Luis Buatois and M. Gabriela Mángano

Ichnology

Organism-Substrate Interactions in Space and Time

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Ichnology is the study of traces, such as burrows, trackways, and borings, created in the substrate by living organisms. It is an increasingly important field, having recently been transformed into a multifaceted science at the crossroads of many disciplines.

This is the first book to systematically cover the conceptual framework of the discipline and the wide breadth of applications in both paleobiology and sedimentology, bridging the gap between the two main facets of the field. It emphasizes the importance of understanding ecological controls on benthic fauna distribution and the role of burrowing organisms in changing their environments.

A detailed analysis of the ichnology of a full range of depositional environments is presented using examples from the Precambrian to the Recent, and the use of trace fossils in facies analysis and sequence stratigraphy is discussed. By presenting ichnological information within a macroevolutionary perspective, the authors provide an up-to-date overview of the subject and highlight the potential of biogenic structures to provide valuable information and solve problems in a wide range of fields.

An invaluable resource for researchers and graduate students in paleontology as well as in sedimentology and sequence stratigraphy, this book will also be of interest to oil industry professionals working in reservoir and exploration geology.

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We dedicate this book to Melanie, Gabriel, Michelle, and also Sebastian and Milly

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Acknowledgments

Ichnology is not only an exciting and vibrant field but also a collective enterprise and multiple collaborations among specialists are, by far, the norm rather than the exception. Throughout our careers we have always counted on the constructive feedback of many colleagues and ichnofriends. In recent years, the enthusiastic support of our graduate students has become a powerful engine. Richard Bromley, Peter Crimes, Tony Ekdale, George Pemberton, and Dolf Seilacher have always been inspiring figures since our years as undergraduate students at the University of Buenos Aires. It all started for us with the arrival at the university library of Tony, Richard, and George's 1984 Short Course Notes and with the visit of Dolf and Peter themselves for a series of talks in Argentina. Richard has devoted countless hours to working and discussing many ichnological (some almost philosophical!) questions with us. Working with him in Patagonia was a real treat. Peter was a wonderful host during a visit to Liverpool (our first ichnological international trip). Sharing field trips and meetings with Tony have always provided us with wonderful experiences, which include not only ichnology but also talks about jazz and science fiction. George has always been extremely supportive and generous both while we were in Argentina and now in our new home in Canada. We enjoyed sharing some time with Dolf and Edith, who visited many localities in northwest Argentina with us, and have opened the doors of their homes (in Tübingen and New Haven) to us many times. John Pollard and Ron Pickerill have been patient reviewers, always providing constructive criticism. Our visit to John in Manchester was also a memorable experience earlier in our careers. All deserve our sincere gratitude.

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Introduction

Worms have played a more important part in the history of the world that most persons would at first suppose.

Charles Darwin
The Formation of Vegetable Mould Through the Action of Worms with Observations on their Habits (1881)

When looking at depositional sequences, no one gets upset when they see a ripple mark, but the presence of a few burrows frequently will divide the field party into two factions. One group falls asleep while the other group begins a lengthy discussion on phylogeny, ontogeny, nutrient upwelling, biochemistry, and the "Voyage of the Beagle".

Jim Howard
"Sedimentology and trace fossils" (1978)

Jim Howard's ironic comment elegantly illustrates both the joys and risks of practicing and communicating the science of organism–substrate interactions to a broad audience. Ichnology is a science located right at the crossroads of paleontology (and biology) and sedimentology (and stratigraphy). Trace fossils link paleontology and sedimentology in ways that most body fossils cannot achieve. In this context, ichnological investigations provide dynamic links among numerous fields. Analysis of specific ichnofaunas results in meaningful contributions to paleoecology, sedimentology, sequence stratigraphy, reservoir characterization, diagenesis, paleoclimatology, paleooceanography, biostratigraphy, evolutionary paleoecology, paleoanthropology, and archaeology. Such studies illustrate how an integrated approach that articulates ichnological information with other sources of data results in a better understanding of depositional setting, stratigraphic architecture, reservoir permeability, organism behavior, and ecosystem reconstruction and evolution. Thus, a multifaceted approach to ichnology will help bridge the gap between biologists and geologists, as well as between theoretical frameworks and applications. Because of this close link between ichnology and several other fields, we will often visit some of these neighboring disciplines in search for connections.

We have subdivided the book into three parts. The first one deals with conceptual tools and methods, and addresses the conceptual background of the field, ichnotaxonomy, burrowing and locomotion mechanisms, the ichnofacies model, and the ichnofabric approach. The second part focuses on spatial trends, and attempts to summarize paleoecological aspects, environmental controls, and the ichnology of different depositional environments. The third part deals with temporal trends, including developments in sequence stratigraphy, biostratigraphy, evolutionary paleoecology, paleoanthropology, and archaeology. In almost every instance, we have tried to avoid including previous illustrations by elaborating new ones or redesigning other author drawings based on our own perspective. Each of the chapters is focused on providing an update of the most pertinent aspects covered in ichnological research. To do so, it is necessary to generalize based on a limited number of case studies. However, some readers may still prefer to learn from specific examples. To avoid that potential problem, we have included boxes that either supply a more in-depth treatment of selected topics or summarize case studies that illustrate significant advances in our understanding of the field.

This book attempts to provide a balance between our own personal experience, and a comprehensive synthesis of previous and current research in the field of animal–substrate interactions. In the first place, our personal experience and interests are reflected throughout the book by the choice of topics and philosophical perspective. The book emphasizes invertebrate ichnology rather than vertebrate ichnology, and bioturbation rather than bioerosion, although a conscious (perhaps not entirely successful) effort has been made to counterbalance our biases. Second, we use many examples drawn from our own work. These include research undertaken in deposits ranging from the Ediacaran to the Recent that have accumulated in a wide variety of environments and geographic locations. We consider ourselves really lucky to have been able to explore such a vast timescale and variety of settings. However, we also offer extensive coverage of the work done by the different working groups in the last few decades.

In *Time's Arrow, Time's Cycle*, Steven Jay Gould (1987) emphasized the tension between time's arrow and time's cycle in our understanding of Earth's history. Time's arrow sees history as an irreversible sequence of unrepeatable events. Time's cycle emphasizes a non-directional time, in which events are repeated according to a recurrent pattern. This dichotomy is expressed in ichnology as a tension between studies that apply ichnofacies models in facies analysis and sequence stratigraphy, and those that underscore the utility of trace fossils in evolutionary paleobiology. The very same notion of ichnofacies recurrence, irrespective of age, is strongly rooted in a cyclic idea of geological time. However, this view of ichnology stands in apparent opposition to the study of secular changes in bioturbation and trace fossils as evidence of the changing ecology of the past and a dynamic landscape, which is never the same. The structure of the book attempts to honor both facets of ichnology.

In that sense, our approach is rather eclectic, trying to incorporate information from the two main schools: that using the ichnofacies model and its wide potential (mostly western Canadian-based), and that employing the ichnofabric approach (rooted in continental Europe and the United Kingdom). One of the advantages of having grown as scientists in such a geographically remote country as Argentina is that one gets a good balance of tradition and freedom. Tradition is revealed by a long and rich history of paleontological research in the country. However, at the same time, being far from the authoritative centers of scientific production gives a sense of freedom that prevents tradition from suffocating critical thinking. Hopefully, by the end of the book eclecticism will have paid, and the gap between the Voyage of the Beagle and the Reservoir Model may have narrowed a little bit.

Part I Conceptual tools and methods

1 The basics of ichnology

> These "-ichnial" ethologic categories are useful tools for organizing important paleoecologic information about a particular organism community. Of course, semantic distinctions between the different categories may be carried to the extreme, and confusion rather than clarification results. For example, imagine the trackway created by a man running across a mudflat at low tide. Do his footprints represent repichnia (perhaps he was jogging for his health) or fugichnia (perhaps he was being chased by someone with harmful intentions) or praedichnia (perhaps he was chasing sea gulls for a special gourmet dinner)? Imagine that the man fell flat on his face in the mud. If he got up and continued his journey, the impression he left behind would be a cubichnial trace. If, on the other hand, he died where he fell and his body decayed away totally, the remaining impression would be a body fossil (i.e., external mould) and not a trace fossil at all!
>
> Tony Ekdale
> "Paleoecology of the marine endobenthos" (1985)

Ichnology involves the study of traces produced by organisms (both animals and plants) on or within a substrate, and includes all issues related to bioturbation, bioerosion, and biodeposition (Pemberton *et al*., 1992a; Bromley, 1990, 1996). As such, ichnology encompasses both the study of processes, and their resulting products. The processes are all those involved in the interaction between organisms and substrates. The products are the traces themselves, which comprise individual and distinctive structures of biogenic origin, particularly those related more or less directly to the morphologies of the producers (Frey, 1973), and any sedimentary fabric resulting from biogenic reworking of the substrate, including non-discrete mottlings (i.e. biodeformational structures). Ichnology comprises two main fields: neoichnology (the study of modern traces or *lebensspuren* of classic German papers) and paleoichnology (the study of their fossil counterparts: trace fossils or ichnofossils). In this chapter, we review the conceptual framework of ichnology. We start by introducing basic concepts and outlining the 10 most important characteristics of trace fossils. Then we discuss aspects of trace-fossil preservation, including different schemes to classify biogenic structures in this respect. Finally, we turn our attention to the potential of trace fossils as sources of behavioral information, providing an in-depth discussion of the ethological classification.

1.1 BASIC CONCEPTS

During the seventies, attempts were made to provide a general classification framework for ichnology and related fields. Biogenic structures, defined as any evidence of organism activity other than the production of body parts (Frey and Wheatcroft, 1989), were regarded as the most inclusive category. The alternative term "ethologic structures" was suggested subsequently to emphasize the behavioral significance of these structures (Pickerill, 1994). In addition, a number of concepts were introduced in order to group trace fossils (Box 1.1). The most popular scheme was proposed by Frey (1971, 1973) and experienced minor modifications in subsequent years (Frey and Pemberton, 1984, 1985; Frey and Wheatcroft, 1989; Pemberton *et al*., 1990, 1992a). This scheme subdivided biogenic structures into three major categories: (1) biogenic sedimentary structures; (2) bioerosion structures; and (3) other evidence of activity. Biogenic sedimentary structures are biogenic structures produced by the activity of an organism upon or within an unconsolidated substrate (Frey and Wheatcroft, 1989). In turn, biogenic sedimentary structures were subdivided into bioturbation structures, biodeposition structures, and biostratification structures. Bioturbation structures are biogenic sedimentary structures reflecting the disruption of stratification features or sedimentary fabrics by the activity of an organism (Frey and Wheatcroft, 1989). Tracks (impressions left by an individual locomotory appendage) and the related term trackway for a series of tracks (Fig. 1.1a), trails (continuous grooves produced during locomotion; Fig. 1.1b), and burrows (more or less permanent structures excavated within the sediment; Fig. 1.1c) fall into this group.

Biodeposition structures (Fig. 1.1e) were not recognized as a separate entity in the original scheme by Frey (1971, 1973), but were later incorporated as a discrete category (Frey and Pemberton, 1984). They were defined as biogenic sedimentary structures reflecting production or concentration of sediment by the activities of an organism (Frey and Wheatcroft, 1989). This category embraces coprolites, fecal pellets, pseudofeces, and fecal castings (Frey and Pemberton, 1984; Frey and Wheatcroft, 1989).

Biostratification structures (Fig. 1.1f) referred to as biogenic sedimentary structures consist of stratification features imparted by the activity of an organism (Frey and Wheatcroft, 1989). Stromatolites, byssal mats, biogenic graded bedding, and thrombolites are included in this category (Frey, 1973; Frey and Pemberton, 1984, 1985; Frey and Wheatcroft, 1989; Pemberton *et al*., 1990, 1992a). Interestingly, experimental studies showed that some organisms (e.g. the pistol shrimp *Alpheus bellulus*) are even able to produce a structure similar to cross lamination (McIlroy, 2010).

Bioerosion structures (Fig. 1.1d) comprise biogenic structures produced mechanically or biochemically in rigid substrates by an organism, such as hardgrounds, clasts, bones, or rocks (Frey and

Box 1.1 Grouping trace fossils

There are many terms currently in use to group trace fossils. Some of these terms are more descriptive, while others involve various degrees of interpretation. Some groupings imply recurrence in time, while others are more restricted in temporal scale. Because there is a need for consistency in terminology, the most important concepts are reviewed here.

Ichnoassemblage or trace-fossil assemblage: Groups of trace fossils preserved in a rock unit or sedimentary facies, with no assumptions in regards to time of emplacement or recurrence in the stratigraphic record.

Trace-fossil suite: A more restricted group of trace fossils that reflects contemporaneous time of emplacement. Traditionally, it has been applied to successive groups of trace fossils emplaced under different degrees of consolidation of the substrate (e.g. a hardground suite cross-cutting firmground and softground suites). It has also been referred to as pre- and post-event suites in the case of environments affected by storms or turbidity currents. In this sense, suite is almost a synonym of ichnocoenose.

Ichnocoenose or ichnocommunity: This term has been used in many different ways. The present consensus is that it refers to a group of trace fossils produced by a biological community.

Ichnofacies: Conceptual construct based on the identification of key features shared by different ichnocoenoses of a wide range of ages formed under a similar set of environmental conditions. To avoid confusion with other terms used to group trace fossils at different scales, ichnofacies are commonly referred to as Seilacherian or archetypal ichnofacies. The archetypal nature of ichnofacies relies on a "distillation" process that extracts the key features shared by actual ichnocommunities (see Chapter 4).

Ichnofabric: Any aspect of the texture and internal structure of a substrate resulting from bioturbation and bioerosion at any scale (see Chapter 5).

Trace-fossil association or ichnoassociation: As with ichnocoenose, this term has been used in a loose way. However, and in contrast to ichnocoenose, there is no present consensus on a more precise meaning. On occasions, it has been used in a temporal sense (i.e. as recording the work of a community), essentially approaching the meaning of ichnocoenose or trace-fossil suite. In other cases, a mere spatial connotation is implied, becoming in practice a synonym of trace-fossil assemblage. In a trace-fossil association, biogenic structures are "associated", but the cause may be merely coincidental (i.e. trace-fossil assemblage) or ecological (i.e. ichnocoenose).

Ichnosubfacies: A group of trace fossils representing a subdivision within an ichnofacies.

Ichnoguild: A group of trace fossils defined on the basis of: (1) bauplan, (2) food source, and (3) use of space. The use of this term is intimately linked to ichnofabric and tiering analysis (see Section 5.4).

Ichnofauna: Very general term to group trace fossils having no scale or genetic connotation.

References: Bromley (1990, 1996); Hunt and Lucas (2007); MacEachern *et al*. (2007a).

Wheatcroft, 1989). Bioerosion structures include macroborings (down to the millimeter scale) and microborings (smaller than a millimeter) (Bromley, 1994). Borings, embedment structures, rasps and scrapes, surface etching scars, durophagous damage, and drill holes define the wide range of bioerosion structures (Bromley, 1992, 1994). Different types of structures are placed under "other evidence of activity", including spider webs and egg cases (Frey and Pemberton, 1984, 1985; Pemberton *et al*., 1990, 1992a).

As with most classifications, some fields are vague and gray zones haunt the researcher who ventures towards the margins of a discipline. Although occasionally ichnology is regarded as the study of all biogenic structures, this is not strictly true. Not all biogenic structures fulfill the requirements to be considered organism traces. Every ichnologist agrees that all biogenic sedimentary structures (both discrete trace fossils and undifferentiated biodeformational structures) qualify, and there is general consensus that biostratification structures (e.g. stromatolites and biogenic graded bedding) do not because they do not reveal the functional anatomy of the producer (Frey and Pemberton, 1985). Accordingly, very few regard stromatolites as trace fossils, and those are only rarely treated in the ichnological literature (e.g. Shapiro, 2007). However, issues become more contentious when we move into the gray zones of the classification. Egg cases are currently regarded outside of the field, but a review on fossil eggs (Hirsch, 1994) was included in a trace fossil book (Donovan, 1994). In any case, eggs may be preserved within fossil nesting sites (e.g. Chiappe *et al*., 2004, 2005), which in turn fall within the realm of ichnology because they provide direct evidence of reproductive behavior.

In addition, some of the research produced during the last decade has expanded ichnology by providing systematic treatment of biogenic structures that were not considered in previous classifications. One of these lines of research is the study of plant–arthropod interactions, as revealed by biogenic structures preserved in wood, leaves, and seeds (e.g. Scott, 1992; Genise, 1995; Labandeira *et al*., 1997; Labandeira, 1998, 2002; Wilf *et al*., 2000). The placement of this group of structures in the traditional scheme of classification of biogenic structures is unclear. Damage of plant tissues preserved in leaves has sometimes been linked to bioerosion (e.g. Labandeira *et al*., 1997). However, plant tissue is not strictly a rigid substrate comparable to rockgrounds or hardgrounds. Traditionally, traces in wood have been regarded as borings produced by bioerosion (e.g. Bromley *et al*., 1984; Mikuláš, 2008; Bertling and Hermanns, 1996; Savrda and Smith, 1996), although it may be argued that traces in

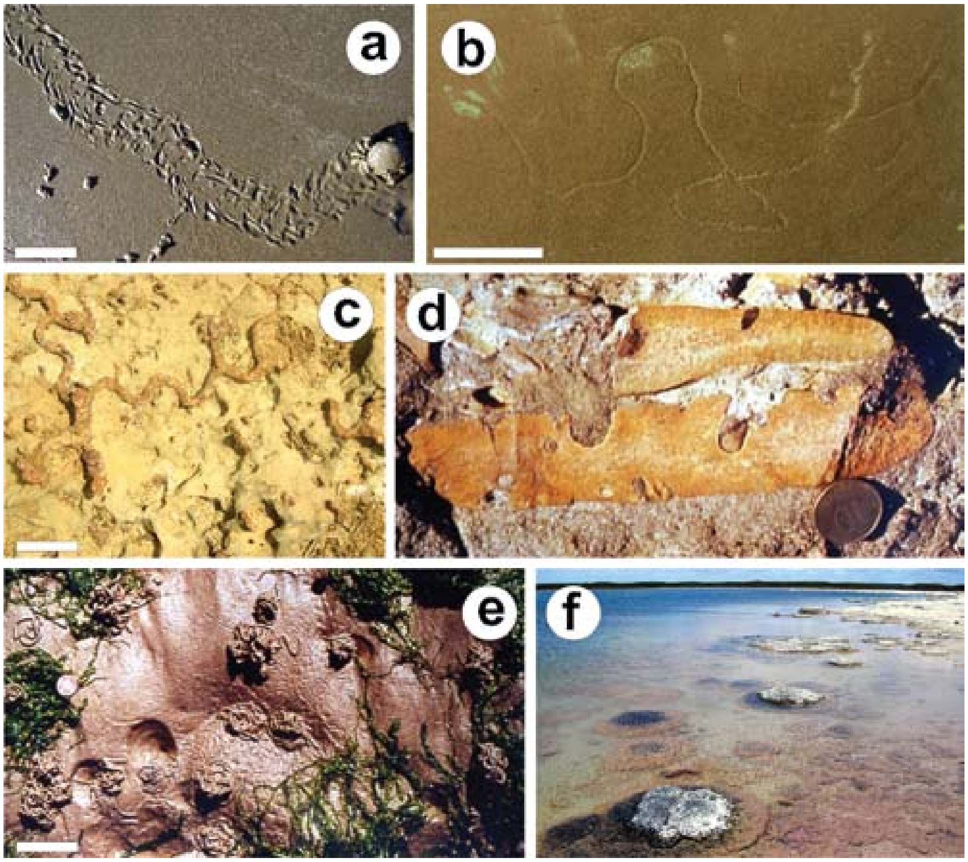

Figure 1.1 Examples of biogenic structures. (a) A trackway produced by a crab (on the right). Tidal flats nearby Estancia Maria Luisa, Tierra del Fuego, Argentina. Scale bar is 5 cm. (b) A trail assigned to the ichnospecies *Gordia marina*. Upper Carboniferous, Guandacol Formation, Río Frío, western Argentina. Scale bar is 1 cm. (c) Burrow system assigned to the ichnospecies *Sinusichnus sinuosus*. Middle Miocene, Socorro Formation, Quebrada El Pauji, northwestern Venezuela. Scale bar is 1 cm. See Buatois *et al.* (2009a). (d) The boring bivalve *Gastrochaenolites* in a clast. Lower Miocene, Chenque Formation, Comodoro Rivadavia, southern Argentina. Coin is 1.8 cm. (e) Fecal casts of *Arenicola marina*. Tidal flats in Gower Peninsula, Wales. Scale bar is 5 cm. (f) Stromatolites, Tethys Lake, western Australia.

wood do not reflect bioerosion in a strict sense. Similiar problems are involved in the study of bioerosion structures in bones (Pirrone *et al.*, 2010). Another line of research focused on the whole array of insect traces produced in terrestrial settings, mostly those of termites, bees, and beetles, but also wasps and ants (e.g. Genise and Bown, 1994a, b; Genise and Hazeldine, 1998; Genise, 2000, 2004). Many of them contribute to destruction of the primary fabric and, therefore, should be considered bioturbation structures. However, placement of some other insect traces within the available classification framework is hardly straightforward. One of these problematic structures is *Chubutolithes gaimanensis*, a nest produced by pompellid wasps (Genise and Bown, 1990). *Chubutolithes* represents an edifice built upon the substrate and constructed with material extraneous to the preserving sediment (see Section 1.4). This structure cannot be regarded as a bioturbation structure, but as a nest constructed by its producer in isolation from the preserving substrate. As such, it may be included within the broad category of "other evidence of activity". Regardless of the precise placement of arthropod traces in plant material and of some of these nests, it is clear that they fulfill the criteria to be considered trace fossils.

Another field of increased activity is the study of microbially induced sedimentary structures (Gerdes *et al.*, 1994, 2000; Noffke *et al.*, 1996; Schieber *et al.*, 2007; Noffke, 2010). These structures record the complex interaction of two sets of processes, those related with the depositional dynamics of the environment and those reflecting the activity of phototrophic microorganisms inhabiting the substrate (Noffke *et al.*, 1996). Stromatolites produced by overgrowth of cyanobacteria are widely recognized examples of microbially induced sedimentary structures in carbonate sediments and, as previously mentioned, have been regarded as biostratification structures (Frey, 1973). This category may also embrace other structures resulting from microbial activity that are commonly preserved in siliciclastic tidal flats. Bacterial activity may contribute to sediment stabilization generating a wide variety of structures, including wrinkled bed surfaces, domal buildups, pinnacles, bulges, and several types of biolaminations in microbial mats (e.g. Schieber, 1999; Gerdes *et al.*, 2000; Noffke, 2010). Although microbially induced sedimentary structures are biogenic structures, they should not be regarded as trace fossils because they fail to reveal any evidence on the morphology of the producers.

There is another group of structures that may be confused with trace fossils, and that, in fact, are not even biogenic structures. These are impressions that result from the passive contact between part of the organism's body and the substrate. Some of these structures are referred to as "death marks", and are illustrated by dead animals dragged by a current along a substrate (Frey and Pemberton, 1985) or carcasses landing on the substrate (Seilacher, 2007a). No behavior is involved; the organism is acting as an inert sedimentary particle. Some of these structures may vaguely resemble animal traces, such as the tilting marks documented by Wetzel (1999), which are produced by wave dragging of shells. Roll and tumbling marks may be produced by ammonites impacting on the sea floor (Seilacher, 1963a). The sweeping motion of a tethered

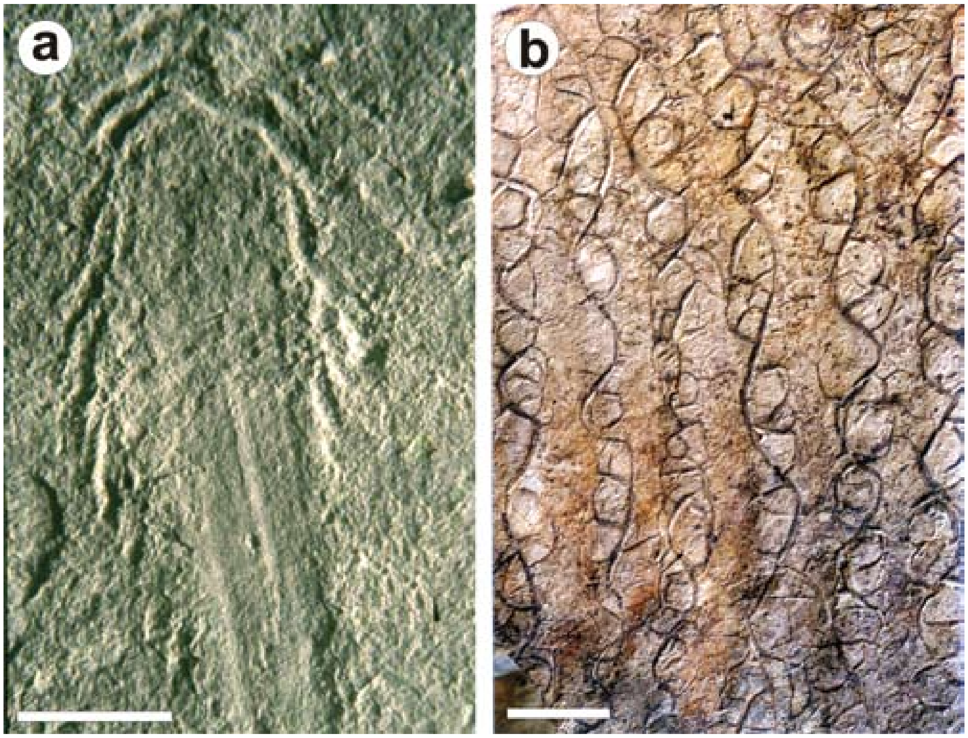

Figure 1.2 Pseudotraces. (a) Inorganic sole mark transitional between groove and chevron mark that superficially may resemble a resting trace. Upper Carboniferous, Agua Colorada Formation, Cantera La Laja, Sierra de Narváez, northwest Argentina. Scale bar is 1 cm. (b) Synaeresis cracks resembling grazing or feeding trace fossils ("Manchuriophycus"). Upper Carboniferous–Lower Permian, Santa Elena Formation, Sierra de Uspallata, western Argentina. Scale bar is 10 cm.

object may be the origin of the supposed trace fossil *Laevicyclus* (D'Alessandro, 1980; Jensen *et al.*, 2002). Scratch circles may be formed by plant stems (Metz, 1991). There is also a gray zone here. Living animals may be dragged by currents leaving marks on the substrate. In most cases, this is just a passive relationship and no behavior is involved, representing a similar situation to that of the death marks. However, it is not unreasonable to suppose that in some instances the animal caught in the current may have raked the sediment. Apparently, this is illustrated by straight to sigmoidal scratch marks, commonly grouped in sets, and repeated laterally that are attributed to trilobites and included in the ichnogenus *Monomorphichnus* (Crimes, 1970a). In order to support this interpretation, the axis of erosional current structures is expected to be parallel to the scratch marks.

Some structures are morphologically similar to organism traces, but careful analysis demonstrates that physical and chemical processes were involved in their production and are, therefore, pseudotraces or pseudo-*lebensspuren*. Turbidite sole marks, particularly chevron and impact marks, are typical examples (Fig. 1.2a). The paleontological and geological literature is plagued with names and descriptions of supposed trace fossils that are actually pseudotraces (e.g. "Manchuriophycus") (Fig. 1.2b). In a few cases, the true nature of some structures remains controversial and even distinction between trace fossils and body fossils may be problematic. Is Ediacaran *Mawsonites* a backfilled burrow system, a medusoid body fossil, or a sand-volcano interacting with a biomat? (Seilacher, 1984, 1989; Seilacher *et al.*, 2005; van Loon, 2008). Finally, there is a nice twist to this story. Some pseudotraces are, in fact, not the result of inorganic processes, but of microbial activity, so they at least qualify as biogenic structures. Corrugations, concentric circles, and spiral and meandering structures are common in microbial matgrounds due to shrinkage of cohesive material on rippled surfaces (Noffke *et al.*, 1996; Pflüger, 1999; Seilacher, 1999; Gerdes *et al.*, 2000). Reinterpretations are made on a regular basis, particularly in the case of Precambrian structures. Beware! Today's trace fossil may become tomorrow's shrinkage crack!

1.2 CHARACTERISTICS OF TRACE FOSSILS

Trace fossils have their own peculiarities that distinguish them from body fossils. These peculiarities, reflecting both their mode of formation and their taphonomic histories, allow the establishment of a rich conceptual framework for ichnology (Seilacher, 1964a; Frey, 1975; Ekdale *et al.*, 1984; Frey and Pemberton, 1985; Pemberton *et al.*, 1990, 2001; Bromley, 1990, 1996; Buatois *et al.*, 2002a). The importance of ichnology in various fields, such as paleoecology, sedimentology, stratigraphy, and macroevolution derives from these basic characteristics. Regrettably, its own limitations also result from this set of main features. In previous studies, this conceptual framework has been expressed as a list of characteristics (Seilacher, 1964a; Frey, 1975) or ichnological principles (Ekdale *et al.*, 1984; Bromley, 1990, 1996). Here, we integrate both schemes to define a series of basic characteristics of trace fossils (Buatois and Mángano, 2008a).

1.2.1 TRACE FOSSILS REPRESENT EVIDENCE OF BEHAVIOR

This is arguably the essence of trace fossils. As expressed by Seilacher (1967a), trace fossils are evidence of fossil behavior.

Analysis of the morphology and architecture of trace fossils reveals valuable information on the anatomy and ethology of their producers (e.g. mode of life, trophic type, and locomotion mechanisms). As outlined below (see Section 1.4), this feature lies at the core of the ethological classification of trace fossils. The behavior involved is, of course, highly variable, from the simple trace of a worm-like animal moving through the substrate (Fig. 1.3a) to the amazing complexities of the work of social insects as illustrated by the termite nest *Termitichnus* (Genise and Bown, 1994b) (Fig. 1.3b). In any case, releasing the behavioral signal unlocked in a biogenic structure is a real challenge in any ichnological analysis.

1.2.2 THE SAME ORGANISM MAY PRODUCE MORE THAN ONE ICHNOTAXON

In a way, this characteristic derives from the former because different behaviors may be attributed to a single animal. Therefore, a single organism may be responsible for producing several ichnospecies and ichnogenera. The classic example is that of the multiple possible behaviors of a trilobite moving through a substrate (Seilacher, 1955a, 1985; Crimes, 1970a) (Fig. 1.4a). The bilobate trail ornamented with scratch marks resulting from the burrowing activity along the sand–mud interface either reflecting simple locomotion or feeding activities is called *Cruziana*. The trackway consisting of series of impressions of individual walking appendages on the substrate due to simple locomotion is referred to as *Diplichnites*. The asymmetrical trackway with two different types of impressions, long straight or sigmoidal (rakers) and short and blunt ones (pushers), attributed to grazing activities, is called *Dimorphichnus*. Short bilobate coffee-bean or heart-shaped traces reflecting resting, nesting, or predation, are known as *Rusophycus*. Deep trilobite burrows are referred to the ichnogenus *Cheiichnus* (Jensen and Bergström, 2000). Cleft-foot deposit-feeding bivalves represent another example of this principle. Chevronate locomotion trace fossils represent the ichnogenus *Protovirgularia*, while the almond-shaped resting or dwelling traces are known as *Lockeia* (Seilacher and Seilacher, 1994; Mángano *et al.*, 1998; Ekdale

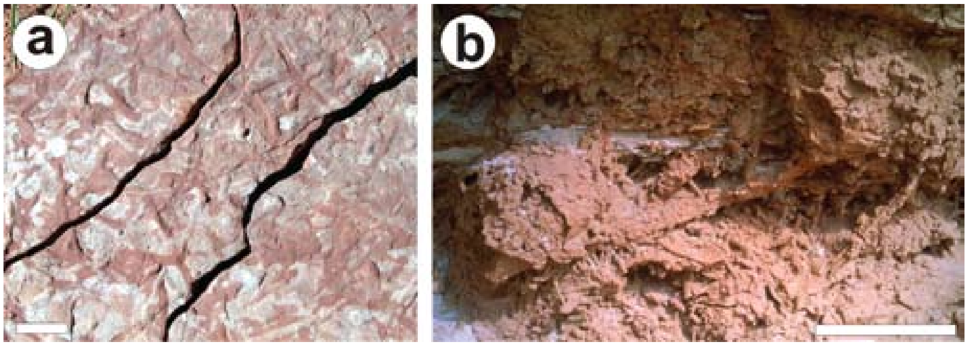

Figure 1.3 Characteristics of trace fossils. Trace fossils represent evidence of behavior. (a) *Palaeophycus tubularis*, a simple trace fossil produced by worm-like animals or insects Lower Permian, Abo Formation, Jemez Mountains, New Mexico. Scale bar is 1 cm. (b) *Termitichnus qatranii*, a termite nest. Upper Eocene–Lower Oligocene, Jebel Qatrani Formation, Fayum Depression, Egypt. Scale bar is 10 cm. See Genise and Bown (1994b).

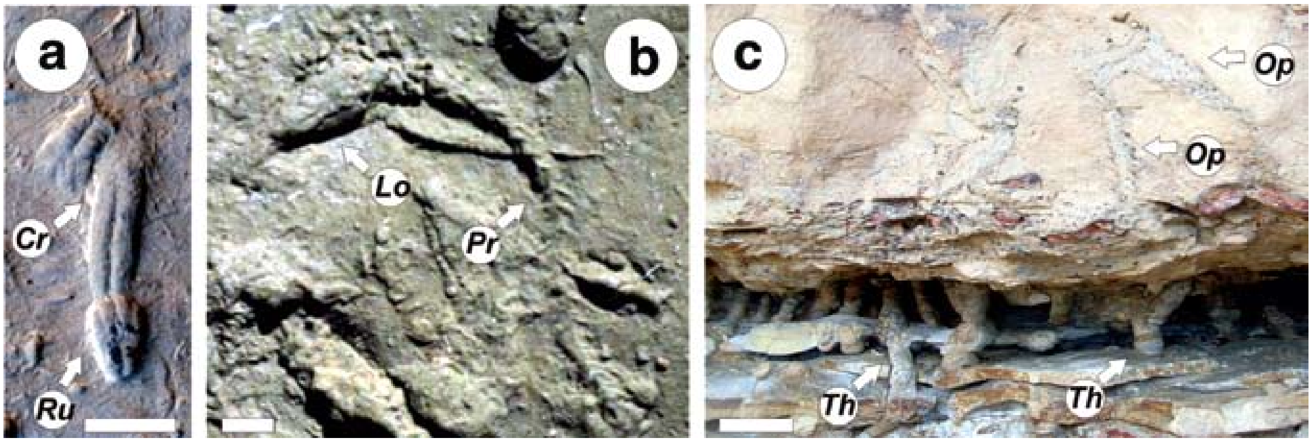

Figure 1.4 Characteristics of trace fossils. The same organism may produce more than one ichnotaxon. (a) Transition between the trilobite locomotion trace *Cruziana* isp. (*Cr*) and the resting trace *Rusophycus* isp. (*Ru*). Upper Carboniferous, Stalnaker Sandstone, roadcut along Kansas Highway 166, United States. Scale bar is 1 cm. See Mángano and Buatois (2004a). (b) Transition between the bivalve locomotion trace *Protovirgularia rugosa* (*Pr*) and the resting trace *Lockeia ornata* (*Lo*). Upper Carboniferous, Stull Shale, Kanwaka Formation, Waverly fossil site, Kansas, United States. Scale bar is1 cm. See Mángano *et al*. (1998). (c) Crustacean galleries showing intergradations between burrows with walls reinforced with pellets in sandy substrates (*Ophiomorpha nodosa*) (*Op*) and burrows with thin lined walls in the underlying more compacted, silty substrates (*Thalassinoides paradoxicus*) (*Th*). Middle Miocene, Socorro Formation, Quebrada El Pauji, northwestern Venezuela. Scale bar is 5 cm.

and Bromley, 2001) (Fig. 1.4b). In addition, associated complex feeding traces have been in some cases referred to the ichnogenus *Lophoctenium* (Ekdale and Bromley, 2001a).

Although common for trails, trackways, and resting traces, this situation is by no means exclusive to this group of biogenic structures. In fact, another common example is that of crustacean burrows (Fürsich, 1973) (Fig. 1.4c). The type of wall in crustacean burrows is largely controlled by substrate grain size and degree of consistency. For example, *Callichirus major* reinforces its burrow wall with pellets in mobile, sandy substrates, and the resulting structure is known as *Ophiomorpha*. However, the same species produces thin burrow linings in more stable sandy or silty sediments, or burrow walls ornamented with bioglyphs in firm, compacted, silty substrates, forming the ichnogenera *Thalassinoides* and *Spongeliomorpha*, respectively. Intergradational forms revealing the transition of one ichnotaxa into another have been called "compound ichnotaxa" (Pickerill, 1994), and are fairly common in the ichnological record (see Section 2.4.1).

In addition to substrate, food supply is another factor that controls burrow morphology. This is illustrated by the amphipod *Corophium volutator*, which is a suspension feeder constructing simple vertical burrows (*Skolithos*) in sandy substrates and a detritus feeder producing U-shaped burrows (*Diplocraterion*) in silty, nutrient-rich sediment (Seilacher, 1953a; Reise, 1985; Bromley, 1990, 1996).

1.2.3 THE SAME ICHNOTAXON MAY BE PRODUCED BY MORE THAN ONE ORGANISM

The same ichnotaxa can be produced by many different animals, revealing behavioral convergence. In most cases, it is simply not possible to establish a one-to-one relationship between producer and biogenic structure. As a general rule, the simpler a trace fossil is, the weaker the link between the biogenic structure and its producer. Simple grazing trails, such as *Helminthoidichnites*, may be produced by nematomorphs, insect larvae, ostracodes, annelids, and many other benthic organisms (Buatois *et al.*, 1998a). The simple vertical burrow *Skolithos* is known to be the product of annelids, phoronids, siphunculids, crustaceans, and probably insects and spiders (Schlirf and Uchman, 2005). The trackway *Diplichnites* records the impressions of multiple undifferentiated locomotory appendages, and has been attributed to many different types of arthropods, including centipedes, millipedes, onicophorans, and trilobites (Buatois *et al.*, 1998b) (Fig. 1.5a). Even burrow systems, such as *Thalassinoides*, which are currently attributed to decapod crustaceans, occur in lower Paleozoic rocks predating the appearance of thalassinideans and callianasids, indicating that other arthropods were probably able to produce similar structures (Carmona *et al.*, 2004).

On the other hand, complex structures can be linked with more confidence to a group of producers. For example, the ichnogenus *Tonganoxichnus* is attributed to apterygote monuran insects based on detailed morphological features and behavioral evidence (Mángano *et al.*, 1997). However, even in this case, a one-to-one link cannot be established because other non-flying insects (e.g. Archaeognatha) are potential producers of *Tonganoxichnus*. Perhaps the closest relationships between trace fossils and their producers can be established with certain insect nests, mostly termites and bees (e.g. Genise, 1997).

Although the precise paleobiological affinity cannot be determined, morphological features may provide enough information on burrowing technique and anatomy to establish a link with a certain group of organisms. Examples of this are represented by *Curvolithus* (turbelarians, gastropods), *Asteriacites* (asteroids, ophiuroids), *Scolicia* (irregular echinoids), *Bichordites* (irregular echinoids), *Protovirgularia* (bivalves), and *Bergaueria* (actinarians, cerianthids, pennatulaceans), among many others. As clearly elaborated by Bromley (1981, 1990, 1996), the practical result of this principle is that biological and ichnotaxonomic classifications should be kept separate.

1.2.4 MULTIPLE ARCHITECTS MAY PRODUCE A SINGLE STRUCTURE

A single structure may reflect the work of more than one producer operating either at more or less the same time or in successive bioturbation events. The first situation typically results from symbiotic or commensalist relationships (see Section 6.7). The

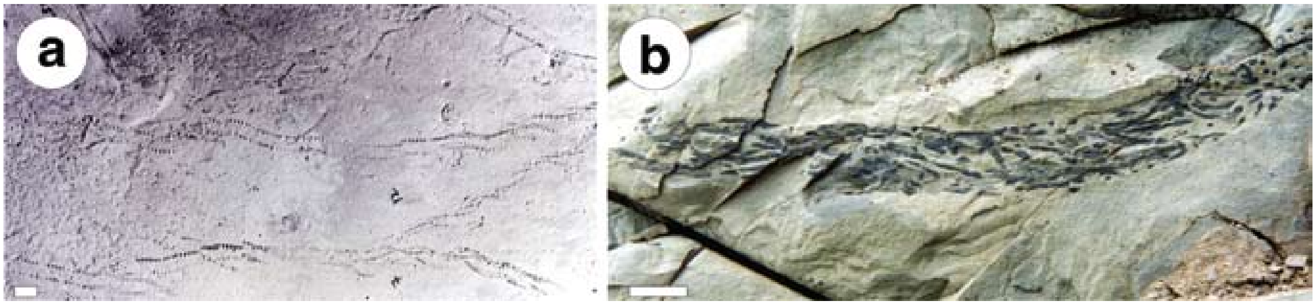

Figure 1.5 Characteristics of trace fossils. (a) The same ichnotaxon may be produced by more than one organism. A wide variety of arthropods, including centipedes, millipedes, onicophorans, and trilobites, are potential producers of *Diplichnites gouldi*. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, United States. See Buatois *et al.* (1998b). (b) Multiple architects may produce a single structure. Concentration of *Chondrites* isp. within "phantom burrows". The high concentration of *Chondrites* helps to delineate the previously emplaced structure that otherwise would have remained undetected. Upper Cretaceous, Horgazu Formation, Covasna Valley, Romania. Scale bars are 1 cm.

standard examples are that of the lobster *Nephrops norvegicus*, the crab *Goneplax rhomboids*, and the fish *Lesueurigobius friessi*, which usually produce independent structures in offshore muds from Scotland, but occasionally construct an interconnected burrow system (Atkinson, 1974). Although this is not uncommon, judging from modern examples, recognition of this type of relationships in the trace-fossil record is extremely problematic. Similar examples are illustrated by burrows constructed by the thalassinidean shrimp *Neaxius acanthus* but also inhabited by the gobiid fish *Austrolethops wardi* (Kneer *et al.*, 2008; Liu *et al.*, 2008). However, in this case the fish apparently does not rework the burrow and, therefore, the resulting structure is essentially the product of the shrimp. The second situation is illustrated by abandoned biogenic structures that are reoccupied by a different organism, which is remarkable common in the trace-fossil record (Fig. 1.5b). A typical example is represented by *Chondrites* and, to a lesser extent, *Phycosiphon*, which may rework the infill of feeding and dwelling burrows, such as *Diplocraterion*, *Cladichnus*, *Gyrolithes*, or *Thalassinoides*, presumably for feeding purposes. This situation is also common in paleosol insect traces (Genise and Laza, 1998; Mikuláš and Genise, 2003). For example, the beetle ichnotaxon *Monesichnus ameghinoi* displays an internal gallery system (*Lazaichnus fistulosus*) probably produced by cleptoparasites (Mikuláš and Genise, 2003). Pickerill (1994) coined the term "composite ichnotaxa" for forms that apparently comprise a single burrow system, but actually result from the interpenetration of individual discrete ichnofossils (see Section 2.4.2), while Mikuláš and Genise (2003) called them "traces within traces".

1.2.5 PRODUCERS ARE COMMONLY SOFT-BODIED ANIMALS THAT ARE RARELY PRESERVED

The body-fossil record is strongly biased towards the groups that have developed hard parts. In contrast, trace fossils commonly record the activities of soft-bodied animals, which make up most of the biomass of a community (Pemberton *et al.*, 1990) (Fig. 1.6a). This principle results from the facts that the trace-fossil record is biased towards the activities of infaunal organisms and that the presence of skeletons is commonly detrimental for infaunal life. Life within the substrate provides protection from environmental stress (e.g. salinity fluctuations, erosion, and desiccation), and biological pressure (e.g. predation). Accordingly, infaunal representatives of many groups of animals, including mollusks, crustaceans, and echinoderms, display a trend to reduce or even eliminate their exoskeleton. For example, efficient burrowers, such as callianassids and upogebids, have significantly reduced calcification of the exoskeleton. In the same vein, deep-infaunal echinoderms have thinner shells than their epifaunal or shallow-infaunal counterparts.

However, examples of the producer preserved in direct association with the biogenic structure have been documented, albeit rarely, in the trace-fossil record. Vertebrate bones preserved inside burrows are related with obrution events (e.g. Voorhies, 1975). The classic example among the invertebrates is that of crustacean claws preserved within *Thalassinoides* burrow systems (Sellwood, 1971; Bromley and Asgaard, 1972a; Mángano and Buatois, 1991). More exceptional are ophiuroids preserved on the resting trace *Asteriacites* (West and Ward, 1990; Mikuláš, 1990) and trilobites on the resting trace *Rusophycus* (Osgood, 1970) (Fig. 1.6b–c). Body fossils of arthropods preserved at the end of their trackway have also been documented. For example, the horseshoe crab *Mesolimulus* is preserved at the end of the trackway *Kouphichnium* in the Jurassic Solnhofen lithographic limestone (Barthel *et al.*, 1990; Seilacher, 2007a).

Figure 1.6 Characteristics of trace fossils. Producers are commonly soft-bodied animals that are rarely preserved. (a) *Bergaueria hemispherica* is produced by burrowing sea anemones. Although these organisms have a remarkably low preservation potential as body fossils, their burrows are common in the fossil record. Lower Cambrian, Gog Group, Lake Moraine, Rocky Mountains, western Canada. See Pemberton and Magwood (1990). (b) *Rusophycus pudicum*. Upper Ordovician, Corryville Formation, Maysville Group, Cincinnati, Ohio, United States. (c) *Flexicalymene meeki* in place associated with the *R. pudicum* specimens shown in (b) One of the unusual cases of producer preserved in connection with the trace fossil. Scale bars are 1 cm. See Osgood (1970).

Because the burrows themselves provide an appropriate microenvironment for body fossil preservation, any shell

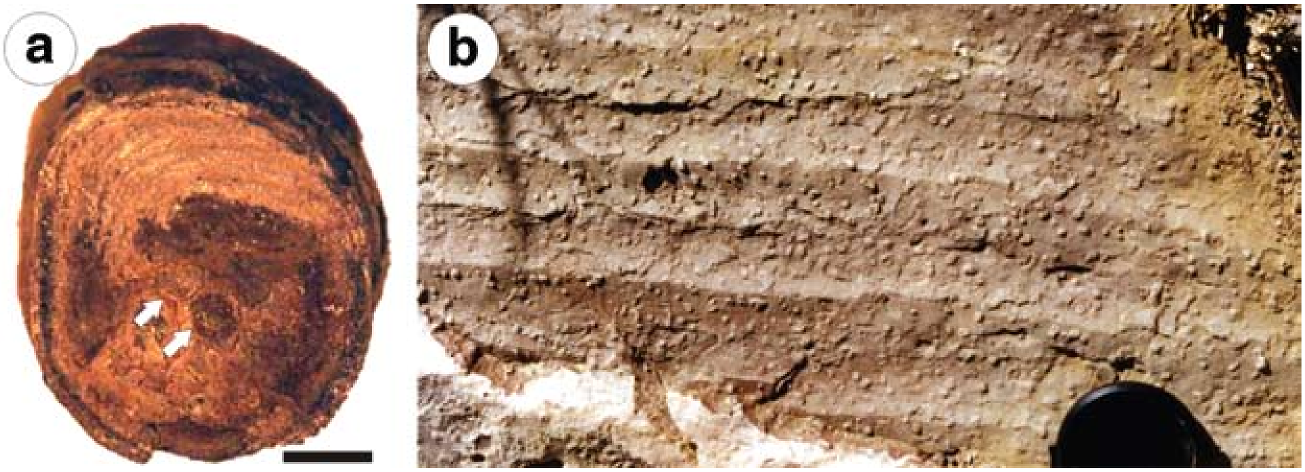

Figure 1.7 Characteristics of trace fossils. Trace fossils are commonly preserved in rock units that are otherwise unfossiliferous. (a) The U-shaped burrow *Tissoa* promotes the formation of minerals that concentrate along tube walls and forms a long axis of conical to cylindrical calcareous concretions. Note the presence of two burrow openings (arrows) indicating a U-shaped morphology. Upper Cretaceous, Hidden Lake Formation, Obelisk Col, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois and López Angriman (1992a). (b) Abundant vertical burrows (*Skolithos linearis*) expressed as circular cross-sections on bedding plane. Lower to Middle Cambrian Campanario Formation, Angosto de Perchel, northwest Argentina. Although trace fossils are abundant in this unit, no body fossils have been recovered with the exception of a few linguliformean brachiopods. See Mángano and Buatois (2004b). Lens cap is 5.5 cm.

that accidentally falls within a burrow may escape destruction by early diagenesis, subsequent bioturbation, and physical reworking, and successfully cross the fossilization barrier (Bromley, 1990, 1996). Repeated storms may lead to accumulation of abundant skeletal material within callianassid burrows producing tubular tempestites (Tedesco and Wanless, 1991). The temptation to establish a genetic link between the burrow system and the preserved body fossils should be resisted at any cost. The standard example here is the delicate preservation of bryozoans trapped inside *Thalassinoides paradoxicus* in chalk (Voigt, 1959, 1974). Another example is the occurrence of the infaunal bivalve *Wilkingia* within *Thalassinoides*-like burrows (Maerz *et al.*, 1976).

1.2.6 TRACE FOSSILS ARE COMMONLY PRESERVED IN ROCK UNITS THAT ARE OTHERWISE UNFOSSILIFEROUS

This characteristic derives, at least in part, from the previously outlined fact that trace fossils being produced by soft-bodied faunas have very low preservation potential. In addition, conditions leading to the preservation of trace fossils are remarkably different than those of body fossils. Accordingly, field parties commonly split into two factions, body-fossil paleontologists rushing into mudstone intervals and ichnologists browsing through sandstone and mudstone interfaces. In particular, diagenetic processes that may lead to destruction of body fossils may enhance trace fossils because burrow walls reinforced with mucus act as focus for mineral precipitation.

In some cases, the biogenic structure may promote the formation of diagenetic minerals (see Section 1.3.2). The U-shaped burrow *Tissoa* forms the long axis of conical to cylindrical calcareous concretions due to the formation of minerals that concentrate along tube walls (Frey and Cowles, 1969; Buatois and López Angriman, 1992a) (Fig. 1.7a). Concretionary flint in chalk results from silicification of burrow systems, such as *Thalassinoides*, *Ophiomorpha*, *Zoophycos*, and *Bathichnus* (Bromley and Ekdale, 1984a).

This differential preservation of trace fossils with respect to body fossils is of great importance because it is not uncommon that biogenic structures represent the only biotic evidence in many rock units. For example, thick successions of Cambrian–Ordovician quartzites commonly devoid of body fossils contain abundant trace fossils that allow paleoecosystem reconstructions (e.g. Mángano and Buatois, 2004b) (Fig. 1.7b). In the case of vertebrates, although footprints and bones may be present separately, there are many examples of co-occurrence (e.g. Lockley, 1991).

1.2.7 THE SAME BIOGENIC STRUCTURE MAY BE DIFFERENTIALLY PRESERVED IN VARIOUS SUBSTRATES

The same burrowing technique may lead to apparently disparate biogenic structures if produced under contrasting substrate conditions, both in terms of degree of consistency of the substrate, grain size, and stratal position. The nature of the substrate is essential to determine the feasibility and efficiency of the burrowing technique, and strongly influences the resultant morphology of the trace fossils. The most significant practical consequence of this characteristic is a persistent taxonomic nightmare for ichnologists. This problem is clearly illustrated by the ichnogenus *Nereites* and its multiple preservational variants, such as *Neonereites*, *Scalarituba*, and *Phyllodocites* (see discussion by Uchman, 1995 and Mángano *et al.*, 2000). Essentially, *Nereites* consists of a central tunnel enveloped by a zone of reworked sediment, but its preservation is highly dependent on substrate. Chamberlain (1971) demonstrated that single specimens could be preserved as lobes or pustules at the base of sandstone layers (*Neonereites* preservation) or as median furrows with reworked lobes on both sides on top of beds (*Scalarituba*, *Nereites*, or *Phyllodocites* preservation).

Another striking example is that of chevronate locomotion traces of nuculoid bivalves represented by the ichnogenus *Protovirgularia* and its plethora of preservational variants, such as *Walcottia*, *Uchirites*, *Imbrichnus*, and *Chevronichnus* (Rindsberg, 1994; Seilacher and Seilacher, 1994; Mángano *et al.*, 1998, 2002a). The morphology of these locomotion trace fossils is highly controlled by substrate consistency (Fig. 1.8a–c). These ichnotaxa do not represent major behavioral differences; they mainly record changes in the degree of dewatering and other related properties of the sediment. The locomotion mechanism of bivalves is based on rhythmic changes of shape performed by their single muscular foot (Trueman, 1966; Seilacher and Seilacher, 1994). In nuculoid bivalves, which have a bifurcated foot, the repetition of this cycle is recorded by the undertrace, which commonly displays diagnostic chevronate morphology (Seilacher and Seilacher, 1994). The distance between two chevrons represents each sequential set of movements and each chevron indicates the site of anchoring of the foot flaps within the sediment. Sharp, closely spaced chevrons account for short steps, with the animal struggling to advance in stiff, resistant sediment. Longer distances between chevrons may reflect relatively coherent, but less resistant substrates, resulting in lower shell friction, and allowing smoother and easier movement during the protraction phase. Sediment that is too fluid may result in irregular and highly deformed trace-fossil morphologies, recording the difficulties of the foot in obtaining a secure anchorage (Mángano *et al.*, 1998; Carmona *et al.*, 2010).

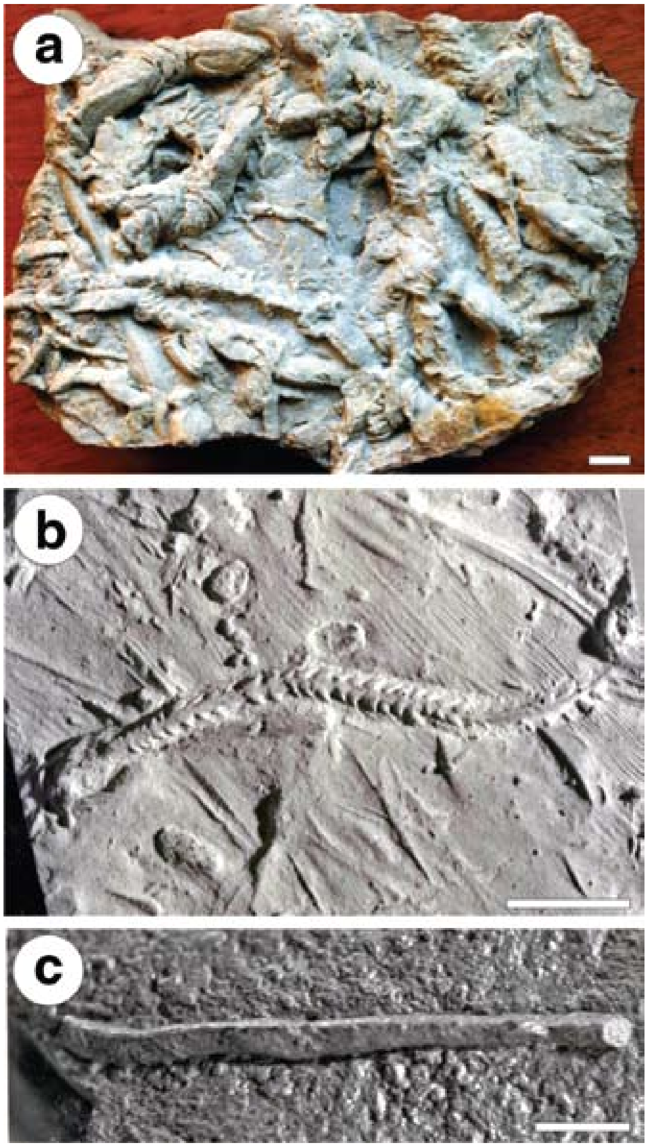

Figure 1.8 Characteristics of trace fossils. The same biogenic structure may be differentially preserved in various substrates. (a) *Imbrichnus wattonensis*. Forest Marble Formation, Jurassic, Forest Marble, Dorset, England. See Hallam (1970). (b) *Walcottia rugosa*. McMillan beds, Ordovician, Cincinnati, Ohio, United States. See Osgood (1970). (c) *Uchirites triangularis*. Guárico Formation, Eocene, Boca de Uchire, Venezuela. See Macsotay (1967). These three forms represent different preservational variants of a chevronate locomotion trace fossil of a cleft-foot bivalve, reflecting various degrees of substrate consistency and corresponding preservation of the chevrons. They are now all included in a single ichnogenus, *Protovirgularia*. Scale bars are 1 cm. See Seilacher and Seilacher (1994) and Mángano *et al.* (1998, 2002a).

1.2.8 TRACE FOSSILS COMMONLY HAVE LONG STRATIGRAPHIC RANGES

The large majority of ichnofossils displays long stratigraphic ranges, commonly spanning most, if not all, of the Paleozoic. A smaller number, including mostly very simple forms, has even originated in the Ediacaran (e.g. *Helminthoidichnites* and *Palaeophycus*) (Fig. 1.9a–c). Interestingly, this fact does not seem to indicate a common producer through geological time, but rather the activity of different types of animals involved in the production of a single ichnotaxon through the Phanerozoic. Accordingly, this characteristic reveals behavioral convergence, and is directly linked to the previously discussed principle that states that a single ichnotaxon may be produced by many different animals. Certain behavioral strategies were established relatively earlier in the history of metazoan life and have remained relatively unchanged. Obviously, this characteristic makes trace fossils of limited use in biostratigraphy (see Chapter 13). As with every rule, this one also has its exceptions (Seilacher, 2007b). Some complex structures produced by insect trace fossils have more limited stratigraphic ranges, representing departures to this principle (Genise, 2004). To a lesser extent, the same can be said of biogenic structures produced by micro and macrobioerosion that commonly have narrower stratigraphic ranges than most burrows, trails and trackways (Bromley, 2004; Glaub and Vogel, 2004). In addition, a fair number of ichnotaxa seem to be restricted to the early Cambrian, including *Psammichnites*

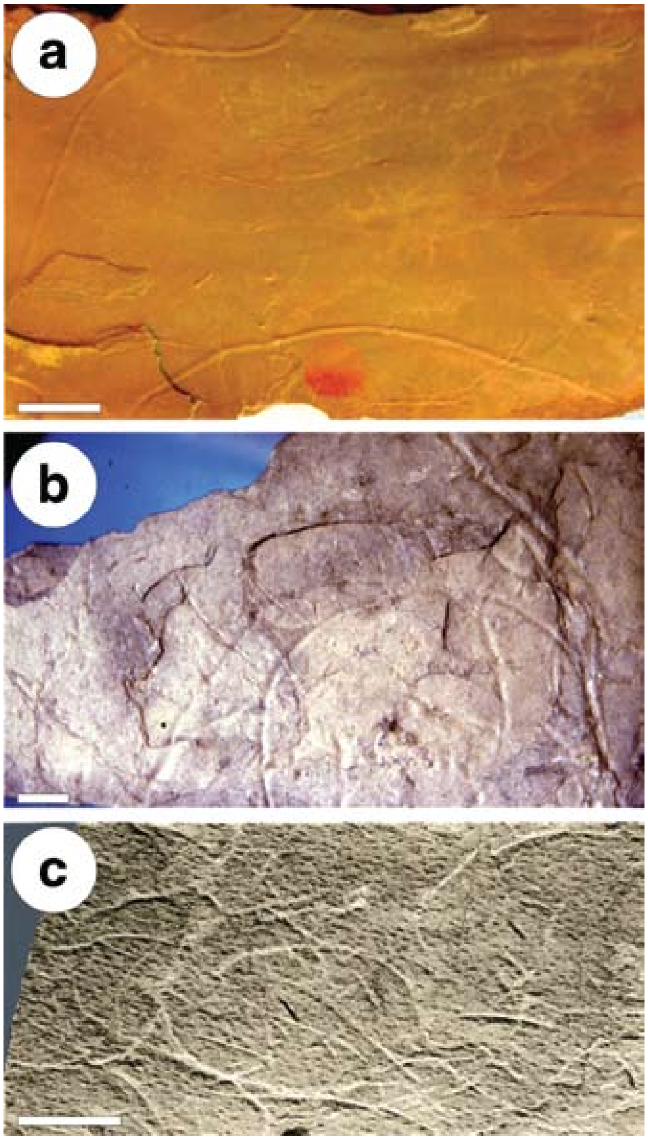

Figure 1.9 Characteristics of trace fossils. Trace fossils commonly have long stratigraphic ranges. *Helminthoidichnites tenuis* (a) Lower Cambrian, Puncoviscana Formation, San Antonio de Los Cobres, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (b) Upper Carboniferous, Agua Colorada Formation, Cantera La Laja, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (c) Lower Cretaceous, La Huérguina Limestone Formation, Las Hoyas fossil site, central Spain. Scale bar is 5 cm. See Buatois *et al.* (2000).

gigas, *Didymaulichnus miettensis*, and several ichnospecies of *Oldhamia* (see Section 13.4).

1.2.9 TRACE FOSSILS COMMONLY HAVE NARROW ENVIRONMENTAL RANGES

Although this characteristic applies more accurately to trace-fossil associations rather than to individual ichnotaxa, it reveals in any case the fact that biogenic structures are strongly controlled by environmental factors and, therefore, they tend to occur preferentially in certain environments of deposition. For example, a number of ichnotaxa are almost exclusively from deep-marine environments, including *Paleodictyon* (Fig. 1.10a), *Helicolithus*, *Spirorhaphe*, *Desmograpton*, *Helminthorhaphe* (Fig. 1.10b), and *Urohelminthoida*. Typical shallow-marine trace fossils include *Psammichnites*, *Curvolithus*, *Daedalus*, and *Arthrophycus*. Another set of trace fossils, such as *Termitichnus*, *Vondrichnus*, *Celliforma*, and *Coprinisphaera*, are exclusive to terrestrial environments. The combination of this characteristic with the fact that trace fossils display long stratigraphic ranges makes them of great importance in paleoecology, allowing comparisons of rocks of different ages formed in similar depositional environments. Certainly, this is at the core of the ichnofacies concept (see Section 4.1).

1.2.10 TRACE FOSSILS ARE RARELY TRANSPORTED

Trace fossils represent the *in-situ* record of biogenic activity. Almost invariably, they have not suffered secondary displacement. Accordingly, trace fossils reveal a more intimate link with the host substrate. This characteristic reveals another of the strengths of trace fossils in paleoecological and paleoenvironmental reconstructions. As with the other principles, some exceptions can be mentioned. First, some trace fossils, most notably borings, can be transported together with the host medium. These include logs bored with *Teredolites* and bioeroded shells and clasts. Second, burrows with strongly reinforced walls are resistant to erosion and reworking, and may be subject to transport. Fragments of crustacean galleries, typically *Ophiomorpha* (Fig. 1.11a–c) and beetle nests, such as *Coprinisphaera*, fall into this category. In particular, the wasp ichnogenus *Chubutolithes* is constructed around plant stems, but subsequently drops to the soil and is reworked by fluvial processes (Genise and Cladera, 2004).

1.3 PRESERVATION OF TRACE FOSSILS

Any trace-fossil description should provide an accurate characterization of preservational aspects. Two main preservational facets can be distinguished: toponomy and physiochemical processes of preservation and alteration (Frey and Pemberton, 1985). Toponomy comprises the description and classification of biogenic structures with respect to their mode of preservation and occurrence. Mode of occurrence is usually defined according to the position of the structure on or within the stratum, or relative to the casting medium. Also included within toponomy are the mechanical processes involved in the fabrication of the structure (stratinomy) and its alteration (taphonomy).

1.3.1 STRATINOMIC CLASSIFICATIONS

Schemes of stratinomic classification (Fig. 1.12) have been proposed by Simpson (1957), Seilacher (1964b), and Martinsson (1970), and are addressed below in chronological order. Summaries and discussions of these classification schemes have been published elsewhere (e.g. Hallam, 1975; Frey and Pemberton, 1985).

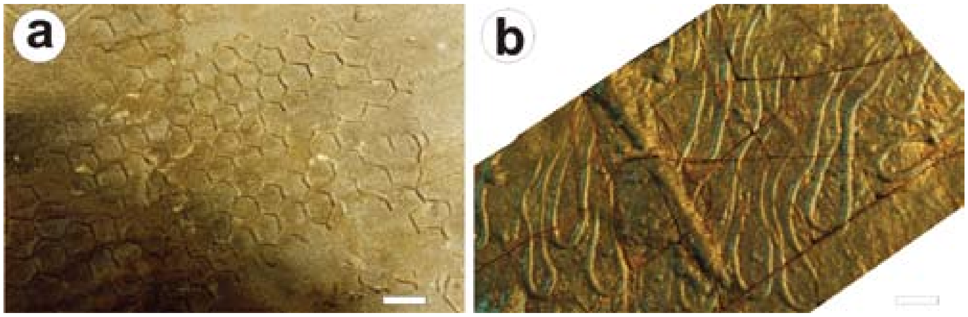

Figure 1.10 Characteristics of trace fossils. Trace fossils commonly have narrow environmental ranges. Some ichnotaxa represent extremely sophisticated feeding strategies that are almost exclusive to deep-marine environments. (a) *Paleodictyon majus*. Zumaya Flysch, Lower Eocene, Guipúzcoa, Spain. See Crimes (1977). (b) *Helminthorhaphe flexuosa*. Lower Eocene, Guárico Formation, Boca de Uchire, Venezuela. See Macsotay (1967). Scale bars are 1 cm.

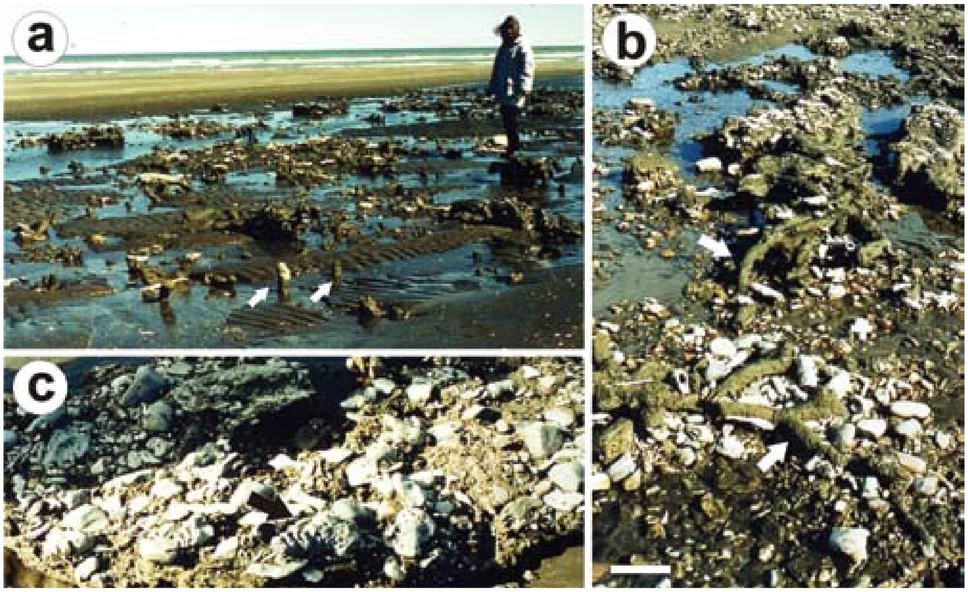

Figure 1.11 Characteristics of trace fossils. Trace fossils are rarely transported. *In situ Ophiomorpha* burrow systems and reworked burrow fragments. Pleistocene, Pehuencó coast, Buenos Aires province, Argentina. (a) General view of *in situ* burrow systems (arrows). (b) Close-up of burrow systems (arrows). Scale bar is 10 cm. (c) Reworked burrow fragments (arrow) in a coastal conglomerate. Lens cap (below arrow) is 5.5 cm.

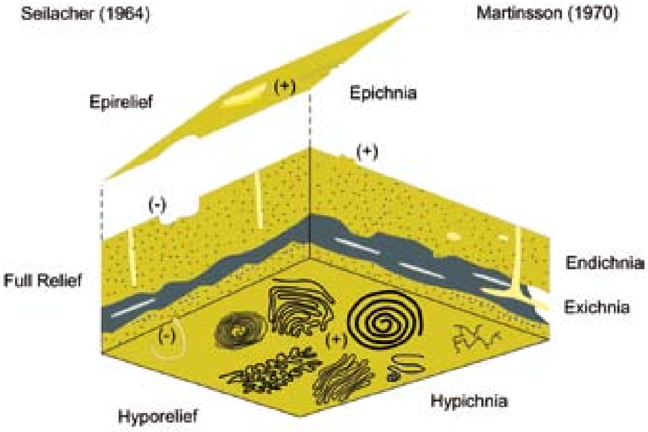

Figure 1.12 Block diagram illustrating the terms used in the stratinomic classifications of Seilacher (1964b) and Martinsson (1970).

SIMPSON'S CLASSIFICATION

Simpson (1957) established four preservational categories: bed-junction, concealed bed-junction, diagenetic, and burial preservations. Bed-junction preservation includes trace fossils preserved in relief at a bed junction. Concealed bed-junction preservation refers to individual burrows that appear to be isolated within an interval of different lithology (Fig. 1.13a). Diagenetic preservation includes ichnofossils preserved as nodule or nodule protuberances formed during early diagenesis (Fig. 1.13b). Burial preservation refers to filled burrows that have been subsequently exhumed by currents winnowing away the associated soft matrix.

SEILACHER'S CLASSIFICATION

Seilacher (1964b) proposed a preservational scheme that comprises two separate sets of terms, descriptive and genetic, which represents a modification of a previous classification (Seilacher, 1953a). Descriptive terms are essentially based on the relationship of the trace fossil to a casting medium, which is usually sandstone. Two main subdivisions, full relief and semirelief, were established. A third category, biodeformational structures, was also defined. Full-relief structures are preserved within the stratum (Fig. 1.13c). Semirelief structures are preserved at lithological interfaces and have been in turn subdivided into epirelief (preserved at the top; Fig. 1.13d–e) or hyporelief (preserved at the base; Fig. 1.13f–g) of the sandstone bed. Additionally, the terms concave (positive) and convex (negative) are used to provide a picture of the trace-fossil relief. Finally, biodeformational

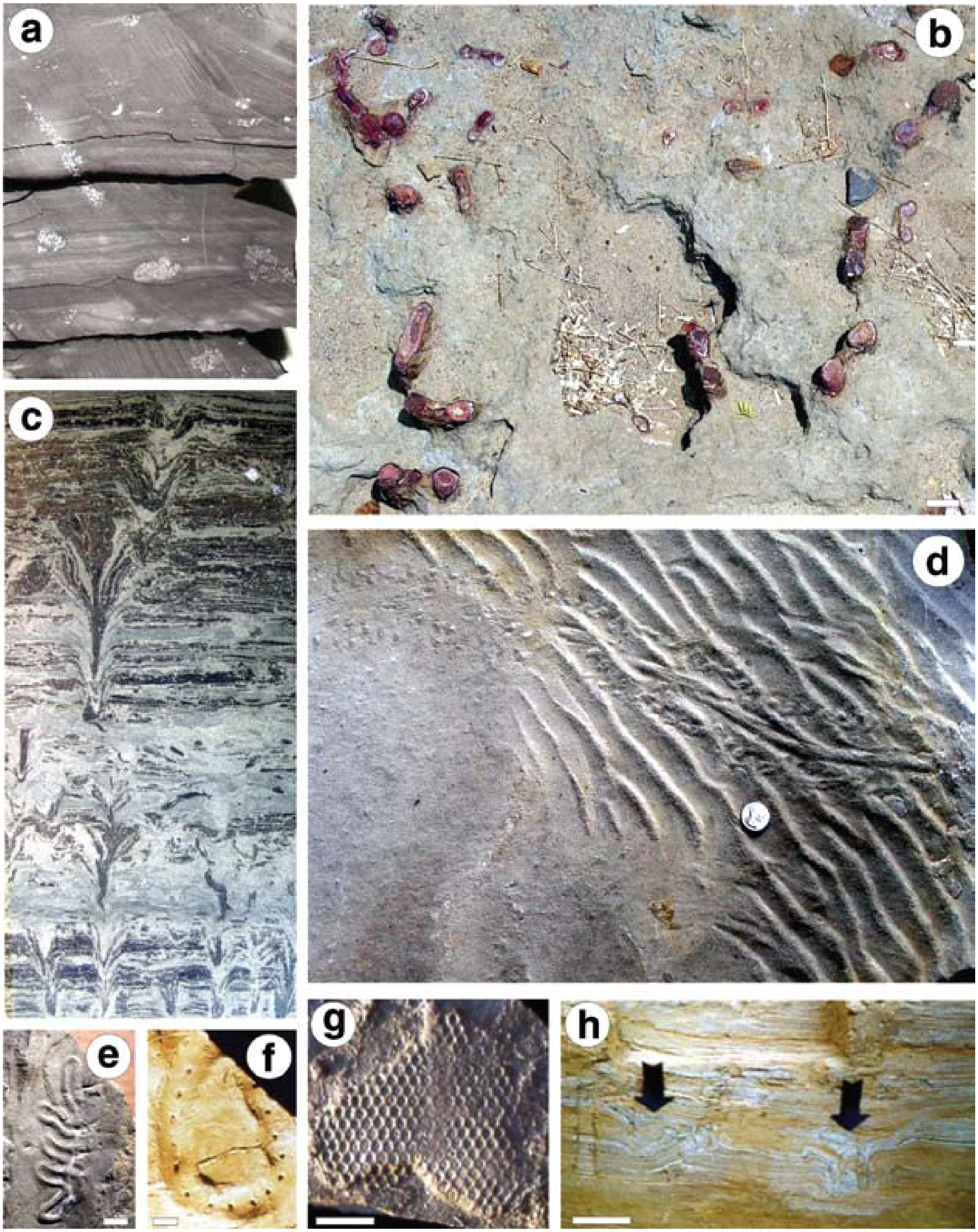

Figure 1.13 Examples of preservational categories. (a) Concealed bed-junction preservation. Firmground *Thalassinoides* filled with coarse-grained sand in prodelta mudstone. Lower Miocene, Tácata Field, Western Venezuela Basin. Core width is 9 cm. See Buatois *et al*. (2008). (b) Diagenetic preservation. Silicified *Diplocraterion parallelum* Middle Miocene, Socorro Formation, Quebrada El Pauji, northwestern Venezuela. Scale bar is 1 cm. (c) Full-relief preservation. *Lingulichnus verticalis* Lower Triassic, Montney Formation, Sturgeon Lake area, west-central Alberta, Canada. Core width is 8 cm. See Zonneveld and Pemberton (2003). (d) Negative epirelief. The arthropod trackway *Protichnites* isp. associated with ripple marks. Upper Cambrian, Cairnside Formation, Postdam Group, slab exhibited at the Fossil Garden at Buisson Point Archaeological Park, Melocheville, Quebec, Canada. Coin is 2.4 cm. (e) Positive epirelief. *Psammichnites implexus* locally preserved along ripple troughs. Upper Carboniferous, Stull Shale, Kanwaka Formation, Waverly fossil site, Kansas, United States. Scale bar is 1 cm. See Mángano *et al*. (2002b). (f) Negative hyporelief. *Psammichnites grumula*. Note well-developed holes (siphon marks) along a median line and prominent levees on both sides of the trace. Upper Carboniferous, Stull Shale, Kanwaka Formation, Waverly fossil site, Kansas, central United States. Scale bar is 1 cm. See Mángano *et al*. (2002b). (g) Positive hyporelief. *Paleodictyon minimum*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Romania. Scale bar is 1 cm. See Buatois *et al.* (2001). (h) Cross-section view of mammoth undertracks (arrows). Mammoth National Park. South Dakota, United States. Scale bar is 10 cm.

structures are not defined with respect to the casting medium, but refer to sediment disturbances of biological origin, such as poorly defined burrow mottling.

Genetic terms refer to the assumed relationship of the trace fossil to the contemporary surface rather than that of the tracemaker. These include exogenic, endogenic, and pseudoexogenic. Exogenic refers to surficial traces covered by sediment that differs from that of the host layer. Endogenic includes those structures actively or passively filled within the host bed. Pseudoexogenic comprises traces formed in a homogeneous medium, but subsequently uncovered by erosion and recast with sand. The terms active and passive can be further added to distinguish between active backfill of the trace fossils from subsequent sedimentation infill. Chamberlain (1971) proposed a slight modification of Seilacher's scheme with the suggestion of replacing the term exogenic by epigenic.

A special case of semirelief preservation has been named cleavage relief and comprises structures seen on cleavage surfaces within intervals of monotonous lithologies (Frey and Pemberton, 1985). This style is commonly associated with preservation of vertebrate and arthropod undertracks (Goldring and Seilacher, 1971; Frey and Pemberton, 1985) (Fig. 1.13h). It has been argued that most fossil trackways are not formed at the sediment surface, but reflect deformation of subsurface laminae during production of the trackway at the surface. This can be typically detected by carefully parting the laminae to reveal vertical repetition of the appendage imprints. Undertrack preservation has been elegantly demonstrated in limulid trackways by Goldring and Seilacher (1971). These authors also detected what was referred to as an undertrack-fallout effect by showing that the most delicate and superficial imprints tend to disappear with sediment depth.

MARTINSSON'S CLASSIFICATION

The classification system proposed by Martinsson (1970) has a lot in common with that of Seilacher (1964b), including the fact that it is also based on the relationship of the trace fossil to a casting medium. Four preservational categories were introduced: epichnia, hypichnia, endichnia, and exichnia. Epichnial preservation comprises structures preserved at the upper surface of the casting strata, while hypichnial preservation includes those preserved at the lower surface of the casting strata. In both epichnial and hypichnial preservations, the terms grooves and ridges are used to denote negative and positive reliefs, respectively. Endichnial preservation refers to structures preserved within the casting medium and exichnial preservation comprises those preserved outside the casting medium.

EVALUATION OF THE CLASSIFICATION SCHEMES

Of these classification systems, those of Seilacher and Martinsson are the ones that have met with most acceptance. Both are very similar and attempt to be comprehensive. Seilacher (1964b) carefully distinguished descriptive and genetic terms. For example, a structure preserved as positive hyporelief may have been formed: (1) as an open burrow system connected to the sediment–water interface that was subsequently filled by sand (e.g. graphoglyptids on turbidite soles); (2) within the sediment along the sand–mud interface (e.g. most specimens of *Cruziana*); or (3) within a homogeneous fine-grained sediment that was subsequently erosionally exhumed and filled by sand. The advantage of Martinsson's scheme relies in its simplicity, but a certain amount of mixing of preservational and genetic aspects in the definition of his terminology represents a problem (Jensen, 1997). Simpson's system is hardly used nowadays, and it is definitely not comprehensive. However, it has been rightly noted that the scheme contains some useful ideas, such as the notion of concealed bed-junction preservation and burial preservation (Frey and Pemberton, 1985). In addition, the classification is not strictly stratinomic because it also takes into consideration diagenetic aspects (see Section 1.3.2) that are overlooked in the other classifications.

1.3.2 PHYSIOCHEMICAL PROCESSES OF PRESERVATION AND ALTERATION

Physiochemical processes of preservation and alteration fall within the realm of diagenesis, and can be quite variable and complex. However, they are still poorly understood although there is an increased recognition of their importance (Simpson, 1957; Frey, 1975; Bromley and Ekdale, 1984a; Frey and Pemberton, 1985; Bromley, 1990, 1996; Schieber, 2002; McIlroy *et al.*, 2003; Pemberton and Gingras, 2005; Needham *et al.*, 2006). Unfortunately, no classification based on diagenetic features is available yet. Early diagenesis is particularly relevant when dealing with trace fossils in carbonates. Organic material and mucus in *Thalassinoides* linings serve as a nucleus for $CaCO_3$ precipitation resulting in the formation of nodular limestones (Fürsich, 1972). Spectacular examples of diagenetically enhanced trace fossils also occur in chalk in the form of flint concretions (e.g. Bromley and Ekdale, 1984a) (see Section 1.2.6). The influence of diagenesis on biogenic structures is also of paramount importance in alkaline lakes (Scott *et al.*, 2007a). These authors evaluated the interplay of diagenesis and animal–sediment interactions, and analyzed the role of efflorescent salt crystallization, substrate wetting and drying, and benthic microbial mats and biofilms. In recent years, different studies have emphasized the links between burrowing and diagenesis (e.g. McIlroy *et al.*, 2003; Pemberton and Gingras, 2005; Needham *et al.*, 2006). In particular, the importance of bioturbation in enhancing permeability in hydrocarbon reservoirs has been stressed (Pemberton and Gingras, 2005).

1.4 ETHOLOGY OF TRACE FOSSILS

Trace fossils are primarily evidence of animal behavior (see Section 1.2.1). Accordingly, understanding the ethological significance of trace fossils lies at the very core of ichnology, and virtually any valuable inference stems from it (Fig. 1.14). It is unsurprising that the ethological classification of trace fossils is one of the most popular in ichnology. This system of classification was proposed

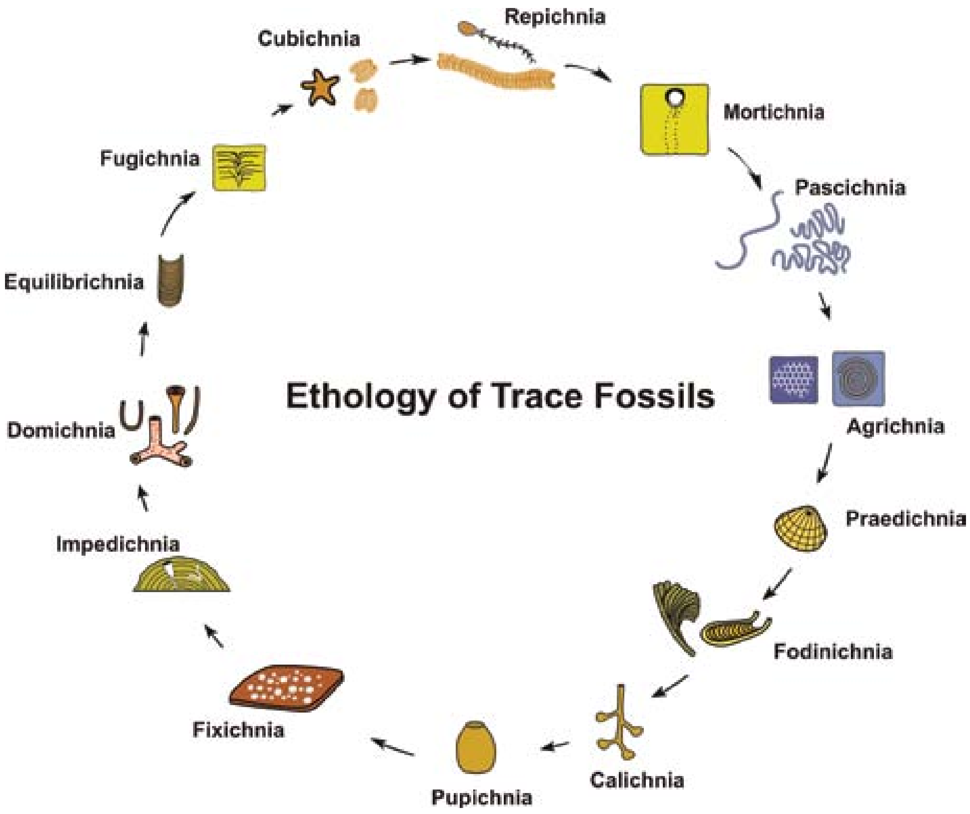

Figure 1.14 Ethological classification of trace fossils. Modified from Bromley (1996).

originally by Seilacher (1953a) and is based on the establishment of a small number of ethological categories. The original system consists of five categories: resting traces (cubichnia), locomotion traces (repichnia), grazing traces (pascichnia), feeding traces (fodinichnia), and dwelling traces (domichnia). These five categories represent the basic building blocks of behavioral interpretations in ichnology. However, refinements have been suggested to take account of additional behaviors. For example, Frey (1973) added a sixth category for escape traces or fugichnia, and Ekdale *et al*. (1984) suggested another one for farming traces and traps or agrichnia. To this list we should add predation traces or praedichnia (Ekdale, 1985) and equilibrium traces or equilibrichnia (Bromley, 1990). In recent years, new ethological categories were added for the work of some terrestrial insects and bioeroders. Nesting traces or calichnia (Genise and Bown, 1994a) and pupation chambers or pupichnia (Genise *et al*., 2007) belong to the first group, while fixation/anchoring traces or fixichnia (Gibert *et al*., 2004) and bioclaustration structures or impedichnia (Tapanila, 2005) fall within the latter. Seilacher (2007a) introduced death traces or mortichnia. Other categories may be considered as subdivisions of the major ones. For example, Genise and Bown (1994a) noted that calichnia may include building traces or aedifichnia, previously proposed by Bown and Ratcliffe (1988). Verde *et al*. (2007) documented aestivation chambers in paleosols, but recommended recognition of further cases to evaluate whether creating a new ethological category is advisable or whether this should be considered a subset of domichnia. In addition, Genise (1995) made the point that substrate selection is an integral part of behavior and introduced xylichnia for wood borings, but placed it as a subcategory of fodinichnia. Unsuccessful attempts at escape have been referred to as taphichnia by Pemberton *et al*. (1992b), but included in fugichnia by Bromley (1996). Needless to say, most trace fossils represent more than one activity and overlap among categories reflects common intergradations. The category polychresichnia was proposed for trace fossils that represent many simultaneous multiple behaviors and uses (Hasiotis, 2003). However, this situation is the rule rather than the exception and, therefore, a discrete ethological category is unnecessary. Excellent summaries of the ethological classification have been published by Frey and Pemberton (1984, 1985), Ekdale (1985), and Bromley (1990, 1996).

1.4.1 RESTING TRACES OR CUBICHNIA

Resting traces are produced by vagile organisms that temporarily dig down, forming shallow depressions, seeking protection from predators or that simply stop their usual activities during quiescent moments. Strictly speaking, few tracemakers actually rest and different subordinate behaviors may be involved (Bromley, 1990, 1996). For example, some resting traces are linked to feeding purposes. Ophiuroids, common producers of *Asteriacites*, dig in the sediment searching for prey and shifting their position at intervals. Resting traces of the ghost crab *Ocypode quadrata* are associated with hydration and respiration (Martin, 2006a). On morphological grounds, resting traces clearly reflect the latero-ventral anatomy of their producers (Fig. 1.15a). As a consequence, resting traces can be ascribed to their

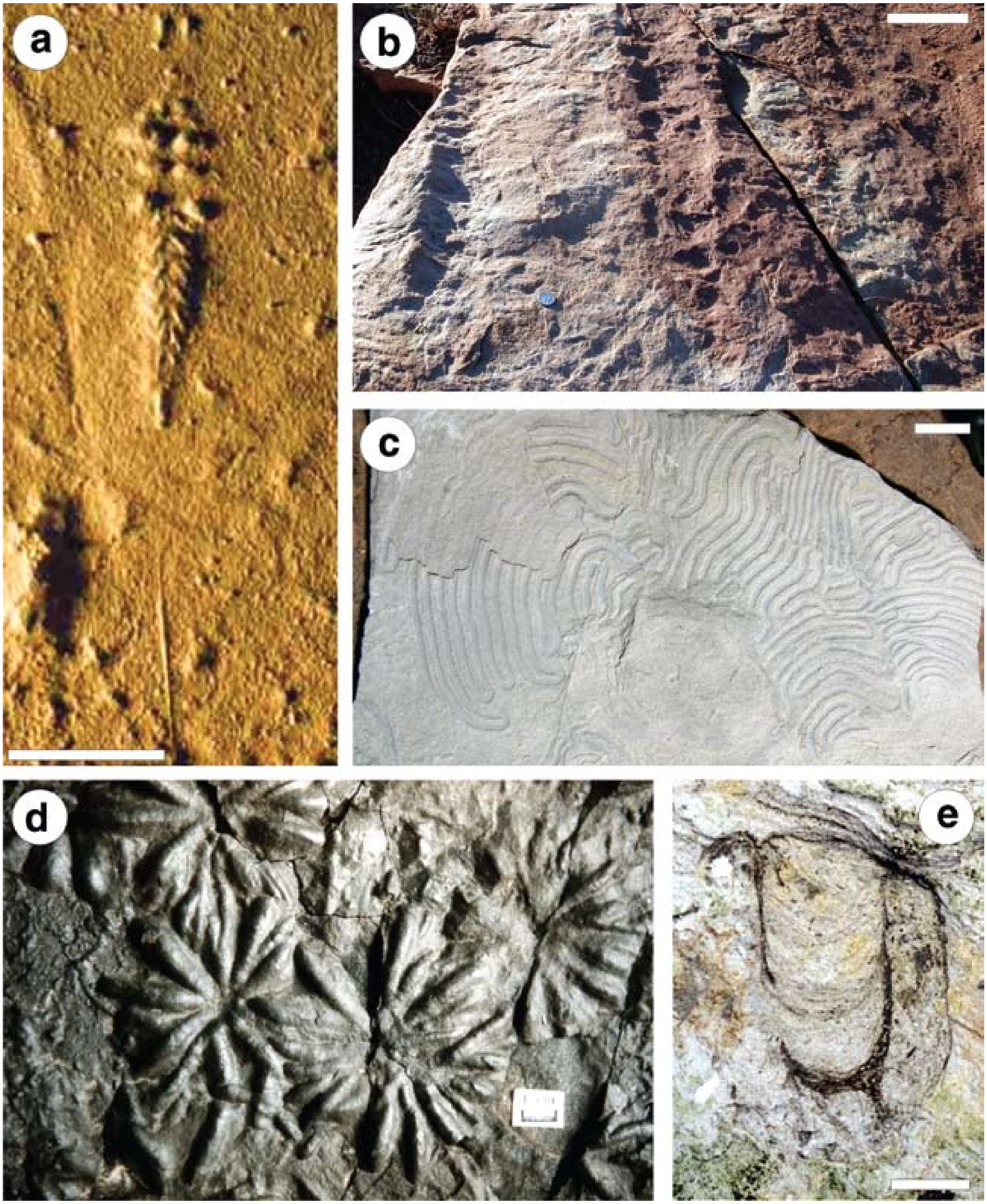

Figure 1.15 Examples of the original ethological categories established by Seilacher (1964b). (a) Resting trace (cubichna) *Tonganoxichnus buildexensis*. Note morphological evidence of the latero-ventral anatomy of its producer, a monuran insect. The anterior region is characterized by the presence of a frontal pair of maxillary palp impressions, followed by a head impression and three pairs of conspicuous thoracic appendage imprints symmetrically opposite along a median axis. The posterior region commonly exhibits numerous delicate chevron-like markings, recording the abdominal appendages, and a thin, straight, terminal extension. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, central United States. See Mángano *et al*. (1997, 2001a). Scale bar is 1 cm. (b) Giant arthropod locomotion trace (repichnia) *Diplichnites cuithensis*. Two rows of imprints produced by the locomotory appendages of a terrestrial myriapod are recorded. Upper Carboniferous, El Cobre Canyon Formation, El Cobre Canyon, New Mexico, southwest United States. See Lucas *et al*. (2005). Scale bar is 10 cm. (c) Grazing trail (pascichnia) *Nereites irregularis*. Note highly specialized guided meanders evidencing efficient covering of the substrate. Paleogene, Rhenodanubian Flysch, Hoflein Wiener Wald, Austria. Scale bar is 1 cm. See Uchman (1999). (d) *Asterichnus* isp., Upper Ordovician, Letná Formation, Chrustenice, Czech Republic. See Prantl (1945) and Mikuláš (1998). Scale bar is 1 cm. (e) The U-shaped dwelling trace (domichnia) *Diplocraterion*. Lower Jurassic, Staithes Sandstone Formation, Staithes Harbour, North Yorkshire Coast, England. See Taylor and Pollard (1999). Scale bar is 1 cm.

makers with a higher degree of certainty than other categories. Although discrete resting traces do occur, intergradations with locomotion traces (e.g. *Rusophycus-Cruziana*) or escape traces (*Lockeia-Protovirgularia wattonensis*) commonly occur. The typical preservation is as positive hyporelief, although negative epireliefs can occur. Examples of resting traces are *Lockeia*, *Tonganoxichnus* (Fig. 1.15a), *Tripartichnus*, *Selenichnites*, *Asteriacites*, *Rusophycus*, *Medousichnus*, *Raaschichnus*, and *Limulicubichnus*. Landing traces or volichnia (Walter, 1983) are best included within cubichnia.

1.4.2 LOCOMOTION TRACES OR REPICHNIA

Locomotion traces result from animals that move from one place to another. The main activity here is displacement of the producer. Other activities, such as feeding, might be involved but they are not reflected by the biogenic structure. As for almost all trace fossils, locomotion traces are typically produced by benthic animals. However, fish swimming close to the sediment–water interface may occasionally touch the bottom leaving locomotion trails (*Undichna*). Because of this, the term "locomotion trace" is preferred to the most widely used "crawling trace". The morphology of the trace fossil is directly related to the locomotion mechanism involved (e.g. locomotory appendages in arthropods and tetrapods, and muscular foot in bivalves). Trackways represent a typical example (Fig. 1.15b), but continuous horizontal trails are also common. Morphologies in this latter case include bilobate traces, simple trails, and chevronate traces. Complex traces suggestive of systematic probing due to feeding activities are excluded. Although less informative of the anatomy of the producers, locomotion traces may shed some light on the type and number of appendages involved in locomotion, as well as on the role of muscles used for displacement. Locomotion traces are invariably preserved as positive hyporelief or negative epireliefs, and are essentially bedding-plane trace fossils formed either at the sediment–water/air interface or along lithological interfaces. Examples include a wide variety of tetrapod and arthropod trackways, such as the ichnogenera *Umfolozia*, *Kouphichnium*, *Diplichnites* (Fig.1.15b), *Permichnium*, *Mirandaichnium*, *Octopodichnus*, and *Paleohelcura*, among many others. Locomotion trails are represented by *Cruziana*, *Gyrochorte*, *Diplopodichnus*, *Didymaulichnus*, and *Protovirgularia*. As indicated by Bromley (1990, 1996), swimming traces (natichnia of Müller, 1962, and Walter, 1983), and running traces (cursichnia of Walter, 1983) are best included under the more general repichnia.

1.4.3 DEATH TRACES OR MORTICHNIA

Death traces reflect the last movements of the makers that are preserved together with their trace fossils. Even post-mortem convulsions may be recorded (Seilacher, 2007a). These are unique cases in which a trace fossil is attributed without any doubt to a producer. They are typically arthropod trackways, such as those of limulids and crustaceans, ending in a body fossil. Less common examples include those of bivalves and gastropods preserved at the end of their burrows and trails, respectively, and tail traces produced by fish. Death traces are almost invariably preserved in anoxic settings as a result of the activity of animals that were transported by turbidity currents into the anoxic zone. With the exception of *Telsonichnus*, which resulted from the final movements of the shrimp *Antrimpos* (Seilacher, 2007a), no formal names have been proposed for death trace fossils. Taxonomic names originally proposed for locomotion structures (e.g. *Kouphichnium*) are commonly used.

1.4.4 GRAZING TRACES OR PASCICHNIA

Grazing traces reflect a combination of locomotion and feeding because the animal searches for food while traveling. They represent the activity of mobile, infaunal deposit feeders or epifaunal detritus- feeding organisms, and typically include forms that are more regular than trails that simply reflect locomotion (Fig. 1.15c). These trails are unbranched and horizontal, varying from simple, straight grooves that may reflect overlapping to, more typically, non-overlapping, curved, circular, and meandering, including tight guided meanders. Trail complexity reveals the degree of sophistication involved in the feeding pattern. In contrast to locomotion and resting traces, anatomic information on the producers of grazing traces is mostly unavailable (although some general morphological information, such as the length of the animal can be readily inferred). As a result, connections between the trace and its producer are difficult to establish. As with locomotion traces, grazing traces are preserved as positive hyporelief or negative epireliefs. They are typical bedding-plane trace fossils formed either at the sediment–water/air interface or along lithological interfaces. Examples of grazing traces are *Gordia*, *Mermia*, *Helminthoidichnites*, *Archaeonassa*, *Psammichnites*, *Helminthopsis*, *Nereites* (Fig. 1.15c), *Bichordites*, and *Scolicia*. *Helminthorhaphe* and *Cosmorhaphe* may belong to this category, although other authors tend to include them in agrichnia.

1.4.5 FEEDING TRACES OR FODINICHNIA

Feeding traces represent combined dwelling and feeding activities. They are typically produced by infaunal deposit feeders that develop an "underground mining" strategy. Morphologies are variable, ranging from simple to extremely complex. Intergradations with dwelling traces are common, and some structures are difficult to place in one category or the other. Common patterns include simple burrows, branched burrow systems, radial structures, and U-shaped tubes. Spreite formation is quite typical. Evidence of active infill (e.g. backfill) by the organism is almost diagnostic. In contrast to the previously described categories, orientation with respect to the bedding plane is highly variable, including horizontal, inclined, and vertical traces. Little, if any, anatomic information is provided by feeding traces. Endichnial preservations are the most common. Examples include *Asterichnus* (Fig. 1.15d), *Asterosoma*, *Arthrophycus*, *Rhizocorallium*, *Treptichnus*, *Dictyodora*, *Lophoctenium*, *Teichichnus*, *Daedalus*, *Syringomorpha*, *Gyrophyllites*, *Dactyloidites*, and *Phycodes*.

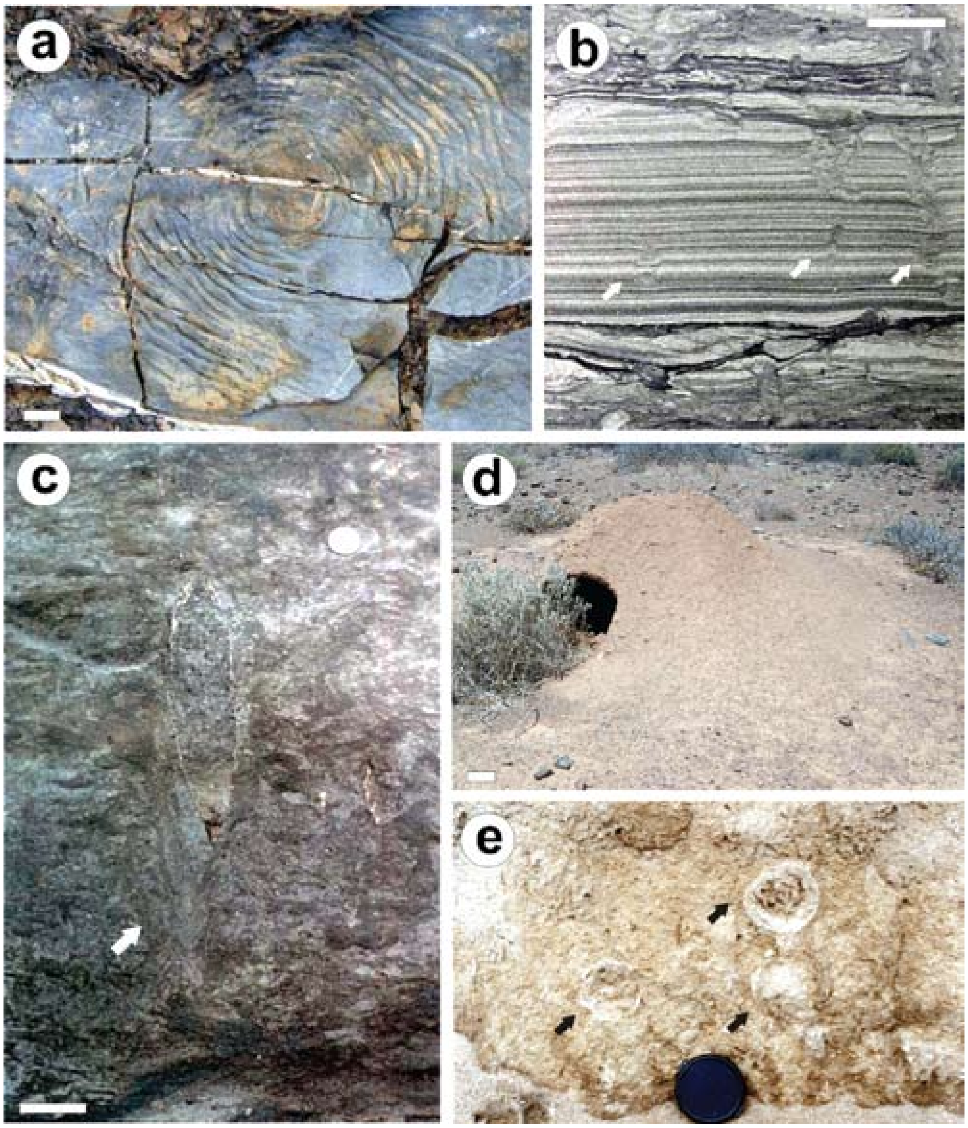

Figure 1.16 Examples of the subsequently added ethological categories. (a) The farming trace (agrichnia) *Spirorhaphe involuta*. Lower Eocene, Guárico Formation, Boca de Uchire, Venezuela. See Macsotay (1967). Scale bar is 1 cm. (b) Escape traces (fugichnia) (arrows) in tempestite. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (c) Equilibrium structure (equilibrichnia) *Scalichnus* (arrow) produced by the bivalve *Atrina* (see body fossil of the producer preserved at the top of the structure). Lower Miocene, Chenque Formation, Caleta Olivia, Patagonia, Argentina. See Carmona *et al.* (2009). Scale bar is 5 cm. (d) Predation trace (praedichnia). Modern termite nest reworked by a myrmecophagous mammal. Matjiesgloof Farm, South Africa. Scale bar is 10 cm. See Fey (2010) (e) The nesting trace (calichnia) *Coprinisphaera ecuadoriensis* (arrows). Pleistocene, Cangagua Formation, Quito, Ecuador. See Laza (2006). Lens cap is 5.5 cm.

1.4.6 DWELLING TRACES OR DOMICHNIA

Dwelling traces comprise permanent domiciles constructed by infaunal organisms, commonly sessile suspension feeders and passive predators. Less commonly, active predators and deposit feeders also construct dwelling traces. Emphasis is on dwelling, but other activities may be involved. The category encompasses not only burrows but also borings in hard substrates. The morphology ranges from simple burrows to U-shaped tubes (Fig. 1.15e) and branched burrow systems. Dwelling traces are typically vertical to oblique, but horizontal burrows may occur. Burrow linings are common, reflecting construction of permanent structures. Burrow diameter tends to be quite constant, reflecting tracemaker width. Dwelling traces are preserved as endichnia. Examples of dwelling traces are *Skolithos*, *Arenicolites*, *Diplocraterion* (Fig. 1.15e), *Ophiomorpha*, *Thalassinoides*, *Monocraterion, Camborygma*, *Lunulichnus*, and *Palaeophycus.*

1.4.7 TRAPS AND FARMING TRACES OR AGRICHNIA

Agrichnia includes complex and extremely regular burrow systems that are referred to as graphoglyptids. These structures represent combined dwelling and feeding activities, and are thought to be produced for bacterial farming or as traps to capture meiofauna or microorganisms (Seilacher, 1977a). Burrow morphologies include branched meanders, spirals (Fig. 1.16a), and nets. These patterns are typical of the deep sea, but have been compared with modern spirals formed in intertidal areas by the polychaete *Paraonis fulgens* for trapping diatoms (Röder, 1971; Papentin and Röder, 1975; Seilacher, 1977a; Minter *et al.*, 2006). However, some graphoglyptids display multiple exits and side branches that suggest bacterial farming rather than trapping (Seilacher, 1977a). The burrows are maintained as open tunnels in hemipelagic mud, very close to the sediment–water interface and, therefore, no active infill occurs. They are subsequently excavated by turbidity currents and

Box 1.2 The ethology of *Zoophycos*

Zoophycos is one of the most complex trace fossils (Fig. 1.17a–h). Several constructional models have been proposed to account for its intricate morphology and its ethological significance. Hardly a year passes without a new paper on *Zoophycos*. Richard Bromley (1991) elegantly summarized the different available models for *Zoophycos*. Because of the large morphological variability of Ordovician to Recent *Zoophycos*, it is likely that there is no single universal "correct" model and, instead, models should be applied on a case-by-case basis. It is even possible that the *Zoophycos* animal displays a behavioral plasticity that allows for shifts in feeding strategies and trophic types if necessary.

Strip-mine model: This model implies a deposit-feeding strategy for the *Zoophycos* producer. In this model, the spreite is the result of sediment feeding and waste disposal occurring simultaneously. This is a low-cost system based on minimal sediment transport. However, the discovery by Nobuhiro Kotake that the *Zoophycos* producer introduces sediment from the sediment–water interface in the form of excreted pellets militates against the strip-mine, deposit-feeding model.

Detritus-feeding model: A detritus-feeding strategy is supported by the downward conveyance of sediment involved in *Zoophycos*. However, this is definitely a high-cost system and its viability remains unclear.

Refuse-dump model: This model attempts to reconcile the two apparently contradictory facts that the *Zoophycos*-infilling material is derived from a higher level and that the spreite is suggestive of a deposit-feeding strategy. Solving this contradiction requires that the preconstructed cavity is the result of deposit feeding and that the resulting material is conveyed upwards, while sediment from the surface is conveyed downwards to maintain the narrow form of the tube. This model is consistent with the generally accepted deep-tier nature of *Zoophycos*. However, as in the previous model, this is a high-cost system.

Cache model: Evidence from marine benthic ecology suggests that the flux of food supply varies periodically and, as a result, some organisms squirrel away food to be used later. The cache model implies that the *Zoophycos* producer feeds at the surface, but also conveys organic material downwards, using the burrow as a storage place for times of reduced food supply. This model is consistent with both the well-accepted downward convection and the deep-tier nature of *Zoophycos*.

Gardening model: This model adds another level of complexity to *Zoophycos* behavior. It has been noted that the thin burrow-fill laminae have a large interface with the surrounding sediment, and that a long marginal tube runs around the perimeter of the spreite. According to the gardening model, the *Zoophycos* animal uses the surface sediment as a carrier of microbes and cultivates bacteria within the marginal tube. This model is consistent with the overall complexity of the burrow.

References: Seilacher (1967a, 2007a); Simpson (1970); Wetzel and Werner (1981); Kotake (1989, 1991, 1994, 1997); Bromley (1991); M.F. Miller (1991); Ekdale and Lewis (1991a); Wetzel (1992); Gaillard and Olivero (1993); Fu and Werner (1995); Olivero and Gaillard (1996, 2007); Bromley *et al.* (1999); Miller and d'Alberto (2001); Bromley and Hanken (2003); Löwemark and Schäffer (2003); Knaust (2004a, 2008); Löwemark *et al.* (2006, 2007).

cast by the turbidite sand. Accordingly, graphoglyptids are preserved as a positive hyporelief at the base of turbidite sandstones. Examples of agrichnia are *Spirorhaphe* (Fig. 1.16a), *Belorhaphe*, *Helicolithus*, *Urohelminthoida*, *Paleomeandron*, *Desmograpton*, *Paleodictyon*, *Megagrapton*, and *Protopaleodictyon*. It has been suggested that some deeper branching burrow systems may be included in agrichnia, such as *Chondrites* (Seilacher, 1990a; Fu, 1991; Bromley, 1996) and *Pragichnus* (Mikuláš, 1997). In addition, farming has been suggested as the feeding strategy involved in the helically coiled spreiten burrow *Zoophycos* (Fu and Werner, 1995) (Box 1.2), and the sinusoidal crustacean burrow system *Sinusichnus* (Gibert, 1996; Buatois *et al.*, 2009a).

1.4.8 ESCAPE TRACES OR FUGICHNIA

Escape traces include structures formed in response to rapid changes in sedimentation, typically event deposition. Animals are forced to rapidly readjust their burrows to avoid burial. Lateral escape from predators may be included in this category (Bromley, 1990, 1996). The polychaete *Scolelepis squamata* forms sinusoidal trails similar to *Cochlichnus* to escape from predators (Behrends and Michaelis, 1977). This latter group of escape traces is difficult, if not impossible, to recognize in the fossil record. In any case, typical escape structures are revealed by the vertical repetition of dwelling traces, commonly forming not only cone-in-cone morphologies (Fig. 1.16b) but also U-in-U traces. Burrow walls are poorly defined and unlined, reflecting rapid sediment reworking. These structures are invariably preserved as endichnial structures. Bivalves and sea anemones usually produce escape traces. Because their morphology is so simple, it is common practice among ichnologists not to give formal ichnotaxonomic treatment to escape traces (e.g. Hanken *et al.*, 2001). As noted by several authors, care should be exercised to avoid confusing escape traces with physical collapse features (Frey and Pemberton, 1985; Buck and Goldring, 2003).

1.4.9 EQUILIBRIUM TRACES OR EQUILIBRICHNIA

Equilibrium traces encompass structures formed in substrates affected by progressive aggradation and degradation. In contrast to escape traces, equilibrichnia comprises more gradual adjustments under background sedimentation reflecting the fact that infaunal organisms live at a certain depth with respect to the sediment–water interface. Displacements include upward

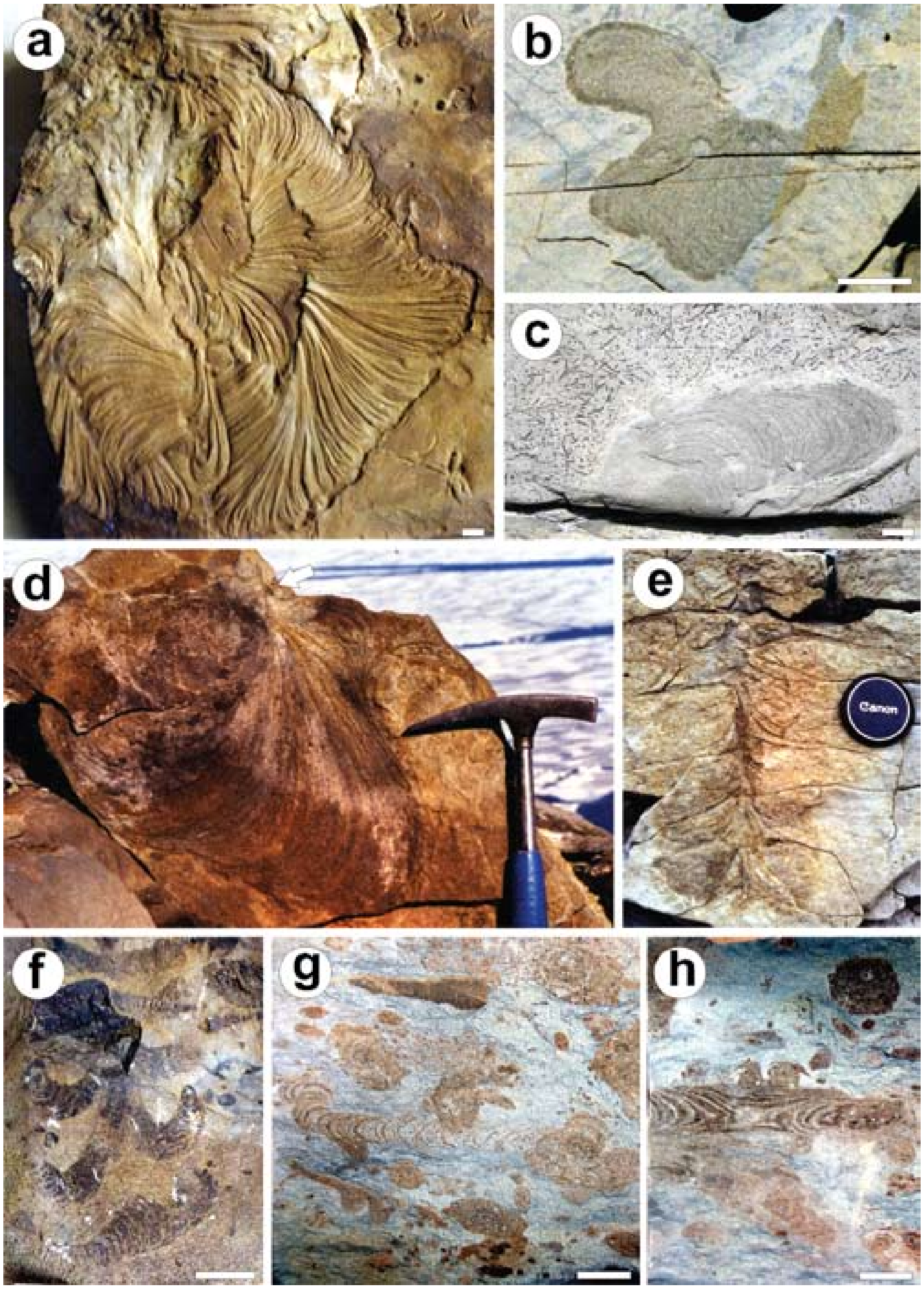

Figure 1.17 Morphological variability and different expressions of *Zoophycos*. (a) Bedding-plane view of a large specimen showing a complex spiral form and lobes with well-developed primary lamellae. Middle Ordovician, Tabuk Group, northern Saudi Arabia. Scale bar is 1 cm. (b) Bedding-plane view of a small specimen showing a complex spiral form and lobes with well-developed marginal tube. Upper Cretaceous, Amden Beds, Fäneren area, Switzerland. Scale bar is 1 cm. See Wetzel (2003). (c) Bedding-plane view of a large specimen showing a simple planar form and lobes with well-developed primary lamellae. Upper Cretaceous, Siliceous Marl, Rzyki, Outer Carpathians, Poland. Scale bar is 1 cm. See Uchman and Gieszkowski (2008a). (d) Bedding-plane view of a large specimen showing a complex spiral form and lobes with well-developed primary lamellae. Note horizontal section of axial shaft (arrow). Upper Cretaceous, Rabot Formation, Rabot Point, James Ross Island, Antarctica. Length of hammer is 33.5 cm. See Buatois *et al.* (1993). (e) Cross-section view of specimen showing axial shaft and successive lobes. Upper Cretaceous, Rabot Formation, Rabot Point, James Ross Island, Antarctica. Lens cap is 5.5 cm. See Buatois *et al.* (1993). (f) Cross-section view of specimen showing successive lobes. Lower Cretaceous, Kotick Point Formation, Kotick Point, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois and Mángano (1992). (g) Cross-section view of specimen in core showing lamina consisting of alternating dark- and light-colored menisci. Lower Cretaceous, Muderong Shale Formation, Pluto Field, Carnavon Basin, offshore Northwestern Australia. Scale bar is 1 cm. (h) Cross-section view of specimen in core showing change in the orientation of the backfilled. Lower Cretaceous, Muderong Shale Formation, Pluto Field, Carnavon Basin, offshore Northwestern Australia. Scale bar is 1 cm.

movement as a response to aggradation and downward burrowing during substrate degradation. Under a rapid increase in sedimentation rate, equilibrium traces grade into escape traces. Vertically oriented, spreite U- or V-shaped burrows represent the typical morphology and are preserved as endichnia structures. The classical example is the vividly named *Diplocraterion yoyo* (Goldring, 1962). *Rosselia socialis*, a vertical fusiform burrow attributed to terebellid polychaetes, is commonly stacked suggesting an equilibrium behavior (Nara, 2002). The bivalve *Panopea* generates equilibrium structures that have been included in the ichnogenus *Scalichnus* (Hanken *et al.*, 2001). The bivalve *Atrina* also produces spectacular equilibrium/adjustment structures by cutting and regenerating its byssum (Carmona *et al.*, 2008) (Fig. 1.16c).

1.4.10 PREDATION TRACES OR PRAEDICHNIA

This category reflects predatory activities. The most common cases are those of borings in hard substrates, such as shells or, less commonly, bones. Round drill holes, gnawings and the chipped margins observed in gastropod and bivalve shells represent typical morphologies. Examples include *Oichnus* and different types of bites and durophagous scars. Predatory holes have also been recorded in the Ediacaran tubular shell *Cloudina* (Bengtsön and Yue, 1992; Hua *et al.*, 2003). Walker and Behrens-Yamada (1993) have even documented structures due to failed predation by crabs in empty gastropod shells. Interestingly, predation by trilobites on worms has been suggested based on ichnological evidence (Bergström, 1973; Jensen, 1990; Brandt *et al.*, 1995). In particular, Jensen (1990) documented examples where the axis of the trilobite trace fossil *Rusophycus dispar* is nearly parallel to the worm burrows. Also, the worm burrows closely follow the curvature of the *Rusophycus dispar* trace and are commonly in contact with only one of its lobes, suggesting active predation. Kramer *et al.* (1995) described trackways of scorpions or spiders (*Octopodichnus*) and insects (*Permichnium*) that abruptly terminate against pelicosaur trackways (*Laoporus*), suggesting predation on arthropods. Modern examples include termite nests that are reworked by myrmecophagous mammals, such as aardvarks and aardwolves (Taylor and Skinner, 2000) (Fig. 1.16d).

1.4.11 NESTING TRACES OR CALICHNIA

Calichnia comprises nests constructed or excavated by the adult insects for breeding purposes (Fig. 1.16e). Insect larvae are confined to cells or chambers that are provisioned by the adults. Nesting traces require specific substrate conditions, particularly with respect to humidity (Genise and Bown, 1994a; Genise *et al.*, 2000). Excessive moisture inside cells leads to the decay of provisions, which are attacked by fungi and other saprobic organisms, whereas insufficient moisture results in the dehydration of larvae, which are not protected by a water-resistant cuticle like adults. Included in calichnia are beetle nests, such as *Coprinisphaera* (Fig. 1.16e) and *Quirogaichnus*, and bee cells (*Celliforma*).

1.4.12 PUPATION CHAMBERS OR PUPICHNIA

Pupichnia consists of structures produced by insects, which mostly live freely in soils or in vegetation, for their protection during pupation (Genise *et al.*, 2007). The same individual that produces the structure, later emerges from it, although in a different developmental stage. Examples include *Fictovichnus*, *Pallichnus*, and *Rebuffoichnus*.

1.4.13 FIXATION/ANCHORING TRACES OR FIXICHNIA

Fixichnia comprises superficial structures formed on hard substrate by sessile epilithic organisms to provide attachment. Two main groups of fixichnia are recognized: those formed by the anchoring of an organism by means of soft parts and those produced by the fixation of its skeleton (Gibert *et al.*, 2004). Examples of fixichnia include *Centrichnus*, *Podichnus*, *Renichnus*, *Stellichnus*, and *Leptichnus*.

1.4.14 BIOCLAUSTRATION STRUCTURES OR IMPEDICHNIA

This category includes structures that record two distinct behaviors during the construction of a cavity in skeletal material (Tapanila, 2005). The resulting structure, referred to as embedment by Bromley (1970) and bioclaustration by Tapanila (2005), is produced by the activity of the endosymbiont that inhibits skeletal accretion of the host and by the host, which alters skeletal growth to accommodate the infesting organism. The bioclaustration structure also serves as a domicile for the endosymbiont. Examples of impedichnia are *Helicosalpinx*, *Tremichnus*, *Chaetosalpinx*, *Hicetes*, *Klemmatoica*, and *Eodiorygma*.

1.4.15 DISCUSSION: COMPLEX TRACES AND EXTENDED ORGANISMS

Undoubtedly, the ethological classification has been extremely successful. As noted by Frey and Pemberton (1985), the classification is intentionally restricted to a small number of categories and proliferation of new ones is not advisable, unless they are well founded. In any case, the more recent additions are valuable because they document behaviors that were not represented in the original Seilacherian scheme. As noted by Genise and Bown (1994a), the fact that the original categories were based almost exclusively on marine ichnotaxa should result in some changes when dealing with behavior peculiar to terrestrial trace fossils.

More recently, some authors suggested that complex trace fossils, such as *Zoophycos*, *Paleodictyon*, and *Phymatoderma*, cannot be accommodated in the traditional classification scheme (Miller, 1998, 2002, 2003). The underlying idea is that these structures have been occupied for long intervals of time and seem to record some sort of active control of the habitat by the tracemaker. In particular, Miller and Vokes (1998) attempted to categorize trace fossils under two main groups: incidental or those that record a single or dominant behavioral activity and deliberate or those that represent restructuring of habitats, modulation of disturbances, and control of food resources. Incidental structures are typically simple, while deliberate structures are complex. These authors advocated a fabricational analysis of trace fossils that involved evaluation of construction, operation, and maintenance of burrow systems. This approach may be framed within the recent view of trace fossils as extended organisms (Turner, 2000, 2003) or the notion of animals as ecosystem engineers (Jones *et al.*, 1994). Although the application of this perspective to the fossil record remains to be tested more extensively, it provides a more active role for the tracemakers rather than a simple passive response to the prevailing environmental conditions (see Section 6.6).

2 Taxonomy of trace fossils

In the final analysis, it is the morphology of the trace as an expression of animal behaviour that is the basis of the name.

Richard Bromley
Trace Fossils: Biology, Taphonomy and Applications (1996)

As ichnologists we must admit that the introduction and discussion of different ichnotaxonomic philosophies reminds us of the inherent subjectivity in any scientific endeavor. Ostensibly the ICZN should constrain such subjective interpretation and bring order to the field. In practice this is difficult, and a certain degree of chaos and ambiguity still reigns. Nonetheless the science progresses, and names, however reliable or controversial, are used for descriptions and dialog between ichnologists.

Martin Lockley
"A tale of two ichnologies: the different goal and potential of invertebrate and vertebrate
(Tetrapod) ichnotaxonomy and how they relate to ichnofacies analysis" (2007)

Although it is not uncommon to find expressions of doubt about the need to use a formal taxonomy to classify trace fossils, ichnotaxonomic classification is an unavoidable companion to preservational and ethological schemes. If a formal name is available, simple descriptors (e.g. vertical burrows and meniscate traces) should be avoided. The ichnotaxonomic classification, albeit imperfect, provides the best common ground on which to base more theoretical elaborations and practical applications (Buatois *et al*., 2002a). In any case, in modern ichnology contrasting philosophical perspectives have been adopted to classify trace fossils. However, exchange of ideas during and after the 1998, 2002, 2006, and 2010. Workshops on Ichnotaxonomy have resulted in a growing consensus among practicing ichnologists (Bertling *et al*., 2006). In this chapter, we turn our attention into the theoretical and practical aspects involved in classifying trace fossils from a taxonomic standpoint. We first address some philosophical problems involved in this approach. Then, we focus on a detailed review of the different ichnotaxobases currently in use and the problems associated with compound and composite trace fossils. Subsequent to that, we move on to some recent ideas and proposals with respect to the uses of hierarchies in trace-fossil taxonomy and the peculiarities of vertebrate ichnotaxonomy. Finally, we review some practical aspects involved in the recognition of trace fossils in both outcrops and cores.

2.1 APPROACH AND PHILOSOPHY

As in the case of body-fossil taxonomists, the lumpers and the splitters represent two opposing ways of weighting trace-fossil morphology (Pickerill, 1994). Lumpers tend to cluster all existing forms in a few essential ichnogenera and splitters find visible morphological differences significant enough to create a plethora of new forms. From a philosophical perspective, lumpers are certainly more inferential and splitters are more empirical. Lumpers tend to favor behavior over morphology, trying to define the basic ethology that relates a group of structures, while splitters remain reluctant to make invisible links among apparently dissimilar forms, tending to adopt morphology at face value. This confrontation is a revisitation of the old debate about the roles of observation and theory in science. In our view, it is impossible to adopt a strictly descriptive procedure to name ichnotaxa. Understanding of the behavioral significance, which implies different degrees of interpretation, is necessary. Although there should be a conscious effort to focus on significant morphological details, there is no such a thing as a purely morphological classification. The ichnotaxonomic classification is permeated by our understanding of the ethology.

We fully agree with Bromley (1996, p. 166) that "in the final analysis, it is the morphology of the trace as an expression of animal behaviour that is the basis of the name". To decipher the behavior of the tracemaker, however, may be quite a difficult task. Very frequently, morphology in itself is considered sufficient to define new ichnotaxa, although its ethological meaning is hardly understood. Some morphological features can be objective in the sense of being observable and easily recognizable, and they may still not deserve any consideration at any ichnotaxonomic level. A drastic difference in morphology may actually provide evidence of extrinsic controls, such as the degree of substrate consolidation, rather than behavioral determinants (see Section 6.1.2). As noted by MacNaughton and Pickerill (1995), taphonomy may negatively impact on ichnotaxonomic precision. As quality of preservation decreases, ichnotaxonomic identifications become less reliable. In most cases, taphonomic overprint may artificially increase trace-fossil diversity, although poor preservation may occasionally induce lumping. These authors introduced the notion of taphoseries to refer to ichnotaxa that could potentially be mistaken for each other (see also MacNaughton and Pickerill, 2003). Only morphological characters that are known to reflect significant behavioral traits should be considered (see Section 2.3).

Because ichnofossils are commonly preserved *in situ*, the relationship established between burrowing organisms and their host substrate is so intimate that both components cannot be studied in isolation. The degree of connection between biogenic structures and the substrate is such that even strict taxonomic studies of trace fossils should not be done without a proper analysis of the associated substrate and the idiosyncrasies of trace-fossil taphonomy. An accurate understanding of the environmental conditions under which a trace fossil is created should illuminate our understanding of the biogenic structure, even if those factors are not formally considered in the nomenclature of trace fossils (Goldring *et al*., 1997). When this guideline is not followed, ichnologists are forced to deal with a large number of poorly defined ichnotaxa whose actual relevance is doubtful. In contrast to standard body-fossil taxonomy, ichnotaxonomy cannot be performed on purely observable morphological grounds. While morphology is observed, behavior must be inferred. The degree of behavioral inference varies with each particular case. For example, in the simplest case, there is almost a continuum from the morphological observation of clearly preserved ventral anatomic features to the interpretation of a trace as a resting structure (e.g. Mángano *et al*., 1997). However, analysis of most trace fossils requires a larger inferential jump, involving knowledge of a complex array of biological, taphonomic, and environmental determinants.

Advantages of a dual nomenclature (i.e. two separate names for biotaxa and ichnotaxa) as well as the risks involved in the biotaxonomic identification of the tracemaker have been stressed by Bromley (1990, 1996) and Bertling *et al*. (2006). Attempts to avoid this approach (e.g. Dzik, 2005) create a large number of problems and give the false impression that a particular trace fossil can be directly linked to a producer [e.g. *Treptichnus* (*Mankyodes*) *rectangularis* invariably to priapulids]. In most cases behavioral convergence rules out establishing a one-to-one relationship between a producer and a trace fossil (see Section 1.2.3). The idea of replacing ichnotaxonomic names with vernacular names, such as “a trail of a worm on the sediment surface” (Dzik, 2005, p. 519) is impractical and represents a step backwards in ichnological practice and communicability. Besides, one is tempted to ask “Was the trail actually produced by a worm?” and “Was it really produced *on* the sediment surface?” In soft substrates, some arthropods can leave a smooth trail undistinguishable from a worm trail (Mángano *et al*., 1996a; Davis *et al*., 2007). In addition, very few trace fossils actually represent the work of an animal moving on the sediment surface (i.e. epigenic); most of them record infaunal activities (i.e. endogenic).

Another complication results from the inclusion of the actual taxonomic identification of the tracemaker as an essential component of naming trace fossils (e.g. Hasiotis and Bown, 1992). In the same vein, introduction of an environmentally based ichnotaxonomy is problematic at best (Hasiotis and Bown, 1992; Hasiotis, 2002). As noted by Buatois *et al*. (1997a), if biological or sedimentological criteria are applied to ichnotaxonomy, it will be virtually impossible to escape from circular reasoning when using trace fossils as an aid to interpret ancient depositional environments. If *Isopodichnus* is named simply because it is present in continental red beds, it is tricky to use its occurrence as an evidence of continental deposition. The establishment of parallel ichnotaxonomic systems for marine, transitional, and continental ichnology proposed by Hasiotis and Bown (1992, p. 71) creates further problems. It is hard to provide a rationale that supports the idea of the same crustacean burrow receiving different names in brackish and fully marine settings. If we restrict *Ophiomorpha* for fully marine environments, which name do we have to use for the same decapod burrow emplaced in the landward side of the barrier island facing the brackish-water lagoon? Such a taxonomic system undercuts the information potential of trace fossils in sedimentology, stratigraphy, and paleoecology (Buatois *et al*., 1997a).

Maintaining the dual nomenclature certainly does not imply that biology does not play a significant role in trace-fossil taxonomy. We strongly advocate a more active role for biology in ichnotaxonomy. Biology provides the “blood” that enlightens the functional-morphology analysis of trace fossils. Although the detailed biology of the producers may remain unknown, understanding the bauplan and biological affinities of the tracemakers is essential. Constructional possibilities are determined by intrinsic biological factors and, therefore, should be helpful in evaluating the relative significance of behavioral traits as reflected by trace-fossil morphology (Mángano *et al*., 2002a). In this sense, the biology of the tracemaker ends up playing a role, albeit indirect, in trace-fossil taxonomy. An adequate ethological interpretation of a morphological feature is impossible without this biological framework.

2.2 SOME PROBLEMS AND PRACTICAL GUIDELINES

The problems that the practicing ichnologists should face result both from historical contingencies, and the intrinsic nature of ichnofossils. Among the historic factors, a large number of ichnotaxa, some of those of widespread use, were introduced during the nineteenth century when trace fossils were still regarded either as animal or plant body fossils (the so-called Age of Fucoids; Osgood, 1975). In accordance, the original diagnosis and descriptions of some of the most representative ichnotaxa include a plethora of zoological and botanical terms to name the morphological elements of these biogenic structures (D’Alessandro and Bromley, 1987; Bromley, 1990, 1996). Another historical peculiarity derives from the fact that the 1964 edition of the International Code of Zoological Nomenclature (ICZN) established that trace-fossil names defined after 1930 should be accompanied by a statement on the identification of the tracemakers. Because fulfilling that requisite was virtually impossible, in practice, post-1930 ichnotaxa became unavailable marking the beginning of what has been referred to as the “Dark Age of Ichnotaxonomy” (Bromley, 1990, 1996). Fortunately, most ichnologists decided to keep a reasonable degree of order and treated valid and invalid ichnotaxa in the same way (Häntzschel, 1975). The requirement of identifying the producer was subsequently eliminated and trace fossils are now bounded by the ICZN.

In addition, ichnotaxa have been introduced frequently in a rather chaotic and careless way. Some ichnotaxa have been poorly diagnosed or illustrated, based on scarce or fragmentary material, or insufficiently compared with similar forms. Taxonomic revisions are extremely useful, but usually cannot keep pace with newly introduced forms. Proliferation of new ichnotaxa based on superfluous features, characteristics of uncertain ethological significance, and poorly preserved or scarce specimens should be avoided. As noted by Bertling *et al*. (2006), trackways are particularly problematic because they are commonly represented by blurred or morphologically deviating undertracks or overtracks. Accordingly, only complete tracks should be used as a basis for establishing an ichnotaxon (see also Minter *et al*., 2007a).

If possible, ichnotaxa should be classified at ichnospecific level to avoid losing potential information (Pemberton and Frey, 1982). However, in some cases, the quality of preservation precludes ichnospecific assignments. In other cases, confusion persists with respect to which criteria should be adopted to classify certain ichnogenera at ichnospecific level (e.g. *Zoophycos*). Open nomenclature (i.e. the use of "cf.", "aff.", and "?") may be used in some cases (Bertling *et al*., 2006). Detailed procedures for the establishment of new ichnotaxa were outlined by Pickerill (1994).

The fact that trace fossils have their own peculiarities that mark significant departures with respect to body fossils (see Section 1.2) further complicates trace-fossil taxonomy. It is fair to say that ichnotaxonomy has all of the problems of body-fossil taxonomy plus their own. The ICZN established that only fossil specimens should be named, and this rule certainly prevents ichnologists dealing with a plethora of ichnotaxa based on recent examples that only have very minor chances of being preserved in the fossil record. One of the underlying reasons is that it is commonly assumed that modern traces can be assigned to their producers on a case-by-case basis. However, continuous attempts to capture the elusive *Paleodictyon* producer demonstrate that this is not always the case (Rona *et al*., 2009). Identification and collection of modern traces, particularly those produced in unconsolidated substrates, are commonly much more difficult than with fossil material. Trace fossils are usually enhanced by diagenetic processes that assist in their recognition (Magwood, 1992). Most important, many biogenic structures are in fact cumulative structures, which consist of both abandoned and active components (Bromley and Frey, 1974). Casts of modern cumulative structures only reflect the morphology of the open components that are actively occupied by the producer, resulting in a simpler pattern than the actual overall architecture (Frey, 1975; Frey and Seilacher, 1980; Magwood, 1992).

However, this ICZN regulation has its problems. Unlike body fossils, the boundary between recent and fossil traces may be, on occasion, quite uncertain (Bromley, 1990, 1996; Bertling *et al*., 2006). For example, ambiguous situations result from the uncertain status of modern borings (which may be considered fossils as soon as their producers die) and from modern burrows excavated in Pleistocene sediments (Bertling *et al*., 2006). The fact that some modern traces are identical to well-established trace fossils has led some ichnologists to refer them to the corresponding ichnotaxa (e.g. Ekdale, 1980; Wetzel, 1984; Gaillard, 1988). Some authors prefer to follow the code and name the producer in connection with the biogenic structure (e.g. burrows of *Upogebia pugittensis*) (Rindsberg, 1990a), while others opt for using the prefix "incipient" before the ichnotaxon (e.g. incipient *Thalassinoides*) (Bromley and Fürsich, 1980). In short, although discrepancies exist with respect to dealing with modern biogenic structures, there is general agreement that ichnotaxa should not be constructed on the basis modern material (Bromley, 1990, 1996; Magwood, 1992; Pickerill, 1994; Bertling *et al*., 2006).

Another distinction, which may be occasionally problematic, is that between body fossils and trace fossils. For example, bivalve internal moulds (*steinkerns*) may be associated with the resting trace *Lockeia*. In other cases, ornamented bivalve resting traces resembling body fossils are connected to the locomotion trace *Protovirgularia*. However, careful examination of the chevron orientation in *Protovirgularia* indicates that the animal exited the resting structure (e.g. Mángano *et al*., 1998). Albeit similar to body fossils, these structures should be regarded as trace fossils. Distinction between plug-shaped burrows and body fossils of ceriancthid or actinarian anemones has been historically problematic particularly with Ediacaran specimens (Jensen, 2003; Seilacher *et al*., 2005). In particular, the ichnogenera *Bergaueria* may be difficult to distinguish from the body fossils *Beltanellifomis* and *Beltanelloides* (e.g. Crimes and Germs, 1982; Fedonkin, 1985; Crimes, 1992; Crimes and Fedonkin, 1996; Jensen, 2003); and the ring-like structure *Intrites* has alternately been regarded as a trace fossil and a body fossil (Fedonkin, 1985; Crimes, 1994; Gehling *et al*., 2000; Jensen, 2003).

2.3 ICHNOTAXOBASES

Bromley (1990, 1996) noted that very little has been written on the characters that should be used to classify trace fossils. In an attempt to shed light on these issues, he introduced the concept of ichnotaxobases. An ichnotaxobase is a distinctive morphological feature of a trace fossil that displays significant and readily detectable variability and, therefore, is commonly used in ichnotaxonomic classifications (Bromley, 1990, 1996; Buatois *et al*., 2002a). Both requirements should be met. Morphological variability should reflect behavioral functions, therefore illuminating our ethological interpretation of a trace fossil. Additionally, an ichnotaxobase should be easily detectable in the sense of allowing uncontroversial identification. Five main ichnotaxobases (general form, wall and lining, branching, fill, and presence or absence of spreite) are discussed here. It should be noted, however, that each of these ichnotaxobases cannot be applied to every group of trace fossils. Arthropod trackways, insect nests, and vertebrate burrows or trackways, commonly pose their own problems to the ichnotaxonomist. For example, Laza (2006) illustrated the significance of the presence and position of the small egg chamber with respect to the large provision chamber in the taxonomy of dung-beetle nests.

In theory, those features that relate to major behavioral aspects should be used to differentiate ichnogenera, while those of lower significance should be applied for ichnospecies (Fürsich, 1974; Pemberton and Frey, 1982; Bromley, 1990, 1996; Bertling *et al*., 2006). In practice, to determine which characters are of main significance is not always straightforward. Characters that are rejected as useful ichnotaxobases are size, producer, type of passive fill, substrate consistency, geological age, geographic location, facies-environment, and any preservational aspect (Magwood, 1992; Pickerill, 1994; Bertling *et al*., 2006). The role of substrate as an ichnotaxobase remains controversial (see Section 2.7). Bertling *et al*. (2006) suggested keeping separate trace fossils formed in lithic, woody, and soft substrates regardless of morphological similarity, but at the same time cautioned against naming a new ichnotaxon based solely on a difference in substrate (see also Carmona *et al*., 2007). Taphonomy also plays a major role because, unfortunately, potentially useful ichnotaxobases may, in some cases, have lower preservation potential.

2.3.1 GENERAL FORM

The general form of a trace fossil represents its basic morphological plan and includes configuration, orientation, and position with respect to stratification (Pickerill, 1994) (Fig. 2.1a–c). Configuration is determined by the spatial arrangements of the trace components and reveals what is usually visualized, at first sight, as a whole (*gestalt*). Examples of descriptors for configuration are hexagonal networks (*Paleodictyon*), meandering traces displaying two orders of meanders (*Cosmorhaphe*), and simple sinusoidal trails (*Cochlichnus*). In these examples, ichnogeneric classification is based essentially on their distinctive configuration. Orientation (e.g. vertical, inclined, or horizontal), and position with respect to stratification or toponomy (e.g. positive hyporeliefs and negative epireliefs; see Section 1.3.1) are also first-order ichnotaxobases that help to classify biogenic structures at the ichnogeneric level. For example, *Rhizocorallium* and *Diplocraterion* share the same configuration (i.e. U-shaped burrows), but differ in their orientation, predominantly horizontal for the former and vertical for the latter. Other structures are essentially similar with respect to their basic configuration and orientation, but differ in stratal position. Examples are some horizontal bilobate trails, such as *Didymaulichnus* (positive hyporelief) and *Gyrochorte* (positive epirelief). In this case, stratal position reflects a completely different mode of construction. Although size may influence our perception of a structure, it should not be considered as a first-rank character, and is certainly a weak ichnotaxobase. However, size has been used in some cases to differentiate ichnospecies substantiated by significant statistical analysis, as illustrated with *Paleodictyon* (Uchman, 1995). Ontogenetic variations should be carefully evaluated (Pickerill, 1994). Bertling *et al*. (2006) expressed their reluctance to use size at the ichnospecies rank, and totally reject it at higher ranks.

2.3.2 WALL AND LINING

Bioturbation results in changes in the sediment and formation of burrow mottlings and discrete structures with different degrees of definition, depending on their function and substrate consistency. For example, a trace that serves as a semipermanent domicile implies certain constructional traits (e.g. burrow lining) that are not present in a trace that reflects a simple incursion through the sediment by a vagile organism (intrusion *sensu* Bromley, 1990, 1996). In particular, details on burrow walls can reveal significant information on trophic type, burrowing technique, and biological affinity (Bromley, 1990, 1996; Ekdale and Gibert, 2010). However, some aspects of the burrow wall lack ichnotaxonomic significance. Although diagenetic haloes may be rather spectacular, they are related to the diagenetic history of the structure rather than animal behavior (Bromley, 1990, 1996). In contrast, more subtle constructional features of burrow walls serve as ichnotaxobases.

Two main components are represented in a wall, internal lining and external deformation in the host sediment (Bromley, 1990, 1996). This author recognized seven main types of walls based on linings, ornamentation, and manipulation of sediment by the organism (Box 2.1): unlined walls (Fig. 2.2a), dust films

Figure 2.1 Examples of general form, illustrating combinations of configuration, orientation, and preservation (a) *Helminthorhaphe* isp., horizontal guided meanders preserved as positive hyporelief. Eocene, Hecho Group, Huesca, Spanish Pyrenees. See Uchman (2001). (b) *Gyrochorte* isp, horizontal biblobate trail preserved as positive epirelief. Upper Cretaceous, Kennilworth Member, Blackhawk Formation, south entrance to Tusher Canyon, Book Cliffs, Utah, United States. (c) *Gyrolithes* isp., Lower Miocene, contact between the Lower Freshwater Molasse and the Upper Marine Molasse, Kobel, St. Gallen area, Switzerland. See Heer (1865) and Wetzel *et al*. (2010). Scale bars are 1 cm.

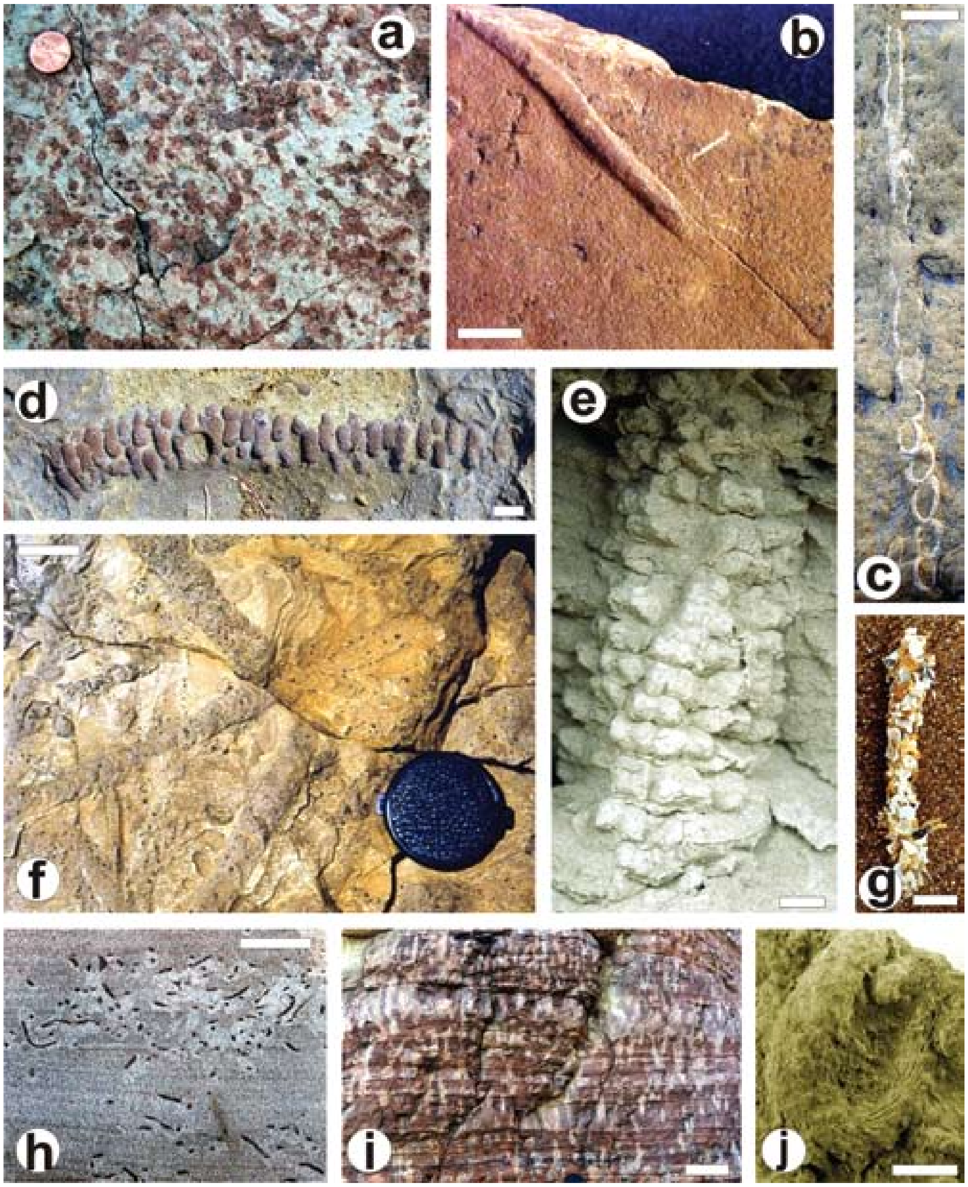

Figure 2.2 Types of walls. (a) Unlined wall in *Planolites montanus*. Upper Carboniferous, El Cobre Canyon Formation, El Cobre Canyon, New Mexico, United States. Coin is 1.9 cm. (b) Thin dust film in *Palaeophycus tubularis*. Permian, De la Cuesta Formation, Los Colorados de Patquía, La Rioja Province, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (2004a). (c) Thick dust film in *Schaubcylindrichnus coronus*. Upper Cretaceous, Panther Tongue Member, Star Point Formation, Kennilworth Wash, Book Cliffs, Utah, United States. Scale bar is 1 cm. (d) Constructional lining with pellets arranged in transverse rows forming relatively continuous rings or annulations in *Ophiomorpha annulata*. Upper Miocene to Lower Pliocene, La Vela Formation, Quebrada el Muaco, La Vela de Coro, northwestern Venezuela. Scale bar is 1 cm. (e) Constructional lining with bilobate pellets in *Ophiomorpha borneensis*. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Chubut Province, Patagonia, southern Argentina. Scale bar is 1 cm. See Scasso and Bellosi (2004). (f) Constructional lining with orbitoid forams. Middle Eocene, Punta Carnero Formation, Airport, Margarita Island, Venezuela. Lens cap is 5.5 cm. (g) Constructional lining with shell material in a modern *Diopatra cuprea*. Gower Peninsula, Wales. Scale bar is 1 cm. (h) Zoned fill characterized by a pale mantle surrounding a dark core in *Phycosiphon incertum*. Lower Jurassic, Plover Formation, Sunrise–Troubadour Field, East Timor Sea, northern Australia. Scale bar is 1 cm. (i) Diagenetic oxidation haloes in *Skolithos linearis* forming a pipe rock. Lower to Middle Cambrian, Campanario Formation, Mesón Group, Maimará, northwest Argentina. Scale bar is 10 cm. See Mángano and Buatois (2004b). (j) Wall ornament of *Fuersichnus striatus* characterized by a powerful bioglyph. Upper Cretaceous, Hidden Lake Formation, Brandy Bay, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois (1995).

(Fig. 2.2b–c), constructional linings (Fig. 2.2d–g), zoned fills (Fig. 2.2h), wall compaction, diagenetic haloes (Fig. 2.2i), and wall ornament (Fig. 2.2j). Bioglyphs, engravings in the ornamented walls of burrows or borings, result from various activities of the tracemaker, including scratching, drilling, plucking, gnawing, poking, and etching (Ekdale and Gibert, 2010). Bertling *et al*. (2006) noted that surface features (sculpture) usually play a secondary role, and are diagnostic mostly at the ichnospecific level. However, surface features and micromorphological characters may be of higher ichnotaxonomic significance in insect nests (Genise and Hazeldine, 1998; Cosarinsky, 2003; Genise, 2004).

2.3.3 BRANCHING

Presence and type of branching are commonly first-rank ichnotaxobases. Three main types of branching are recognized: secondary successive, primary successive, and simultaneous (Bromley and Frey, 1974; D'Alessandro and Bromley, 1987; Bromley, 1990, 1996). The so-called "false branching" simply consists of overlap between two specimens giving the false impression of branching. Secondary successive branching results from an animal that revisits a previously formed structure (Fig. 2.3a). Primary successive branching is a cumulative structure formed by successive probings and implies a series of movements by the producer, such as rotating and moving back and forth

Box 2.1 Types of wall

Seven main types of walls are commonly recognized:

- Unlined walls: The burrow fill abuts against the enclosing sediment at a clean discontinuity surface (Fig. 2.2a). Examples: *Planolites*, *Taenidium.*
- Dust films: The burrow is lined with mucus, introducing dust that adheres on the wall. Linings may be thin (Fig. 2.2b) to thick (Fig. 2.2c). Examples: *Palaeophycus, Schaubcylindrichnus*.
- Constructional linings: The burrow wall is constructed with sediment and special grains. Building materials include sediment pellets of various shapes (Fig. 2.2d–e) and shell fragments (Fig. 2.2f–g). Examples: *Ophiomorpha, Diopatrichnus*.
- Zoned fills: The apparent burrow lining is in fact the outermost layer of a concentrically zoned fill resulting from deposit feeding (Fig. 2.2h). Examples: *Ancorichnus*, *Phycosiphon*.
- Wall compaction: The wall is bounded by an external zone showing disturbance as a result of burrowing.
- Diagenetic haloes: The burrow wall has been affected by special diagenesis, enhancing visibility of the structure (Fig. 2.2i). Examples: *Bathichnus*, some specimens of *Thalassinoides* and *Skolithos*.
- Wall ornament: Walls are characterized by bioglyphs (Fig. 2.2j). Examples: *Spongeliomorpha*, *Scoyenia*.

Reference: Bromley (1990, 1996).

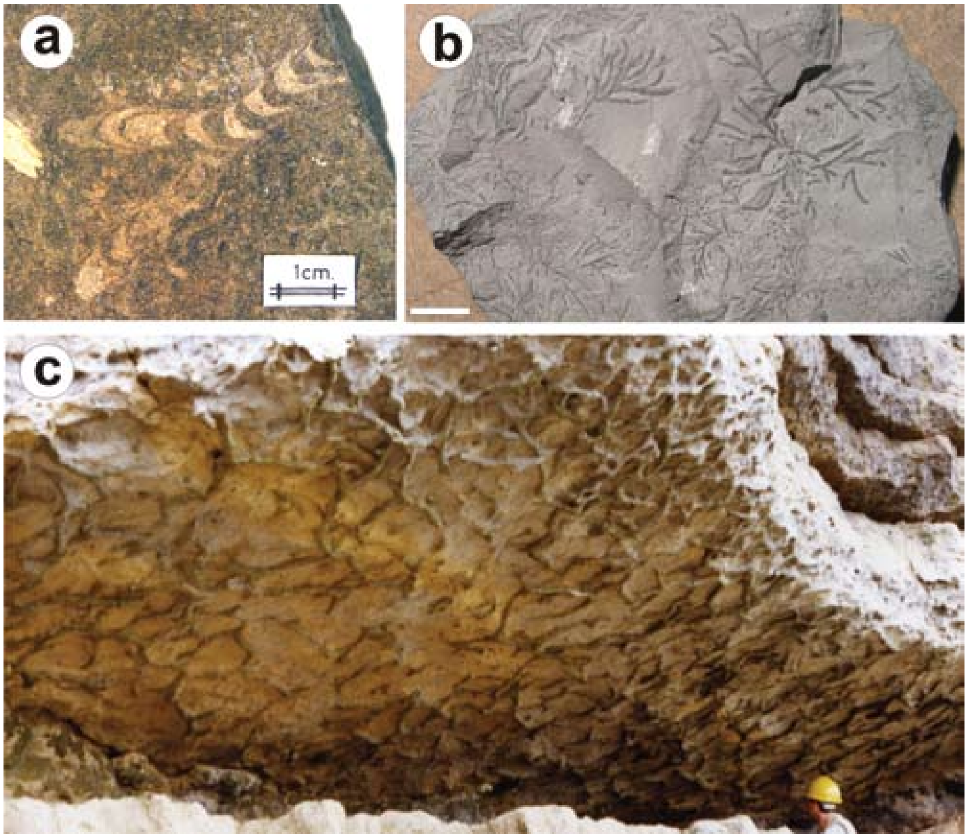

Figure 2.3 Types of branching (a) Secondary successive branching. *Taenidium* isp. Upper Cretaceous, Santa Marta Formation, Santa Marta Cove, James Ross Island, Antarctica. Scale bar is 1 cm. See Scasso *et al.* (1991). (b) Primary successive branching. *Chondrites arbuscula*. Upper Cretaceous, Rhenodanubian Flysch, Voralpen, Austria. Scale bar is 1 cm. See Uchman (1999). (c) Simultaneous branching. Burrow systems assigned to the ichnospecies *Thalassinoides suevicus*. Upper Jurassic, Coralline Oolite Formation, Filey Brigg, North Yorkshire Coast, England. Person for a scale on the lower right. See Fürsich (1972).

(Fig. 2.3b). Simultaneous branching is represented by open passages in permanent or semipermanent domiciles, such as in galleries constructed by crustaceans (Fig. 2.3c).

2.3.4 FILL

Fills can be classified into two main categories: passive and active (Box 2.2). Such distinction, and the type of active fill are first-rank ichnotaxobases because they reveal information on trophic types and feeding strategies. On the other hand, the type of passive fill may provide sedimentological and sequence-stratigraphical information (see Section 12.2) rather than ethology and, therefore, should not be used as an ichnotaxobase (Bromley, 1990, 1996).

Passive fill results from material entering the burrow gravitationally, and mostly characterizes the dwelling structures of suspension feeders and predators. Different types of passive

Box 2.2 Types of burrow fill

Passive and active fill are the two major categories of burrow fill. While passive fill enters the burrow gravitationally, active fill is emplaced by the burrower. In turn, these two major categories are subdivided into many other types.

- Passive massive fill similar to the host sediment: Material from the host sediment is introduced gravitationally into the burrow (Fig. 2.4a). It is a common type of burrow fill in open gallery systems. Example: *Palaeophycus*.
- Passive massive fill contrasting with the host sediment: Material from an overlying layer, typically coarser-grained, is introduced gravitationally into the burrow (Fig. 2.4b). This is also known as bed-junction preservation (Simpson, 1957) (see Section 1.3.1). It is typical of open burrows formed at discontinuity surfaces. Example: Firmground *Thalassinoides*.
- Passive laminated fills: Lamination results from sedimentation within the burrow (Fig. 2.4c). An example of passive laminated fills is tubular tidalites, which consist of rhythmically bedded alternating layers of fine-grained and coarse-grained laminae deposited within open burrows resulting from tidal action (Gingras, 2008). Examples: *Thalassinoides, Ophiomorpha*.
- Draught fill canals: Laminated fill in open burrows having a narrow entrance (Seilacher, 1968) (Fig. 2.4d). The narrow draught canal may be confused with a burrow itself reworking the fill of the larger. Example: *Thalassinoides.*
- Irregularly concentric fills: Intermediate between passive and active because the structure results from gravitation, and sediment manipulation by the animal (Goldring, 1996).
- Active massive fill: Structureless fill typically contrasting with the host sediment, resulting from mechanical manipulation or ingestion (Fig. 2.4e). It may be pelleted. Examples: *Planolites, Macaronichnus*.
- Active meniscate fill: Fill forming a characteristic structure, commonly packed as backfill meniscae, resulting from mechanic manipulation or ingestion (Fig. 2.4f). Examples: *Scolicia, Taenidium*.
- Active concentric fill: (both simple or multiple): Burrow fill formed by concentric alternating layers of contrasting material (Fig. 2.4g). Examples: *Rosselia*, *Cylindrichnus*, *Asterosoma.*

Reference: Bromley (1990, 1996).

fills are recognized, including massive fills similar to the host sediment (Fig. 2.4a), massive fills contrasting with the host sediment (Fig. 2.4b), laminated fills (Fig. 2.4c), and draught fill canals (Fig. 2.4d) (Seilacher, 1968; Bromley, 1990, 1996; Goldring, 1996; Buatois *et al*., 2002a). Irregularly concentric fills are intermediate between passive and active because the structure results from gravitation and sediment manipulation by the animal (Goldring, 1996).

Active fill implies active manipulation of material by the animal, and commonly results in lithological contrasts between the trace and the host sediment. Most commonly, active fill is produced by deposit and detritus feeders. Different types of active infill include massive fill (Fig. 2.4e), meniscate fill (resulting from mechanic manipulation or ingestion) (Fig. 2.4f), and concentric (both simple or multiple) (Fig. 2.4g).

2.3.5 SPREITE

Spreite refers to a lamination that results from closely spaced successive tunnel walls formed by the lateral shifting of a burrow (Bromley, 1990, 1996). Presence of spreite reveals either the ability of an animal to adjust its burrow as a response to instability at the sediment–water interface or to actively mine in search for food (Figs. 2.5, 2.6a–b, and 2.7). Its presence is useful as an ichnogeneric ichnotaxobase. The classic example is the distinction between the U-shaped burrows *Diplocraterion* (with spreite) (Fig. 2.6a) and *Arenicolites* (without spreite) (Fig. 2.6b).

Two types of spreite are recognized, protrusive and retrusive. Protrusive spreite is formed due to distalward movements (i.e. away from the apertures), while retrusive spreite is produced by proximalward movements (i.e. toward the apertures) (Bromley, 1990, 1996) (Fig. 2.5). Careful analysis of the spreite may be useful in ichnotaxonomy of feeding structures (Fig. 2.7) both at ichnogeneric (e.g. *Lophoctenium*, *Zoophycos*, *Teichichnus*, *Phycosiphon*, and *Oldhamia*) and ichnospecific (*Oldhamia alata* and *O. geniculata*) levels. However, the type of spreite is of no use at all for the ichnotaxonomy of equilibrium traces. In this latter case, a retrusive spreite reflects upward burrow migration as a response to increased sedimentation rate, while a protrusive spreite records downward burrow migration resulting from decreased sedimentation or slight erosion. Although of use for paleoenvironmental reconstructions (Goldring, 1964), its value in ichnotaxonomy is limited in this situation (Bromley, 1990, 1996).

2.4 COMPOUND AND COMPOSITE TRACE FOSSILS

2.4.1 COMPOUND TRACE FOSSILS

Another peculiarity of trace-fossil taxonomy is the presence of compound and composite trace fossils (Pickerill, 1994; Pickerill and Narbonne, 1995). Compound trace fossils result from the changing behavior of a single producer, and can represent two different situations: successive or simultaneous formation (Bertling *et al*., 2006) (Fig. 2.8). More commonly, the tracemaker behaves in distinct ways in chronological order, comprising intergradations of one ichnotaxon into another one either at ichnogeneric or ichnospecific level (see Section 1.2.2). The typical example is the transition between locomotion and resting

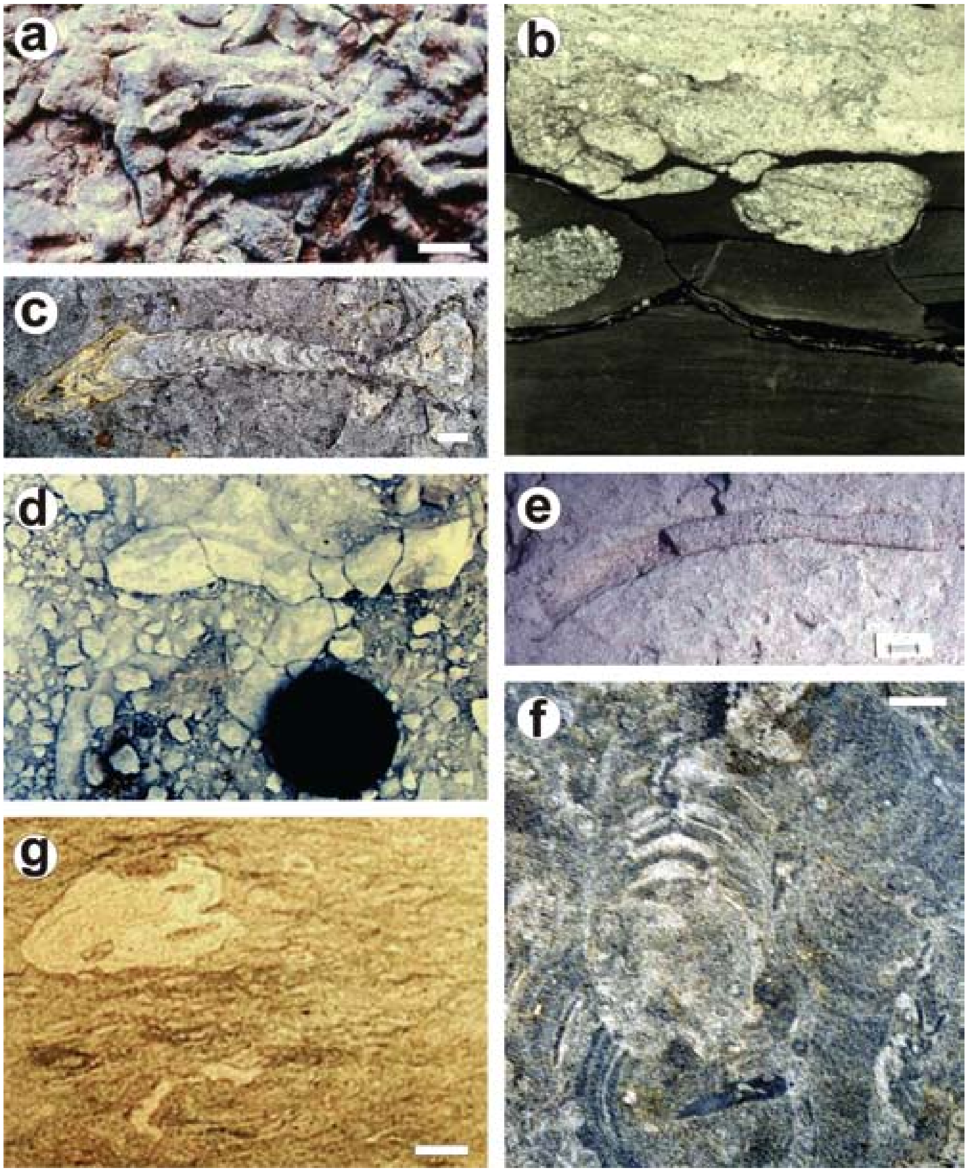

Figure 2.4 Different types of burrow fills. (a) Passive massive fill similar to the host sediment in *Palaeophycus tubularis*. Upper Cambrian, Pico de Halcón Member, Santa Rosita Formation, Quebrada del Salto Alto, Purmamarca, northwest Argentina. Scale bar is 1 cm. See Mángano *et al.* (1996b). (b) Passive massive fill contrasting with the host sediment in firmground *Thalassinoides*. Contact between the Upper Cretaceous Burguita Formation and the Middle Eocene Gobernador Formation, Caipe Field, Barinas Basin, western Venezuela. Core width is 8 cm. (c) Passive laminated fill in *Ophiomorpha nodosa*. Cretaceous, Quiriquina Formation, Cocholgüe, Chile. Scale bar is 1 cm. See Buatois and Encinas (2011). (d) *Thalassinoides suevicus* with draught fill canal Upper Cretaceous, Gramame Formation, Poty Quarry, northeast of Olinda, northeast Brazil. Lens cap is 5.5 cm. (e) Active massive fill illustrated by *Planolites beverleyensis*. Upper Carboniferous, Malanzán Formation, Cuestita de la Herradura, La Rioja Province, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (1995a). (f) Active meniscate fill resulting from ingestion in *Scolicia* isp Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, southern Argentina. Scale bar is 1 cm. See Carmona *et al.* (2008). (g) Active multiple concentric fill in *Asterosoma* isp. Lower Miocene, Oficina Formation, Oritupano field, Eastern Venezuela Basin. Scale bar is 1 cm.

traces, such as trilobite locomotion traces (*Cruziana*) and resting traces (*Rusophycus*) (Crimes, 1970a; Mángano *et al.*, 1996b), and bivalve locomotion traces (*Protovirgularia*) and resting traces (*Lockeia*) (Mángano *et al.*, 1998). Other ethological categories may be involved, such as transitions between the echinoid grazing trace *Scolicia* and its resting counterpart *Cardioichnus* (Smith and Crimes, 1983) (Fig. 2.8). In other instances, intergradations may occur within an ethological category as illustrated by crustacean dwelling burrows, such as *Ophiomorpha*, *Thalassinoides*, and *Gyrolithes* (Bromley and Frey, 1974; Muñiz *et al.*, 1995). Typical examples at ichnospecific and ichnosubspecies levels are shown by transitions between trilobite trace fossils, such as *C. rugosa furcifera* and *C. rugosa rugosa*.

Bertling *et al.* (2006) noted that these compound structures pose two problems in ichnotaxonomy if methods of biological taxonomy are applied: (1) an exceptional intergradation of ichnotaxa that are normally found separately would imply synonymization in all other occurrences, leading to invalidation of at least one established ichnotaxon, and (2) if the constituents of a normally compound ichnotaxon are found separately, they would have to be named differently, as they form discrete trace fossils. However, following procedures of biological taxonomy is not advisable here. The standard practice with compound specimens is to name the whole structure for its predominant component, taking careful note of the intergradations (Pickerill, 1994; Pickerill and Narbonne, 1995).

Another situation results when the producer may simultaneously behave in various distinct ways. For example, Bromley *et al.* (2003) documented the trace fossil of a bivalve that used its foot to dig into the substrate and its siphons to collect food. A collective name, *Hillichnus*, was given in this case (Fig. 2.8). Most of these simultaneously produced compound trace fossils are complex trace fossils (*sensu* Miller, 1998, 2002, 2003) (see Section 1.4.15). However, not all complex trace fossils are

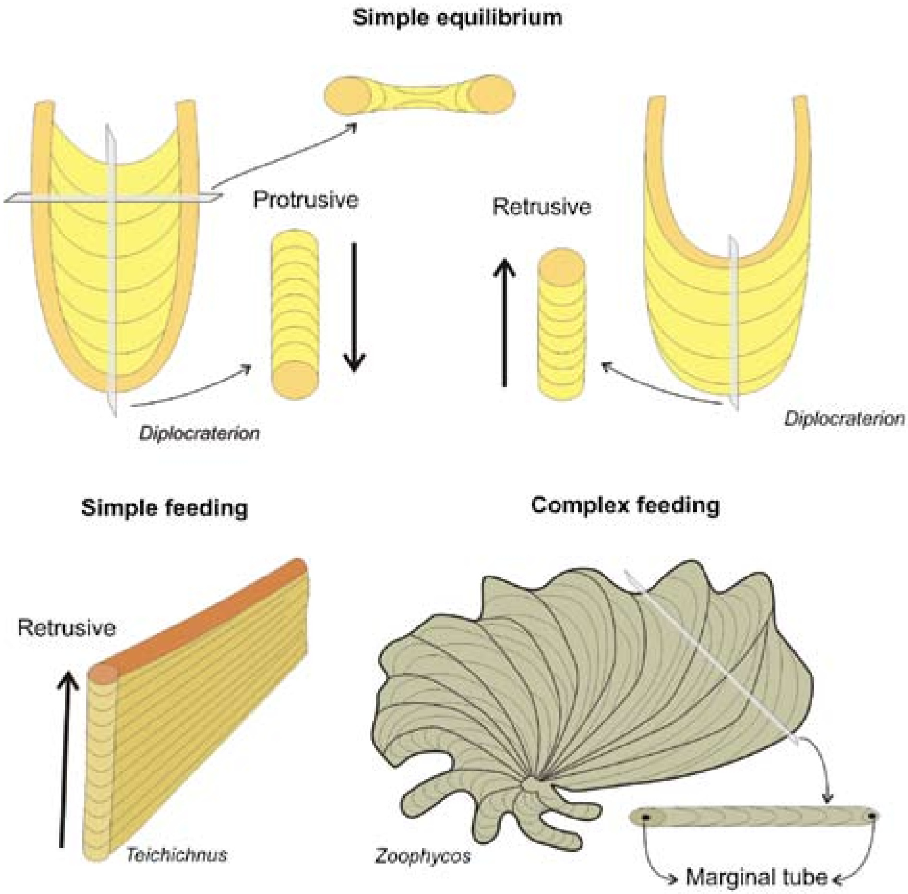

Figure 2.5 Types of spreite. In equilibrium structures the spreite reveals the ability of an animal to adjust its burrow as a response to instability at the sediment–water interface, while in feeding structures the spreite reflects an organism actively mining in search for food.

Figure 2.6 Use of spreite to differentiate U-shaped trace fossils. (a) Spreite in *Diplocraterion parallelum*. Lower Cambrian, Dividalen Group, Imobekken, northern Norway. See Bromley and Hanken (1991). (b) Absence of spreite in *Arenicolites*. Lower to Middle Cambrian, Hanneh Member, Burj Formation, Dead Sea, Jordan. Scale bars are 1 cm.

compound structures, because although more than one behavior is involved, discrete components cannot be identified, and some behaviors may not be strictly simultaneous. Bertling *et al*. (2006) stated that if these compound superstructures mirror a recurrent pattern of behavior, then they deserve their own name, as illustrated by *Hillichnus*.

2.4.2 COMPOSITE TRACE FOSSILS

Composite trace fossils apparently comprise a single system, but actually result from the interpenetration of discrete ichnotaxa (Pickerill, 1994; Pickerill and Narbonne, 1995) (see Section 1.2.4) (Fig. 2.8). A typical example is a structure that was referred to as *Mixoteichichnus* by Müller (1966), but that, in fact, consists of a specimen of *Teichichnus* intersected by *Planolites* (Pemberton and Frey, 1982). Common examples are discrete feeding or dwelling traces (e.g. *Thalassinoides*, *Diplocraterion*, *Gyrolithes*, and *Cladichnus*) that are reworked by *Chondrites* or *Phycosiphon* (e.g. Bromley and Frey, 1974; Ekdale and Bromley, 1991; Buatois and Mángano, 1992) (Fig. 2.8). In some cases, a high concentration of trace fossils reworking a burrow helps to delineate the previously emplaced structure ("phantom"

Figure 2.7 Feeding spreite in long specimens of *Rhizocorallium irregulare*. Upper Jurassic, Lastres Formation, cliffs west of Playa de España, Quintes, Villaviciosa, Asturias, northern Spain. Scale bar is 5 cm.

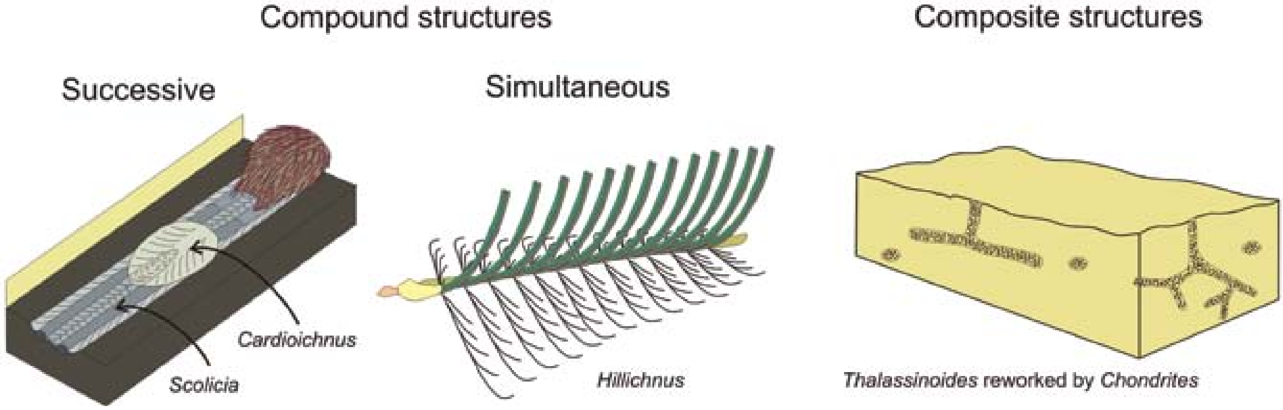

Figure 2.8. Examples of compound (successive and simultaneous) and composite trace fossils.

burrow) that otherwise would have remained undetected. Wood fragments with *Teredolites* enclosing sand-lined tubes produced by sabellariid polychaetes represent another example (Miller, 1996). The feeding trace *Piscichnus* excavated by rays, and reworked by polychaetes (producers of *Macaronichnus*) also illustrates a composite structure (Kotake, 2007). In the realm of paleosol insect trace fossils, composite structures seem to be very common as illustrated by beetle nests (*Monesichnus ameghinoi*) that have been reworked by cleptoparasites, which in turn produced open galleries (Genise and Laza, 1998). Composite structures should not be named as a whole. Rather, discrete components should be named separately (Pickerill, 1994; Pickerill and Narbonne, 1995; Bertling *et al.*, 2006).

2.5 HIERARCHIES IN ICHNOTAXONOMY

Although trace fossils are different from body fossils, the classical binominal scheme has been adopted. In contrast to body fossils, however, the terms ichnogenera (ichnogen. or igen.) and ichnospecies (ichnosp. or isp.) are used to make clear that the entity is a trace fossil rather than a body fossil. Traditionally ichnologists have treated trace fossils at these two main hierarchical levels. However, in recent years, it has become increasingly clear that additional categories may be of use (Buatois *et al.*, 2002a) and a growing consensus is building in support of their importance (Bertling *et al.*, 2006). In fact, ichnofamilies are formally accepted by ICZN (1999, Art. 10.3), and some have been proposed since the end of the nineteenth century (e.g. Chondriteae, Rhizocorallidae, and Arenicolitidae) based on morphology, albeit with limited ethological insights (e.g. Schimper and Schenk, 1890; Fuchs 1895, 1909). More recently, new ichnofamilies have been suggested (e.g. Walter, 1983; Fu, 1991; Seilacher and Seilacher, 1994; Genise, 2000, 2004).

Bromley (1996) noted that three main criteria have been used to group trace fossils in ichnofamilies: a common producer at high taxonomic level (e.g. Pelecypodichnia), morphological similarities based on anatomy of the producers (e.g. Multipodichnia), and functional similarities based on morphology (e.g. Alectoruridae). The present consensus is that ichnofamilies should be based on trace-fossil morphology, not on the biology of the potential producer (Bertling *et al.*, 2006). As indicated by Buatois *et al.* (2002a), the present challenge is to define ichnofamilies based on a common set of morphological traits of functional significance that allow links to be established among trace fossils related on constructional grounds, regardless of phylogenetic relationships (Buatois *et al.*, 2002a). Bertling *et al.* (2006) noted that many of the morphological groups of flysch ichnotaxa recognized by Książkiewicz (1977) and Uchman (1995, 1998) could be formalized as ichnofamilies.

On the other side of the taxonomic spectrum, ichnosubgenera and ichnosubspecies are allowed in trace-fossil taxonomy, but have been rarely used, particularly the former (Rindsberg 1990a). However, ichnosubspecies have been occasionally employed, and may be advisable in certain cases. For example, Mángano and Buatois (2003a) treated the components of the so-called *Cruziana rugosa* group as ichnosubspecies (*C. rugosa rugosa*, *C. rugosa furcifera*, and *C. rugosa goldfussi*), following a suggestion by Seilacher (1996). They noted that although these ichnotaxa are morphologically distinct, they are best regarded as ethological variations at the ichnosubspecies level rather than at the ichnospecies level. This scheme reflects more adequately the fact that differences among these ichnosubspecies are less significant than those between them and other *Cruziana* ichnospecies (e.g. *C. semiplicata*). Ichnosubspecies have been also suggested for some *Arthrophycus* ichnospecies (Seilacher, 2000).

2.6 VERTEBRATE ICHNOTAXONOMY

The relationship between vertebrate and invertebrate ichnology is one of the present hot topics in ichnology (e.g. Melchor and Genise, 2004a, b; Hunt and Lucas, 2007; Lockley, 2007; Lucas, 2007; Minter *et al.*, 2007a). Central to this debate is the idea of unity or disunity of ichnology with respect to concepts and methods. In practical terms, invertebrate and vertebrate ichnology developed independently, to a large extent (Lockley, 2007). Ichnology textbooks tend to cover either one topic or the other, and only rarely (e.g. Ichnia 2004 and 2008) vertebrate and invertebrate ichnologists gather together in the same scientific meetings. One of the central issues is how to keep a balance between unification of the ichnological field on one side, while giving enough room for diversity of approaches on the other. While some authors favor "one ichnology" (e.g. Melchor and Genise, 2004a, b), others regard this as a nice, but impractical, idea (Lockley, 2007).

Ichnotaxonomic problems are at the core of this topic. Hunt and Lucas (2007) noted that invertebrate ichnologists mostly use an ethological approach, while vertebrate ichnologists favor a biotaxonomic approach. In other words, the focus of invertebrate ichnology is in classifying biogenic structures based on the ethological significance of their morphology, while vertebrate ichnologists attempt to relate traces to their producers. The word "mostly" in this context means that these two approaches work essentially as end members with some groups of trace fossils occupying an intermediate position (e.g. arthropod trackways and insect traces in paleosols). However, Minter *et al.* (2007a) noted that the field of vertebrate ichnology also uses an ethological approach because the same ichnotaxonomic name should not be assigned to a burrow and a trackway produced by the same vertebrate, or to a resting trace and a trackway also sharing the producer. In this regard, at least theoretically, vertebrate and invertebrate ichnology do not seem to be so far apart. More controversial gray zones include trackways produced by the same animal, but reflecting a change in speed. In any case, this is also a contentious issue with arthropod trackways (e.g. Braddy, 1995), so it is a problem inherent to trackways not strictly to vertebrate traces.

However, in practical terms the problem persists because the vast majority of vertebrate traces identified in the fossil record are trackways and, therefore, locomotion is the main behavior involved. Lockley (2007) specifically raised the question of whether it is reasonable to apply the same conventions and expectations of invertebrate ichnotaxonomy to vertebrates. The morphology of a footprint is determined not only by the structure of the foot of the producer but also by foot–substrate interaction, the latter resulting in extramorphological variation (Lucas, 2007). Haubold (1996) proposed the name phantom taxa for tetrapod footprint taxa based on such extramorphological variation, while Lucas (2001) suggested the name taphotaxon for a taxon based on distinctive morphological features that result from taphonomic processes, noting that this situation is more common with trace fossils than with body fossils. There is consensus among vertebrate ichnologists that extramorphological features should not be used in ichnotaxonomy, and it has been argued that this may be a problem with most taxa defined at ichnospecific level (Lucas, 2007). Assuming that the vast proportion of vertebrate trace fossils record locomotion, it is hard to see how a completely morpho-ethological system can be applied in practice to vertebrate ichnotaxonomy.

Carrano and Wilson (2001) summarized the main methods employed by vertebrate ichnologists to relate tracks to their producers. These authors noted that the three main approaches that have been employed are phenetic correlation, coincidence correlation, and synapomorphy-based correlation. Phenetic correlation is the standard method, and is based on the similarity between the track and the foot skeleton. Coincidence correlation uses information other than morphology (e.g. geological age, geographic provenance, or local faunal composition) to establish the link between track and producer. Synapomorphy-based correlation applies cladistic methods to classify trackways assigning ichnotaxa to biological taxa using shared derived characters. Although Carrano and Wilson (2001) favored this latter approach, Lucas (2007) raised some doubts about the benefits of applying synapomorphy-based correlation instead of the more standard phenetic correlation. Coincidence correlation, although useful in the search of potential tracemakers, should not be used as a taxonomic criterion because it may lead to circular reasoning (see Section 2.1). The challenge in vertebrate ichnotaxonomy seems to be to formulate ichnotaxobases based on morphology, which allows the establishment of ichnotaxa at different hierarchical levels avoiding circular reasoning.

2.7 THE UNCERTAINTY PRINCIPLE IN ICHNOTAXONOMY

Since its original formulation by Werner Heisenberg, physicists have been forced to deal with the uncertainty principle, which establishes that certain pairs of physical properties of an electron, such as position and momentum, cannot simultaneously be known. Perhaps ichnologists may be allowed to play with an analogy in ichnotaxonomy. No matter how hard we try, it seems that we cannot establish an ichnotaxonomic system that simultaneously fulfills the following requirements: (1) internal consistency and (2) applicability. The search for internal consistency is desirable, but occasionally the system may lose applicability if consistency is pushed too far.

There is general consensus that ichnotaxonomic classifications should be based on intrinsic properties of trace fossils that are of enough ethological significance. Accordingly, extrinsic parameters, such as stratigraphic age, facies, or geographic location, play no direct role. However, this sharp boundary gets blurred when substrate is addressed. It seems that substrate in itself cannot be considered an ichnotaxobase because of its extrinsic character, although it is the behavior that results from the influence of substrate that is at play. In any case, substrate plays an indirect role in naming trace fossils, essentially in the same way that the biology of the producer influences behavior (see Section 2.1). Regardless of this, substrate has been historically considered significant enough to form the basis on which ichnotaxa are established; vertical burrows in sediment are called *Skolithos* while vertical borings in lithified substrates are called *Trypanites*. These problems were raised by Ekdale and Bromley (2001b) when defining the ichnospecies *Gastrochaenolites oelandicus* because some of their specimens seem to be borings and some burrows. Carmona *et al.* (2007) noted that Miocene specimens of *Gastrochaenolites ornatus* formed in firmgrounds were identical to *G. ornatus* produced in hardgrounds. Accordingly, these authors concluded that using substrate as an ichnotaxobase in this case would be artificial and misleading. Substrate may qualify as a high-rank ichnotaxobase when morphology reflects distinct ways of organism–substrate interactions, but when the same organism is able to excavate and bore, and the excavation technique is identical to the mechanical perforation technique, the validity of the substrate vanishes (Carmona *et al.*, 2007).

There is widespread agreement that general form is a high-rank ichnotaxobase. Accordingly, some authors (Fürsich, 1973; Schlirf, 2000) have suggested that general form should be used to classify crustacean burrow systems, such as *Ophiomorpha*, *Thalassinoides*, and *Spongeliomorpha*, ichnogenera that at present are distinguished on the basis of the nature of burrow wall, a character of lesser significance. If this view is adopted, then the ichnogenera *Thalassinoides* and *Ophiomorpha* should become junior synonyms of *Spongeliomorpha*, which is the oldest available name. It is undeniable that this approach aims for internal consistency in ichnotaxonomy. However, it has been met with little acceptance (e.g. Bromley and Frey, 1974; Bromley, 1990, 1996; Carmona and Buatois, 2003). Besides other possible reasons to keep the three ichnogenera, reluctance to abandon *Thalassinoides* and *Ophiomorpha*, two ichnotaxa firmly entrenched in the literature and of widespread recognition in outcrop and cores, undoubtedly plays a huge role.

2.8 CLASSIFICATION OF TRACE FOSSILS IN OUTCROPS AND CORES

Outcrops and cores are two very different realms and comparison of ichnological information may represent a challenge (Bromley, 1990, 1996). However, in the same way that sedimentological observations in outcrops should be integrated with core data in order to produce more accurate depositional models, subsurface and surface ichnological information should be evaluated using similar criteria and ichnotaxonomic standards. With an increasing recognition that ichnological information is of paramount importance in petroleum exploration and reservoir characterization, studies addressing trace fossils in cores have become common practice, and a series of atlases has been published (e.g. Chamberlain, 1978; Pemberton *et al.*, 1992c, 2001; Gérard and Bromley, 2008). Commonly, trace fossils in cores are classified at ichnogeneric level (e.g. Ekdale, 1977). However, in many other cases ichnospecific assessments are possible when dealing with ichnogenera whose ichnospecies are classified according to features that are easy to detect in cores, such as the type of burrow wall in some ichnospecies of *Ophiomorpha* (Bromley, 1990, 1996).

The fact that ichnologists working with cores have to deal with narrow two-dimensional views represents a departure with respect to the study of trace fossils in outcrops. As noted by Gerard and Bromley (2008), the probability of a single burrow being detected is related to its orientation, its size, and the core diameter. Some of these peculiarities pose a problem, but others may represent an advantage. Some ichnotaxa that are easily identified in outcrops may be impossible to recognize in cores. Biogenic structures preserved in semirelief, such as graphoglyptids, locomotion traces (e.g. trackways), and shallow grazing trails, fall into this category. These structures are revealed along bedding planes in outcrops. On the other hand, full relief ichnofossils, such as endichnial feeding and dwelling traces, are easy to visualize in cores. Furthermore, cores commonly reveal subtle details of burrow boundaries that may be overlooked in outcrops, as illustrated by haloes in *Phycosiphon*. The lack of weathering in cores is particularly helpful to examine biogenic structures in mudstone. In outcrops, where sandstone interbeds are absent in fine-grained successions, it is often difficult to evaluate the ichnological content. On the other hand, discrete structures emplaced in mudstone are easily detected in cores.

Besides their classification in cores, paleoenvironmental interpretation of trace fossils is enhanced by the amount of additional information available in subsurface. For example, biofacies data (e.g. foraminiferans, palynofossils, and calcareous nanoplankton) from regularly selected core intervals are currently available, as well as geochemical and petrophysical information. These additional datasets can be employed to integrate ichnological information with other lines of evidence, promoting more robust depositional models. Also, where core recovery is good, one is able to examine relatively continuous intervals. Unfortunately, some oil companies tend to take cores only from the reservoir interval (sandstone and carbonate) and associated mudstone facies, whose characterization would be essential to understand depositional conditions and paleoenvironments, cannot be examined.

Finally, in many cases cores represent the only available information. This is the case with modern offshore areas (e.g. Ekdale, 1978, 1979; Wetzel, 1983, 1984), and some rock units that are only known from the subsurface (e.g. Buatois *et al.*, 1999, 2002b). In recent years, subsurface information also become available through the study of borehole images and various core-imaging techniques. Ichnological data can also be evaluated from borehole images, albeit with a lower level of resolution than in cores (e.g. Salimullah and Stow, 1995; Bockelie *et al.*, 1998; Gerard and Bromley, 2008). Calibration of these images is highly recommended, as elegantly illustrated by Gerard and Bromley (2008). Also, scanner-imaging techniques may help to visualize the three-dimensional morphology of trace fossils in cores (Gerard and Bromley, 2008).

3 Paleobiology of trace fossils

> This success stems mainly from the intimate connection of ichnology with sedimentology and the importance of both fields for paleoenvironmental and basin analysis, which becomes more and more important in petroleum exploration. This useful connection, however, also had its price. In the hand of biogeologists, trace fossils easily lose their significance as unique biological documents.
>
> Dolf Seilacher
>
> *Trace Fossil Analysis* (2007)

> One of the triumphs of the palaeobiological approach to palaeontology is the insight functional morphology has given us about the life activities of long dead organisms.
>
> Richard Bambach, Andrew Bush, and Douglas Erwin
>
> "Autecology and the filling of ecospace: key metazoan radiations" (2007)

Although the significance of trace fossils in paleoenvironmental reconstructions is responsible for the rapid development of ichnology, we should not forget that ichnofossils are produced by living organisms and, as such, the biological nature of trace fossils is at the core of any study on animal–substrate interactions. In this chapter, we analyze the paleobiological facet of trace fossils. In order to do so, we revise concepts from benthic ecology and paleoecology. First, we explore the concept of modes of life, addressing feeding strategy, position in relation to the substrate–water interface, and level of motility. Second, we elaborate on the different modes that organisms have to interact with and, in particular, penetrate into the substrate. Third, we look at basic locomotion and burrowing mechanisms from a historical perspective, revisiting the pioneering work of Schäfer and the synthesis by Trueman. We exemplify all these mechanisms with examples form the trace-fossil record. Finally, we close this chapter by introducing the new paradigm of movement ecology and its potential implications in ichnological studies.

3.1 MODES OF LIFE

Animals burrow in order to solve four basic problems: respiration, feeding, reproduction, and protection (Bromley, 1990, 1996; Mángano and Buatois, 1999a). The diverse modes of life in the living world reflect viable strategies to deal with these problems. Mode of life includes feeding strategy, position in relation to the substrate–water interface, and level of motility (Bambach *et al.*, 2007; Bush *et al.*, 2007). These modes of life reveal all possible combinations of ecological parameters, allowing a multidimensional analysis of theoretical ecospace. The combination of these elements results in 216 potential modes of life. In practice, only 92 of these modes of life are recorded as utilized (Bambach *et al.*, 2007).

3.1.1 FEEDING STRATEGY

Food is an essential requirement for life and, according to their structural possibilities, each invertebrate group has developed a repertoire of feeding mechanisms and strategies in order to get the necessary nutrients from the surrounding environment. The questions what does an animal eat, where is this food resource located in relation to the animal life-site, and how common is this resource (availability) determine the specific adaptations for food acquisition (Mángano and Buatois, 1999a). Trace fossils provide valuable information on trophic types and feeding strategies.

Marine biologists have recognized incredibly diverse and ingenious ways of feeding. However, their perspective is quite different from that of a paleobiologist or an ichnologist. Biologists are largely focused on particular characteristics, such as food particle size, and less attention is paid to what, where, and how something is eaten (Crame, 1990). In other cases, exquisite details about a peculiar behavior have been observed by marine ecologists, but very little of that behavior is recorded in the sediment and has preservation potential. From a paleobiological and ichnological standpoint, the signal left in the substrate is a simplified version of the behavior involved, and can be interpreted in terms of a few major trophic types and feeding strategies. Trophic categories can be broadly defined as groups of organisms that feed, in general, in the same fashion (Walker and Bambach, 1974; Bambach, 1983; Bambach *et al.*, 2007). In other words, a certain source of food is exploited in a similar manner. Although the classification commonly adopted by ichnologists (e.g. Bromley, 1990, 1996) is mostly based on marine invertebrates, it can be modified to include feeding strategies in terrestrial environments. Trophic types are based on the type of food, source location in relation to the sediment–water interface, and the general feeding mechanism involved.

There are five major feeding categories: suspension feeding, detritus feeding (also known as surface deposit feeding), deposit feeding (also known as mining), grazing, and predation (Bambach *et al.*, 2007). However, other unconventional categories, such as trapping, farming, photo- and chemosymbiosis, and parasitism have also been recognized. In particular, parasitism is discussed in the context of animal–animal interactions (see Section 6.7). In addition, some organisms are able to

Box 3.1 *Tasselia ordamensis*, a complex deposit-detritus feeding-gardening structure of maldanid polychaetes

Studies involving three-dimensional CT scan and X-ray analyses of incipient *Tasselia* recovered from shallow- to deep-water settings off the coast of Africa and deep-water sediments from eastern Canada revealed its complex internal structure, and provide strong evidence to support a maldanid polychaete origin. However, the ethological meaning of this peculiar structure has remained elusive until recently. Based on the detailed analysis of over 400 exquisitely preserved specimens of *Tasselia ordamensis* from the Upper Cretaceous to Cenozoic marine deposits of Tierra del Fuego and Antarctica, a new feeding strategy has been proposed. This trace fossil, unquestionably related to maldanid worms, illustrates the complex feeding strategies developed by representatives of this polychaete group. *Tasselia ordamensis* is a pear-shaped structure characterized by an axial thickly lined tube surrounded by vertically stacked sediment disks and continuing downward into a basal chamber (Fig. 3.1). Composition, geometry, and the cross-cutting relationships of internal elements reveal the existence of two domains within each sediment disk: the outer and the inner burrow-fill domains. The outer domain contrasts with the host rock in grain size and composition of particles, consisting of a fine-grained, micritic matrix enriched in microfossils, such as radiolarians, calcispherules, and diatoms, and tiny plant debris. The internal structure of the outer domain consists of radially arranged, subhorizontal to oblique petal-like elements. Coarse particles (e.g. microfossils) are re-oriented parallel to the petaloid elements. The boundary between the outer-fill domain and the host rock is sharp, but no particle orientation is visible. The inner-fill domain has a higher concentration of coarser particles than the outer burrow-fill domain. Its internal structure consists of short, subvertical and strongly arched petaloid elements, which are confined to the sediment disk. The boundary between the outer- and the inner-fill domain is also sharp with clear evidence of the inner-fill-domain laminae cross-cutting the outer-fill domain. *Tasselia ordamensis* has been traditionally interpreted as a retrusive domichnion/equilibrium structure produced by suspension-feeding or microcarnivore organisms. However, detailed analysis of the internal structure of *Tasselia* clearly indicates that it is constructed protrusively (i.e. in a downward direction), and that is most likely a complex structure resulting from the deposit feeding, detritus feeding and microbial-gardening activities of maldanid polychaetes. The outer-fill domain, mostly formed of fine-grained particles, suggests a deposit-feeding mode with ingested particles passing through the gut of the producer up to the surface (i.e. upward advection), and non-ingested particles (large size particles, medium and coarse-grained sand) remaining in the basal chamber or on the central part forming part of the inner fill domain. Microfossils and plant debris within the outer-fill domain are clearly oriented. They may have been collected at the surface and placed within the petaloid elements (i.e. downward advention), documenting the role of detritus feeding. Densely packed microfossils and plant debris in discrete levels within the structure most likely reflect pulsed delivery of organic matter to the seafloor, followed by rapid subduction and redistribution by the tracemaker (detritus-feeding mode). After excavation and deposit-detritus feeding resulting in the formation of a burrow fill disk, a new feeding chamber is excavated below. The old feeding chamber is now situated above, and functions as "culturing compartment". The distinct structure of the inner domain results from reworking of particles stored in previous feeding chambers. Therefore, *Tasselia ordamensis* illustrates the feeding plasticity of maldanid polychaetes, producing complex structures, resulting from a combination of deposit-detritus feeding and gardening activities, and most likely as a response to fluctuating food supply.

References: Olivero and López-Cabrera (2010).

switch feeding strategies. For example, some suspension- and surface-deposit feeding bivalves are able to switch mechanisms facultatively (Skilleter and Peterson, 1994). Combined feeding strategies may result in complex trace fossils, as in the case of the ichnogenus *Hillichnus*, which has been attributed to a combination of deposit feeding and chemosymbiosis with sulfide-oxidizing bacteria (Bromley *et al.*, 2003). Behavioral plasticity in terms of feeding strategies is also common in decapod crustaceans and polychaetes (Box 3.1).

Suspension feeders capture suspended particles from the water column, and are commonly sessile forms that do not move around to get the necessary nutrients. Filter feeding is a subdivision of suspension feeding, in which an organic filtration mechanism is involved in food acquisition (Walker and Bambach, 1974). In the trace-fossil record, suspension feeding is revealed by simple (e.g. *Skolithos*) or U-shaped (*Diplocraterion*) vertical burrows with lined walls preserved in clean sandy substrates. In modern environments, these structures are produced by polychaetes, sabellariids, spionids, and phoronids, among other organisms (Alpert, 1974; Gingras *et al.*, 2008a). Suspension-feeding strategies have been envisaged for some simple horizontal burrows, such as *Palaeophycus*, which is thought to have been produced by a wide variety of organisms, including polychaetes (Pemberton and Frey, 1982).

Various devices and adaptations have been developed by suspension feeders to attain the appropriate position in the water column for trapping particles. Some suspension-feeding brittle stars (ophiuroids) can coil their arms and hence are well-adapted for clinging onto corals and other elevated structures. Other ophiuroids (e.g. the basket star) display delicate branching arms that form a mucus-trapping basket directed towards the current (Barnes and Hughes, 1999). The ophiuroid trace fossil *Asteriacites aberensis* is characterized by long rays frequently oriented parallel to the inferred paleocurrent (Crimes and Crossley,

Figure 3.1 *Tasselia ordamensis*, a complex trace fossil attributed to the detritus- and deposit-feeding, and gardening activities of maldanid polychaetes. Visible internal structural elements are the axial, lined tube, the stacked sediment disks, the outer and inner fill domains, and the terminal chamber. Upper Eocene-Lower Oligocene, Punta Gruesa Beds, Punta Gruesa, Tierra del Fuego, southern Patagonia, Argentina. Scale bar is 5 cm. See Olivero and López-Cabrera (2010).

1991), suggesting a suspension-feeding trophic type (Mángano *et al*., 1999). Preferential orientation with respect to the predominant current (i.e. rheotaxis) by clusters of resting traces has been commonly invoked to infer suspension feeding. Examples include *Rusophycus* in freshwater environments attributed to notostracan crustaceans (Bromley and Asgaard, 1972b) and in marine environments presumably produced by trilobites (Pickerill, 1995).

Some suspension-feeding body plans, such as those of sponges and cnidarians, include chambers or an internal cavity lined with tissue, whose cells, by means of cilia, seta, flagella, or amoeboid pseudopodia, capture particles trapped within the cavity. This strategy is illustrated by the clionid sponge-boring *Entobia* (Bromley, 1970). Brachiopods exhibit a more complex design, in which anatomical structures are particularly adapted for filtering. In particular, the lophophore with ciliated filaments performs three interrelated functions as a pump, a sieve, and a respiratory organ. Although it is a well-established dogma that brachiopods are sessile epifaunal organisms, modern lingulide brachiopods live within a vertical to inclined, mucus-lined burrow; the anterior part of the shell at or slightly projecting from the water–sediment interface and anchored, via a flexible pedicle, into the substrate (Emig *et al*., 1978; Savazzi, 1991). As documented by Zonneveld and Pemberton (2003), the dwelling trace fossil *Lingulichnus* illustrates a wide range of behaviors, including stationary suspension feeding, escaping from burial, and reburrowing after erosional exhumation, all behaviors known in extant lingulide.

Suspension-feeding bivalves display complex gill morphologies, which are used for both respiration and particle collection from the mantle cavity. A set of morphological features, such as a streamlined shape, deep pallial sinus, marginal posterior gape, and absence of prominent shell ornamentation characterize suspension-feeding bivalves (Stanley, 1970). The presence of a deep pallial sinus is related unequivocally to posterior siphons. The posterior gape signals the existence of a long siphon that cannot be withdrawn entirely into the shell, forcing the animal to be confined permanently in a deep burrow safe from the hazards of the shallower tiers. This type of siphon is almost invariably linked to a suspension-feeding strategy. The ichnospecies *Lockeia siliquaria* has been interpreted as the basal part of a dwelling structure of suspension-feeding bivalves (Mángano *et al*., 1998). A similar interpretation can be made for freshwater bivalve traces because almost all lacustrine representatives are suspension feeders (White and Miller, 2008). Another example of trace fossils produced by a suspension-feeding bivalve is represented by the occurrence of *Panopea faujasi* within its equilibrium structure *Scalichnus phiale* (Hanken *et al*., 2001).

Detritus feeders or surface deposit feeders capture loose particles on the depositional interface, which is rich in organic matter (Bromley, 1990, 1996; Bambach *et al*., 2007). Both vagile organisms that move around in search of food and sessile animals that explore around their burrows are represented. Non-specialized grazing trails (e.g. *Mermia* and *Gordia*) in freshwater environments have been attributed to detritus-feeders, most likely insect larvae (Buatois and Mángano, 1993a). Snails in both marine and freshwater environments graze on organic matter and algal material at the sediment surface, producing structures akin to the ichnogenus *Archaeonassa*. Tellinid bivalves are common surface deposit feeders living below the sediment–water interface and using the inhalant siphon to collect particles at the surface. These structures are well documented in modern tidal flats (e.g. Schäfer, 1972). However, the only trace fossil attributed to tellinid bivalves, the ichnogenus *Hillichnus*, is remarkably complex and has not been regarded as reflecting a *Macoma*-like detritus feeding strategy (Bromley *et al*., 2003). Surface deposit feeding is also adopted by various worms, such as some terebellids, maldanids, and glycerids (Gingras *et al*., 2008a). Concentrically filled burrows assigned to the ichnogenus *Rosselia* have been attributed to detritus-feeding terebellid polychaetes (Nara, 1995, 2002).

Deposit feeders or miners ingest organic matter within the substrate to recover buried food. Because most of the sediment is composed of inorganic mineral grains (even organic-rich sediment can be 95% inorganic in matter) animals may wander through the sediment in search of organic food particles or construct complex and more permanent burrows to systematically mine the sediment. Because the surface and uppermost parts of the substrate are richer in nutritious particles, they are heavily populated by deposit feeders (Bromley, 1990, 1996). Deposit feeders can be selective (i.e. those that only extract nutritious grains from the sediment) or non-selective (i.e. those that engulf the sediment uncritically and digest what they can from it). Most infaunal organisms (i.e. endobenthos) are deposit feeders that rework the sediment to get nutritious particles producing biogenic reworking (Bromley, 1990, 1996). In many cases, the morphology and nature of the infill of trace fossils record unquestionable support for a deposit-feeding habit of the tracemaker. For example, an actively infilled burrow (i.e. a fill that has been subject to biological processing, passing through the animal's gut) commonly contrasts in organic content or grain size with the host rock (e.g. *Planolites*), or is packed as backfilled menisci (e.g. *Taenidium*, *Scolicia*).

Marine benthic ecology and neoichnological studies indicate that deposit feeding is a widely represented feeding strategy among many vermiform organisms. Various polychaetes, such as terebellids, maldanids, glycerids, and opheliids, feed within the sediment (Gingras *et al*., 2008a). The latter are known to produce the ichnogenus *Macaronichnus* (Clifton and Thompson, 1978; Pemberton *et al*., 2001). In continental settings, oligochaetes and various annelids, such as tubificids and lumbriculids, are typical deposit feeders (White and Miller, 2008). Protobranch bivalves and many echinoids are also well-known deposit feeders with an extensive representation in the ichnological record. Combined locomotion and feeding activities of protobranch bivalves are represented by the chevronate trace fossil *Protovirgularia* (Seilacher and Seilacher, 1994; Mángano *et al*., 1998; Carmona *et al*., 2010). Structures attributed to spatangoid echinoids are illustrated by the backfilled ichnogenera *Scolicia* and *Bichordites* (Bromley and Asgaard, 1975; Smith and Crimes 1983; Bromley *et al*., 1995).

Some complex gallery systems produced by decapod crustaceans reveal adaptations for deposit feeding (Ekdale, 1992). According to Gingras *et al*. (2008a), some thalassinid shrimps construct tiered boxworks and networks using the vertical shaft to maintain a connection to the sediment–water interface and the basal network for deposit feeding.

A number of biogenic structures known from the fossil record have been attributed to deposit feeders based on design, although the actual affinities of the producer remain unknown in the absence of modern analogues. Examples include ichnogenera from the ichnofamily Arthrophycidae, such as *Arthrophycus* and *Phycodes* (see Section 13.3), as well as other feeding burrows, such as *Halopoa*, *Phycosiphon*, and *Heimdallia*, among many others (Seilacher, 2007b).

A deposit-feeding trophic type has been inferred for extinct organisms based on combined ichnological and functional morphological evidence. One of the most remarkable examples is trilobites, which are regarded for the most part as deposit feeders, although some may have developed other feeding strategies, such as scavenging, predation, and suspension feeding (Seilacher, 1985; Jensen, 1990; Whittington, 1992; Fortey and Owens, 1999). Deposit feeding is suggested on morphological grounds, such as the absence of mandibles and chelate appendages, and the presence of multiple undifferentiated biramous limbs. The so-called trunk-limb feeding mechanism involves the rhythmical inward motion of the endopodites (inner branch of the limb), which convey the gathered particles to the mouth through the intercoxae food groove (Seilacher, 1985; Clarkson, 1992; Levi-Setti, 1993). Some features, such as the presence of a spinose coxae and the backfacing mouth at the rear of the hypostome, suggest that larger size particles were probably squeezed and shredded along the intercoxae groove and subsequently pushed forward to the mouth (Whittington, 1992). The abundance of cruzianids in lower Paleozoic rocks also provides a strong evidence for deposit feeding. These structures not only involved high-energy requirements inconsistent with simple locomotion, but also, in some cases, display scribbling or circling patterns best explained by food searching (e.g. Seilacher, 1970; Fortey and Seilacher, 1997; Mángano and Buatois, 2003a; Neto de Carvalho, 2006). Functional morphological analysis of the trace fossils *Cruziana* and *Rusophycus* has provided valuable information to elucidate the mechanics involved in trilobite deposit feeding (Seilacher 1970, 1985) (see Section 3.3.1). Bilobate trails are also produced by various other invertebrates, many of which are deposit feeders, such as isopods, which move through sediment to extract organic matter (Hauck *et al*., 2008; Gingras *et al*., 2008a).

Grazers are basically herbivores who scrape or nibble plants, algae, or even microbial material from the depositional surface, or chew or rasp larger plants or seaweeds (Mángano and Buatois, 1999a). Ecologists tend to link the feeding strategy of grazing to the development of grasslands, mammals being the archetypal grazers (Owen, 1980; see also Thomasson and Voorhies, 1990). In the sea, limpets, sea urchins, and fishes are well-established grazers on hard substrates. In modern coral reefs, grazing fish are major determinants of the benthic community structure (Bellwood and Wainwright, 2006). Reef structures have been related to the activities of grazers throughout the Phanerozoic, the most marked change being in the Cenozoic when diverse grazing fishes accompanied by some groups of invertebrates, such as deep-grazing limpets and sea urchins, resulted in a drastic increase in grazing pressure (Bellwood and Wainwright, 2006). The use of the term "grazing" in ichnology may be somewhat misleading. In ichnology, the strategy of "grazing" refers to a combination of feeding and locomotion being recorded by the ethological category pascichnia (see Section 1.4.4). Archetypal grazing structures commonly reflect that the animal is feeding while moving on or within the substrate, so from a trophic-type perspective detritus- or deposit-feeding, and, less commonly, true grazing may be involved. In soft marine substrates, grazers commonly eat some superficial organic detritus, so this category is actually transitional to detritus feeding. Organisms that feed on large particles of dead animals found at the sediment–water interface are referred to as scavengers. As particle size decreases, this category also grades into detritus feeders. On the other hand, some carnivores may eat dead, undecayed animals and, therefore, scavengers may grade into predators (Walker and Bambach, 1974). Although grazers, detritus feeders, and scavengers are not easily differentiated in terms of their trace-fossil record, in some contexts, it is possible to point to a grazing trophic type. For example, Ediacaran simple trails, some of the first metazoan structures, are best interpreted as the product of grazers on microbial mats (Seilacher, 1999; Buatois and Mángano, 2003a) (see Section 14.1.2). The trace fossil *Radulichnus*, a rasping structure, is a typical example of grazing feeding strategy in the ichnological record. In Carboniferous tidal flats, grazing trails may be directly associated with fossil leaves and other plant material (see Section 8.1.2).

Terrestrial arthropods feed on living and dead plants using multiple strategies, including piercing-and-sucking, chewing, galling, scraping, and boring. While there are few primary decomposers in marine food chains and webs, primary decomposers are essential elements of terrestrial ecosystems, giving rise to a second food chain. Woody, supporting tissues, which form the bulk of vegetation, only become available as food once they are dead. Arthropod adaptations to consume plant material are documented in the fossil record not only by the study of arthropod body fossils but also by the trace-fossil record of plant–arthropod interactions (Labandeira, 1998, 2007) (see Section 14.2.7).

Predators, also known as carnivores, get their food by capturing prey that is capable of resistance (Bambach *et al*., 2007; Bush *et al*., 2007). They represent the highest levels of the food chain. Predators can be passive or active, according to whether they wait in a fixed position for prey or they actively pursue it. Passive predation is illustrated by some polychaetes, sea anemones, and other anemone-like anthozoans (Ceriantharia). Some tube-dwelling worms are typically carnivores, they use the tube as a protective retreat and extend from the opening to seize passing prey. Vertical burrows, such as *Skolithos*, are commonly attributed to suspension feeders, but passive predation cannot be disregarded. Sea anemones live attached to corals, shells, or hide in rock crevices, and some burrow in sand or mud. They prey on various invertebrates, such as bivalves and crustaceans, swept by currents or waves, and some large species are even able to capture fish. The prey is paralyzed by nematocysts, caught by the tentacles, and carried to the mouth (Barnes and Hughes, 1999). Plug-shaped burrows (e.g. *Conostichus*, *Bergaueria*, *Conichnus*) are typically attributed to anthozoan cnidarians, including sea anemones (Actinaria) and tube anemones (Ceriantharia) (Pemberton *et al*., 1988; Bromley, 1990, 1996). Most recent anthozoans are microcarnivores, however, and the distinction between passive predation and suspension feeding based on morphology of biogenic structures is difficult.

Active predation is the main mode of predation. This strategy is illustrated by many invertebrates and all vertebrate predators. In terms of biomass, predators are commonly underepresented in the fossil record, but they have played a critical role in shaping long-term trends in adaptation (Vermeij, 1987). Several phases are involved in predation, namely, search, capture, penetration, ingestion, digestion, and defecation (Bishop, 1975). Direct evidence of predation in the fossil record includes trace fossils of penetration and ingestion of preys, and digestive contents and fecal products of predators (Mángano and Buatois, 1999a) (see Section 1.4.10). Bites or crush marks on the prey exoskeleton result from pre-ingestive breakage, and circular and parabolic bore holes are produced by drilling. Crustaceans have developed various techniques to kill their prey, including peeling (i.e. piece by piece breakage), crushing between the claws, or pounding their prey with expanded segments of their maxillipeds (Brett, 1990). Drilling is a specialized mode of predation, as illustrated by many marine mollusks (Brett, 1990). Circular drilling holes (ichnogenus *Oichnus*) are well known in the trace-fossil record, and may be produced by a number of organisms, including carnivorous gastropods and octopodid cephalopods (Bromley, 1981, 1994).

Evidence of predators *in situ* on prey is fascinating, but extremely uncommon. Sublethal predation scars and biogenically induced broken fragments of trilobites provide evidence of trilobites being preyed upon (Babcock and Robinson, 1989; Babcock, 1993; Pratt, 1998). Moreover, right–left behavioral asymmetry recorded by predation scars, preferentially on the right side, indicates the existence of predators with a lateralized nervous systems since at least the Early Cambrian (Babcock and Robinson, 1989). Ichnological evidence of predation by trilobites has been suggested by Jensen (1990), who documented the recurrent association of the trilobite resting trace *Rusophycus dispar* and worm trace fossils. This author noted that the trilobites consistently positioned themselves so that only the legs of one side were in contact with the worm burrow, suggesting a capture technique in which the legs of one side were flexed around the prey, squeezing it against the spinose inner part of the coxae. Although, this predation interpretation has been questioned by Rydell *et al*. (2001), further case studies documenting ichnological evidence of predation by trilobites have been published (e.g. Brandt *et al*., 1995; English and Babcock, 2007).

Ingested prey within the gut and gastric contents is another source of information, mostly restricted to fossil deposits of exceptional preservation (e.g. Viohl, 1990; Habersetzer *et al*., 1994; Zhu *et al*., 2004). Coprolites, however, are a more widespread evidence of diet, being found both in fossil lagerstätten (Vannier and Chen, 2005) and in terrestrial red beds (Hunt *et al*, 1994, 1998). Although the nature of coprolites was recognized very early by William Buckland (Pemberton and Frey, 1991), only recently has their potential in paleoecology and biostratigraphy started to be explored. Coprolites and gut contents provide crucial data to reconstruct ancient trophic webs (Richter and Baszio, 2001; Richter and Wedmann, 2005; Habgood *et al*., 2003; Vannier and Chen, 2005).

Trapping, farming (also referred to as gardening), photosymbiosis, and chemosymbiosis are unconventional feeding categories (Mángano and Buatois, 1999; Bambach *et al*., 2007). Trapping is the passive capture of migrating meiofauna or other microrganisms within spiral or complex structures (see Section 1.4.7). A typical example of trapping is represented by the paraonid polychaete *Paraonis fulgens*, which produces spiral burrows within intertidal sediment (Röder, 1971; Risk and Tunnicliffe, 1978). This polychaete selectively feeds upon diatoms as indicated by analysis of its gut contents and by its small size (Röder, 1971; Levin *et al*., 1999). The spiral burrows are used as traps to capture diatoms as they migrate vertically within the sediment. The gaps between the whorls are interpreted as an area from which new diatoms can move into the trap, and so repeated visits can yield additional food (Röder, 1971). Although these intertidal biogenic structures have very low preservation potential, they have recently been described from the fossil record (Minter *et al*., 2006).

Farming is a feeding adaptation that involves the culturing of suitable bacteria or fungi to provide food (Seilacher, 1977a) (see Section 1.4.7). Both farming and trapping can be inferred from complex, regular architectural patterns of biogenic sedimentary structures that are difficult to explain in terms of deposit feeding and are illustrated by the ethological category agrichnia (see Section 1.4.7). Complex three-dimensional network designs with secondary undulations, side branching, and anastomoses are commonly suspected to represent trapping or farming structures (Seilacher, 1977a). Examples include the ichnogenera *Paleodictyon*, *Protopaleodictyon*, *Acanthorhaphe*, *Desmograpton*, and *Urohelminthoida*, among many others. In particular, the ichnogenus *Spirorhaphe* has been modeled on the *Paraonis* spiral trap. Although commonly overlooked, these feeding adaptations may be the cornerstone of some sophisticated food chains. These specialized strategies are developed in response to depleted food conditions and absence of sunlight, and are typical of base-of-slope environments (see Sections 9.2 and 9.3).

Photosymbiosis and chemosymbiosis are feeding adaptations, which, until recently, have been overlooked in the paleontological literature. Photosymbiosis has been recognized in corals and several recent bizarre bivalves (e.g. *Tridacna*, *Corculum*) (Seilacher, 1990a). Chemosymbiosis involves animal endosymbiosis with chemoautotrophic bacteria. This adaptation has been extensively studied in relation to deep-sea vents, where chemosymbiotic bacteria allow the development of real oases of life in an otherwise life-depleted setting (Grassle, 1985). Chemoautotrophs use different inorganic sources (e.g. hydrogen sulfide, elemental sulfur, ammonia, ferrous iron, hydrogen) to produce energy. For example, sulfuricant bacteria occur within the soft tissue of the host (e.g. gills, mantle) where they are able to oxidize vent-derived H_2S in the presence of sufficient oxygen. Other reactions used by bacteria to obtain chemical energy are hydrogen oxidation and methane production. Chemosymbiosis is also an effective strategy in other environments such as anoxic muds (e.g. anoxic fjords, seagrass meadows, mangrove swamps) where oxygen and hydrogen sulfide are found in close proximity. In these environments, recent amphisiphonate lucinids (e.g. *Thyasira*, *Codakia*) are known to host chemoautotrophic bacteria in their gills. Chemosymbiosis is an unusual mode of nutrition that requires physiological adaptations and protection from the toxic surrounding environment. The recent bivalve *Solemya* has its gills packed with bacteria and its gut is reduced or absent (Yonge, 1936). These modifications in the soft parts, however, are not reflected by the shell morphology, which is largely unaffected (Seilacher, 1990a).

In the fossil record, photo- and chemosymbiosis have been inferred based on morphological and behavioral adaptations, and are well represented in some invertebrate groups, such as bivalves (Seilacher, 1990a). While photosymbiosis does not involve a particular interaction with the substrate and, accordingly, has not been documented from the trace-fossil record, some ichnofossils have been related to chemosymbiosis. Many odd burrows, such as the ichnospecies *Solemyatuba ypsilon*, have been interpreted as specialized chemosymbiotic designs, and modeled based on analysis of the bivalve *Solemya*. *Solemyatuba ypsilon* displays a basic U-shaped design that allows burrow ventilation and oxygen intake and a downward blind extension, presumably used for pumping hydrogen sulfide from the surrounding sediment (Seilacher, 1990a). The ichnogenus *Chondrites*, whose branching design cannot be satisfactory explained as the work of a deposit feeder, may actually represent "sulfide wells" constructed by the activity of a chemosymbiotic worm-like animal (Seilacher, 1990a; Fu, 1991).

3.1.2 POSITION WITH RESPECT TO THE SUBSTRATE–WATER INTERFACE

The position in relation to the substrate–water interface or tiering is a central concept in ichnology (see Section 5.1). It identifies the setting where an animal lives and, as such, it is intimately related to its feeding type. Six basic situations can be recognized (Bambach *et al.*, 2007; Bush *et al.*, 2007). These are pelagic (living in the water column as either plankton or nekton), erect (benthic, extending into the water mass), epifaunal or surficial (living on the surface, not extending significantly upwards), semi-infaunal (partly infaunal, partly exposed to the water column), shallow infaunal (living in the upper 5 cm of the substrate), and deep infaunal (living below the upper 5 cm of the substrate). The 5-cm boundary reflects approximately a depth above which organisms are challenged by disturbance rather than maintaining contact with the sediment–water interface and below which these difficulties are reversed in severity (Bush *et al.*, 2007). In any case, this boundary may be highly variable as it is highly dependent on several parameters, such as hydrodynamic energy (see Section 6.1.1) and depth of the redox discontinuity surface (see Section 6.1.3).

All the latter five categories include organisms living on and/or within the substrate, and are regarded as benthic (Walker and Miller, 1992). The terms epibenthic (= epifaunal, living at the sediment–water interface) and endobenthic (i.e. living within the sediment) are widely used in ichnology. Although occasionally some nektonic organisms may be revealed in the trace-fossil record (e.g. the fish trail *Undichna*), ichnology deals essentially with the activities of benthic organisms. In ichnological studies a more detailed subdivision of the infaunal ecospace is attainable because a finer-grained zonation can be obtained by careful study of tiering of biogenic structures that are produced not only by animals with hard parts but mostly by soft-bodied organisms (see Section 5.1).

3.1.3 LEVEL OF MOTILITY

The level of motility is the capability of an animal to move under its own power (Bambach *et al.*, 2002). Motility level is essential in ecological reconstructions because it determines an animal's range of physical activities (Bush *et al.*, 2007). It has been subdivided into six main categories: freely fast (regularly moving, unencumbered); freely slow (regularly moving, intimate contact maintained with substrate); facultative unattached (moving only when necessary, free-lying); facultative attached (moving only when necessary, attached); non-motile unattached (not capable of self-propulsion, free-lying), and non-motile attached (not capable of self-propulsion, attached) (Bambach *et al.*, 2007; Bush *et al.*, 2007).

Motility level is reflected by the basic ichnological categories of sessile and vagile used in ichnoguild characterization (see Section 5.4). However, not all the categories established based on body-fossil analysis are recorded in the ichnological realm.

Tracemakers are for the most part motile animals, either fully or facultatively motile. The only exception is attachment structures (e.g. *Podichnus*). In this case, the brachiopod tracemaker is a non-motile attached organism. Overall, those fully motile in intimate contact with the substrate are the most effective burrowers. Those motile animals that are less encumbered and that move by pressing the substrate with their appendages (e.g. many epibenthic arthropods) are less effective burrowers or do not burrow at all, but may produce trackways under appropriate substrate conditions. Facultatively motile animals can move to escape a threat or to reposition if affected by environmental disturbance (Bush *et al.*, 2007), therefore producing biogenic structures (e.g. escape traces).

3.2 MODES OF INTERACTION WITH THE SUBSTRATE

There are several classifications that account for the many ways that animals interact with the substrate (e.g. Hanor and Marshall, 1971; Bromley, 1990, 1996; François *et al.*, 1997; Solan and Wigham, 2005). Each of these schemes emphasizes different aspects, but to a certain extent equivalencies between the different frameworks can be proposed.

Bromley (1990, 1996) defined four main types of interactions between infaunal animals and the substrate: intrusion, compression, excavation, and backfilling (Fig. 3.2a–k). These categories are based on increasingly more complex animal–sediment

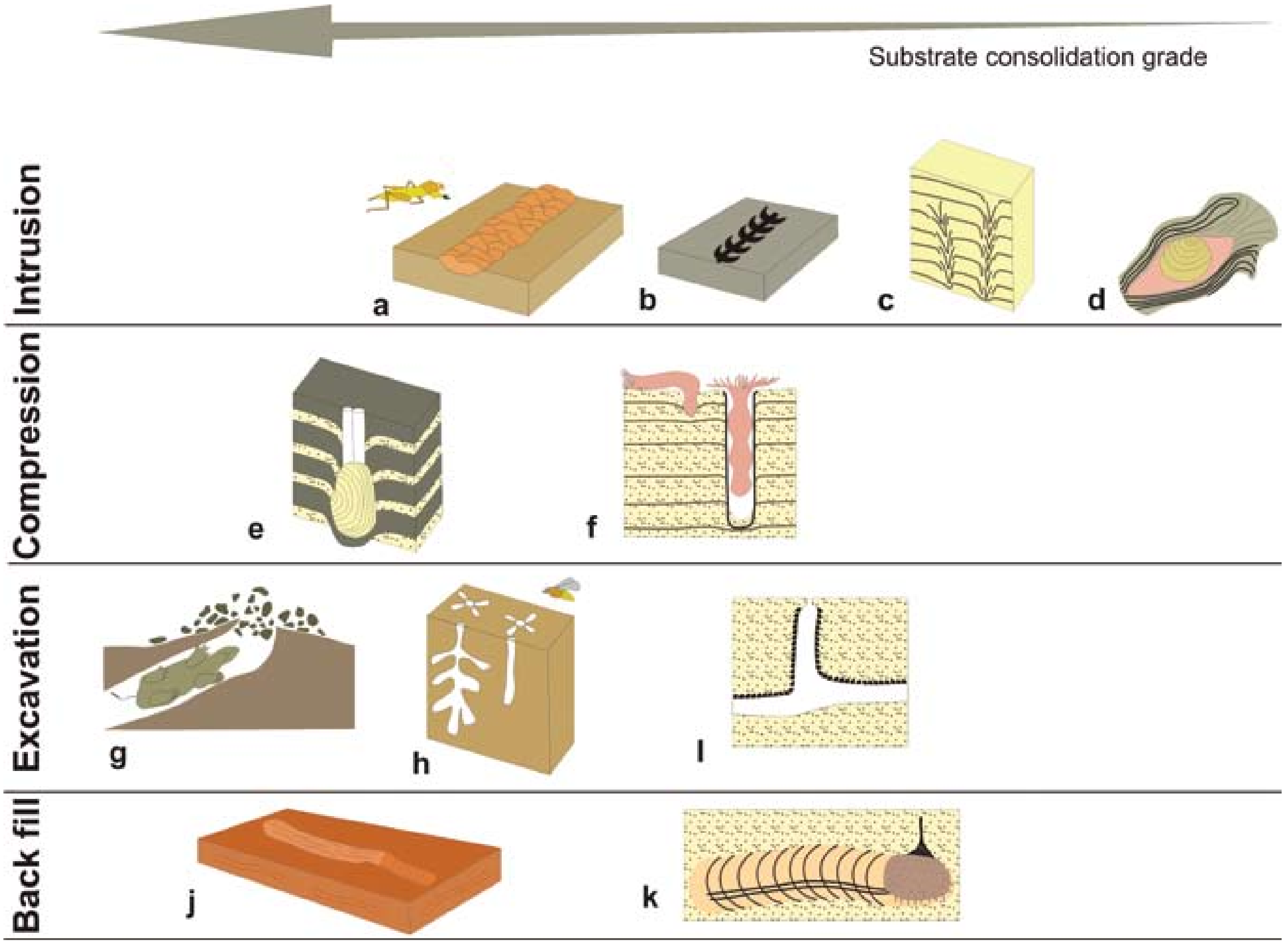

Figure 3.2 Some classic trace fossils interpreted within the categories of animal–substrate interactions of Bromley (1990, 1996). Note the relation with substrate consolidation. (a–d) Intrusions may form under a wide range of sediment consistencies from soupy to firm. (a) Shallow insect tunnel produced in a stiff sediment (stabilization may be related to sediment dewatering and/or microbial binding). (b) Bivalve trace in softgrounds. (c) Escape structures typically record intrusions in soft-to-soupy substrates. (d) Carnivore gastropods may intrude into soft-to-soupy sediment in search of prey producing biodeformational structures. (e–f) Compression structures are typically formed in partially dewatered sediment with enough shear strength. Compression action re-orients sediment particles at the structure boundary. Mucus can be used to bind the sediment grains. (e) Bivalve burrow. (f) Sea-anemone burrow. (g–l) Excavations can be formed in a wide range of consistencies, but are commonly not effective in soupy substrates. (g) Many mammals are well-adapted for excavating in firm terrestrial settings. (h) Excavation is the most common type of construction by insects in soils. (i) In soft sediments, excavations require reinforcement of the burrow boundary by a construction wall. (j–k) Backfilling is an efficient way of advancing through sediment while feeding, the loosened grains ahead being transported backwards via digestion or mechanical transport, and packed in a meniscus structure. Backfills can be found in soft to firm substrates. (j) Striated and meniscate burrow. (k) Irregular echinoid burrow.

interactions, namely the sediment is simply displaced, pushed aside and reorganized, manipulated and transported somewhere or digested and redeposited during burrowing. He noted that this approach is essentially from an ichnological standpoint.

During intrusion an animal simply displaces sediment temporarily with its body (Bromley, 1990, 1996) (Fig. 3.2a–d). As the animal moves on, the medium closes behind (i.e. no cavity is left open). In soupy or soft sediments, this burrowing strategy results typically in biodeformational structures rather than permanent and distinct burrows. This mode of interaction is also adopted by many different organisms producing escape traces (see Section 1.4.8). According to Bromley (1990, 1996), intrusion is also accomplished by some terrestrial vertebrates (e.g. moles, some reptiles) and insects (e.g. crickets and beetles), when they move close to the sediment surface. In this case, the uncompacted roof sediment is simply moved up and, in many cases, the structure collapses behind the animal. However, if these structures are produced at a slightly deeper level within a firmer substrate, a compression structure rather than an ephemeral intrusion will be produced.

Compression records the activity of an infaunal organism that forces a passage through the sediment by pressing material aside and compacting it (Fig. 3.2e–f). This mode of interaction typically results in relatively permanent and distinct burrows. The burrow boundary is typically smooth and only exceptionally ornamented (e.g. *Lockeia ornata*). Hydrodynamic deformation of the body (or part of the body) may result in compression on the boundary if sediment consistency is appropriate. In marine environments, this mode is adopted by bivalves, cnidarians, and many worms that move using a hydraulic mechanism through a firm substrate. Bivalve resting structures (e.g. *Lockeia*) and cnidarian resting and dwelling structures (e.g. *Bergaueria*, *Conostichus*) are examples, while in continental environments, tunnels made by earthworms and many vertebrates (e.g. rodents) are produced by compression.

Excavation is the most efficient way to deal with somewhat compacted sediment (Fig. 3.2g–i). The animal loosens the sediment ahead and relocates the material elsewhere, typically onto the substrate surface. Crustaceans use a basket formed by their anterior appendages to transport sediment outside the burrow, while fish use their mouths (Bromley 1990, 1996). Crustaceans may also use mucus and their anterior appendages to produce construction pellets that are pressed into the boundary of the structure to form a reinforced wall (e.g. *Ophiomorpha*). In some cases, part of the sediment may be ingested and the feces deposited outside the burrow, into the wall, or stored somewhere within the structure. In terrestrial settings, this burrowing strategy is commonly adopted by many fossorial mammals and insects.

Backfill consists of active manipulation by the animal in which sediment ahead is loosened, transported backwards around or through the body and redeposited behind as the organism moves forward (Fig. 3.2j–k). In the case of sediment being moved around the body, the sediment is mechanically manipulated, while sediment transported through the body of the organism involves ingestion and excretion. Burrow fill may be either meniscate, showing alternation of layers of different grain size (e.g. *Taenidium*), or homogeneous (e.g. *Planolites*) (see Box 2.2). Backfill is typically employed by worms, but it is also common in arthropods and irregular echinoids. Although some insects are able to backfill their structures by mechanical manipulation (Smith *et al.*, 2008a), they do not ingest and excrete sediment (Bromley *et al.*, 2007).

The ichnological classification by Bromley (1990, 1996) can be easily related to the approach of Hanor and Marshall (1971), who identified four mechanisms by which organisms can induce mass transport: turbulent diffusion, shear, advection, and molecular diffusion. More than one of these mechanisms may be involved in the generation of a biogenic structure. The first three mechanisms correlate well with distinctive categories in Bromley's scheme, the fourth one involves chemical reactions, inducing mixing on a molecular level and can be favored by any of the three types of physical transport processes.

Turbulent diffusion (also known as eddy diffusion) is produced when an organism moves through sediment generating turbulent stirring. This may occur around the margin of the animal and within its digestive tract in the case of deposit feeders. Turbulent diffusion takes place during intrusion in soupy substrates and commonly produces biodeformational structures (Bromley, 1990, 1996).

Shear takes place if the movement generates a laminar flow of sediment that predominates over turbulence. Some structures may display a central core of turbulent disturbance surrounded by a region of shear at the boundary of the structure. Shear is involved at the boundary of structures generated by compression *sensu* Bromley (1990, 1996). Internally, within the organism, shear is involved during mastication and digestion where solid grains are crushed and ground (Hanor and Marshall, 1971).

Advection refers to the bulk transport of a component, and may involve downward, upward, and axial movements. Burrows filled by sediment collapse or passive infill of open galleries involved downward advection. Many compression structures left open are infilled by collapse and downward advection. Upward advection is involved when an organism excavates a burrow and transports sediment up to the sediment–water interface. Some worms select what they eat, indigestible material is advected through the worm and excreted at the other end. Conveyor burrowers, such as maldanid worms in marine environments and earthworms in terrestrial settings, provide excellent examples of selective advection. If the organism ingests sediment at one end and excretes it out at the other or transports it mechanically along the structure, we are dealing with axial advection. This type of mass transport is recorded in backfill *sensu* Bromley (1990, 1996).

Sediment particle redistribution by the activities of benthic invertebrates and the evaluation of the bioturbation capacity of extant assemblages have received considerable attention by marine ecologists (e.g. Rhoads, 1974; Snelgrove and Butman, 1994; Pearson, 2001; Solan *et al.*, 2004a, b). However, many of the resulting models and classification schemes may be of limited application in paleoichnology as the identity of the tracemaker is in most cases a fundamental incognita. However, Solan and Whigam (2005) modified a previous classification by François *et al.* (1997), which provides a mechanistic understanding of biogenically induced mixing irrespective of the species identity that can be applied more generally. Seven basic modes of bioturbation are recognized: epifaunal bioturbators, surficial modifiers, biodiffusive bioturbators, gallery biodiffuse bioturbators, upward conveyors, downward conveyors, and regenerators. Some of these categories (e.g. upward conveyors and downward conveyors) closely match the basic mechanisms of Hanor and Marshall (1971) and categories of Bromley (1990, 1996), but others deserve further comments and clarification. Epifaunal bioturbators refer to organisms whose activities occur predominantly above the sediment–water interface, and therefore have a negligible contribution to vertical particle transport, but may contribute to lateral heterogeneity by redistribution of fine particles over very short distances along the surface. In contrast, the surficial modifiers of this scheme are actually very shallow-tier bioturbators that inhabit the uppermost 1–2 cm of the sediment, and generate more disturbance than the epifaunal bioturbators. Biodiffusive bioturbators move particles through every level of the sediment profile resulting in a down gradient vertical transport of particles analogous to molecular and eddy diffusion. Gallery biodiffusive bioturbators account for rapid transport of particles from the upper regions of the sediment to the lower limit of burrow penetration. Regenerators excavate holes and transfer sediment from depth to the surface where it is removed by physical processes, such as currents; and is replaced by surficial sediment and burrow collapse material; this is analogous to the typical excavations described by Bromley (1990, 1996) involving upward advection of material during excavation followed by passive infill by downward advection. Solan and Whigam (2005) also explored the interactions between biogenic reworking and microbial activity, emphasizing the necessity of including the microbial component in our understanding of animal–sediment interactions at different scales.

3.3 LOCOMOTION AND BURROWING MECHANISMS

We can approach to the problem of animal–substrate interactions analyzing the many ways in which animals move on and through the substrate. In order to decipher the ethological meaning of a biogenic structure, it is essential to have an understanding of the locomotion and burrowing mechanisms available to the different groups of benthic organisms. Movement is a fundamental characteristic of life, driven by processes that act across a wide variety of spatial and temporal scales (Nathan *et al.*, 2008). Constrains on movement are both intrinsic (i.e. morpho-structural and behavioral) and extrinsic (environmental). The locomotion and burrowing techniques employed by different groups of invertebrates have been analyzed using different frameworks based on experimental work and observation of extant species (e.g. Trueman and Ansell, 1969; Trueman, 1975; Ott *et al.*, 1976), a combination of modern and body-fossil material (e.g. Savazzi, 1982) or reconstructed based on the analysis of biogenic structures both, modern and ancient (e.g. Seilacher, 1953b; Yochelson and Fedonkin, 1993; Mángano *et al.*, 1999). In recent decades, biomechanics and analysis of muscle-skeletal form and function have made a major contribution to our understanding of vertebrate locomotion and feeding strategies, in particular, in extinct groups such as dinosaurs and South American mammals (e.g. Vizcaíno and Fariña, 1999; Vizcaíno *et al.*, 2001; Vizcaíno and De Iuliis, 2003; Sellers and Manning, 2007; Manning, 2008; Manning *et al.*, 2009; Falkingham *et al.* 2009).

In invertebrates, only a handful of studies have dealt with the issue of defining general categories of locomotion and burrowing mechanisms (e.g. Schäfer, 1972; Trueman, 1975; Carney, 1981). There are essentially three ways of looking at this problem. One is an exhaustive documentation of the multiple modes of moving on and through the substrate (Schäfer, 1972). Another possibility is to focus on a reduced number of functional morphological traits (i.e. intrinsic constraints) that allow an organism to move (Carney, 1981). Finally, it is possible to distil a few archetypal mechanisms that can account for the locomotion and burrowing capabilities of invertebrates (Trueman, 1975).

3.3.1 MULTIPLE MODES OF LOCOMOTION: THE EMPIRICIST APPROACH

In a pioneer study on the tidal flats of the Wadden Sea, Schäfer (1962, 1972) identified 12 mechanisms of locomotion in marine invertebrates: amoeboid, ciliar, undulatory, peristaltic, glide-crawling, push-and-pull-crawling, bolting, multiple circular shoveling, pacing, drilling, chimney climbing, and jumping. Although this list is based on extant species, with some adjustments, it can be extrapolated to understand the production of a wide variety of biogenic structures in the fossil record. Although a monumental effort, this classification does not attempt to be comprehensive. As the focus of this classification is providing an analogical link to interpret biogenic structures in the fossil record, locomotion mechanisms of nektonic invertebrates (e.g. jet propulsion) were excluded from this classification (see Trueman, 1975). In practice, many organisms may employ a combination of more than one mechanism.

Schäfer's studies were performed within the framework of the so-called actuopaleontology, a research field that involves the study of marine benthic ecology from a perspective that incorporates a strong paleobiological interest (see Cadée and Goldring, 2007, for a historical study). His empirical approach, based on decades of meticulous observations in modern tidal flats, remains a classic in marine neoichnology.

The breadth of this classification is impressive, from both organism and substrate standpoints. It aims to cover protozoans to vertebrates, and softgrounds to hardgrounds.

Amoeboid locomotion is characterized by the flowing of the body. It is performed by protozoans lacking a shell or rigid pellicle. The mechanism is based on the formation of pseudopodia as a result of local expansion of the protoplasm, ectoplasm, or plasma gel of the protozoan. Locomotion structures produced by amoeboid protozoans in soft tidal-flat mud can be more conspicuous than their producers. In the case of foraminiferans, the plasma body is enclosed by a rigid shell and locomotion is due to rhizopodia extending out of the shell. Schäfer (1962, 1972) noted that little empirical support was available, but suggested that foraminiferan traces may consist of narrow and deep furrows in mud; this has been recently corroborated based on observations of the deep-sea floor (Matz *et al.*, 2008).

Another mechanism used by very small organisms is ciliary locomotion. In this type of locomotion cilia project beyond the surface of the cell membrane and generate a beat that commonly consists of a movement within a single plane. Because the plane of the ciliary beat is diagonal to the longitudinal axis of the body, small ciliate organisms rotate during locomotion. Forward locomotion is achieved via coordination of cilia by a metachronal rhythm, in which a wave of simultaneously beating groups of cilia moves from the anterior to the posterior end of the organism. Although a ciliary epithelium is common in many multicellular animals, ciliary locomotion is only effective in small organisms, protozoans, small metazoans, and larvae. Ciliary locomotion is common in meio- and microfauna inhabiting the uppermost layers of oxygenated sediment. Most of the structures produced are not persistent, although ciliary movement is responsible for the grain dislocation and displacement involved in cryptobioturbation. Some gastropods moving on hard substrates use ciliary movement to complement to glide-crawling (Trueman, 1975).

In undulatory movement, propulsion is achieved by sine waves that propagate along the body, typically in a single plane. The most common type of undulatory motion involves waves traveling from head to tail as the organism moves forward, but backward motion can be achieved by reversing the direction of wave motion from tail to head. The active contraction on one side of the body is responsible for the passive stretching of the opposite side. The wavelength is constant at a given time, although it may change from time to time. This locomotion mechanism is employed by different groups of organisms, such as nematodes, nemertines, errant annelids, cephalocordates (lancelets), fish, limbless lizards, and snakes (although a more complex variant: lateral undulation), moving in a wide variety of substrates, from completely dry (e.g. thixotropic sand) to fluid (i.e. soupy substrate). Undulatory movement is not exclusive to benthic animals, but is also employed by nektonic fish. This wide array of organisms shares a basic morphology consisting of an elongate body, but does not require the presence of an internal cavity (e.g. coelom). To move efficiently within the substrate, undulation can be used in combination with other mechanisms. For example, the polychaete *Nereis*, shoots its proboscis forward (bolting) while the posterior part undulates, helped by the use of large parapodia that act as walking legs (pacing) beating a backstroke on the convex side and a forward stroke on the concave side (Schäfer, 1972). In short, nereids can propel themselves through the sediment using a combination of three locomotory mechanisms: bolting, undulating, and pacing. If the sediment is soupy, some animals can essentially "swim" through it using pure undulations (Bromley, 1990, 1996). The sinusoidal ichnogenus *Cochlichnus*, produced by both nematodes and insect larvae (e.g. ceratopogonids), is a typical example of a trace fossil produced by simple undulatory movement. The sinusoidal trail *Undichna* is another well-known biogenic structure generated by the undulatory movement of a fish with the fins touching the sediment–water interface (e.g. Anderson, 1976; de Gibert *et al.*, 1999).

Peristaltic movement characterizes worm-like animals that have an elongate body, circular cross-section, and double layer of muscles in the body wall. Locomotion is attained by the coordination of this double layer of muscles that work antagonistically (longitudinal in the inner layer and circular in the outer layer), involving contraction of one layer accompanied by relaxation of the other. In the simplest situation, the muscles of all segments contract at the same time, alternatively thickening or lengthening the body. Contraction of the circular muscles reduces the diameter and causes the extension of the worm, while recovery is attained by contraction of the longitudinal ones. In most complex cases, the animal stretches and telescopes section by section. This mechanism is employed by a wide variety of vermiform organisms displaying an internal cavity, including marine polychaetes and earthworms. Waves can move along the body to the head (direct waves in *Arenicola*) or vice versa (retrograde waves in earthworms). In contrast to undulatory movement, peristalsis requires the presence of an internal cavity essential for a hydrostatic mechanism of propulsion. In worms, peristalsis can be combined or alternated with other mechanisms, such as bolting, pacing, and undulatory movement. In the trace-fossil record, peristaltic movement has been inferred for a number of vermiform structures (e.g. *Planolites*), although diagnostic indicators of peristalsis are commonly absent. In other cases, the presence of constrictions in the burrow boundary suggests a deformable body and the use of peristalsis. Perhaps the best available evidence of peristalsis is found in ichnotaxa included in the ichnofamily Arthrophicidae (i.e. *Arthrophycus*, *Phycodes*, *Daedalus*) (Seilacher, 2000). These trace fossils exhibit a distinctive ornamentation ("fingerprints") that tell us about the locomotion mechanism involved: evenly spaced transverse rings visible to the bare eye (the "arthrophycid signature") and fine, submillimetric wrinkles only exceptionally preserved (Seilacher, 2007a). This fine ornamentation was imprinted by the animal cuticle on the burrow wall as a result of peristaltic movement.

Glide-crawling consists of the passage of a series of muscular waves along the body or the part of the body responsible for locomotion. A flat morphology or a flat foot that allows ample contact with the substrate is essential in glide-crawling. This is typically illustrated by gastropods, but also by other groups (e.g. turbelarians and nemertines). The gastropod foot is a hollow muscular organ consisting of numerous variable oriented fibers, which moves over the substrate through waves, locomotion being assisted by mucus secretion. In the trace-fossil record, a number of superficial and very shallow structures, such as *Archaeonassa*, have been assigned to gastropods employing a glide-crawling strategy (Knox and Miller, 1985; Buckman, 1994), although attribution to gastropods has been questioned by others (Yochelson and Fedonkin, 1997). Glide-crawling is commonly complemented by ciliary movement.

In push-and-pull-crawling (or the "double-anchor mechanism"), the penetration and the terminal anchors are applied alternately to produce a stepping motion. To work efficiently this mechanism requires organisms with an internal fluid cavity.

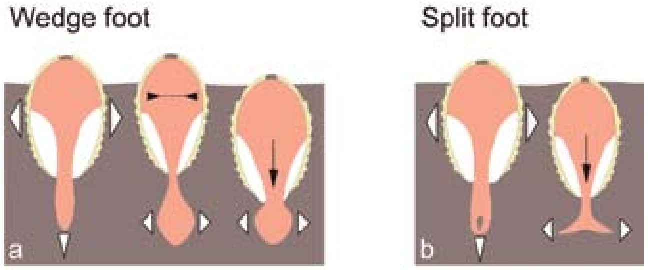

Figure 3.3 Bivalve push-and-pull-crawling ("double-anchor mechanism"). In this technique, the penetration and the terminal anchors are applied alternatively to produce a stepping motion. (a) Wedge foot bivalve burrowing cycle: extension of the food, shell opened against the sediment providing a penetration anchor (left), followed by contraction of adductor muscles and fluidization of the substrate (center), and final expansion of the foot (terminal anchor) and protraction of the shell. (b) Burrowing cycle in a protobranch bivalve: penetration anchor (left) and terminal anchor (right) displaying the open flaps of a split foot. Based on Seilacher and Seilacher (1994).

Bivalves represent the archetypal example, but other mollusks, such as gastropods and scaphopods, and many polychaetes push and pull, albeit in some cases in combination with other mechanisms. In the case of bivalves, the locomotion mechanism is based on rhythmic changes of shape performed by a single muscular foot (Trueman, 1966, 1975; Seilacher and Seilacher, 1994) (Fig. 3.3a–b). Trueman (1975) reconstructed the stages of the digging cycle based on the analysis of film and recordings of pressure measured by an electronic transducer. First, the foot makes a major probe downwards to penetrate into the sediment and be able to pull the shell into an erected position (initial penetration, see Trueman, 1975). Then, the animal moves into the substrate repeating regularly a digging cycle (Trueman, 1975) involving a sequence of steps: (1) adductors relaxed, siphons are closed (to avoid water from passing out during subsequent adduction), and the foot is extended into a slender blade-like structure; (2) valves are closed by contraction of adductor muscles and water is ejected from the mantle cavity through the pedal gape (fluidizing the sediment), at the same time a pulse of pressure causes dilation of the foot to form a terminal anchor; (3) contraction of foot retractor muscles results in the shell being dragged into the sand (siphon reopen at the end of retraction); (4) adductor muscles relax and the shell reopens (by the energy stored in the ligament), pressing into the sand to form a penetration anchor, and (5) the shell is static and the foot is protracted (plateau in cycle curve, Trueman, 1975). The cycle is repeated during the entire burrowing period. This digging cycle can be understood in terms of two phases: the penetration and the terminal anchor (Fig. 3.3a–b). During penetration, the foot is extended into a slender blade-like structure, the shell acts as a penetration anchor by opening the valves to avoid backslippage (Fig. 3.3a). Hydrostatic pressure generated by contraction of the adductor muscles and closure of the valves produces expansion of the foot generating a terminal anchor (Fig. 3.3b). Once a firm foot anchorage is obtained, pedal retractors (i.e. shell protractors) are contracted and the shell is pulled forward. Anchorage of the foot is generated by a pressure pulse which may produce a broad flat area of contact with the sand (e.g. *Donax*), a bulbous swelling (e.g. *Ensis*), or the outward spreading of the cleft foot of protobranchs. The locomotion trace *Protovirgularia* commonly associated with the resting structure *Lockeia* is interpreted as the product of a push-and-pull mechanism by protobranch bivalves (Seilacher and Seilacher, 1994; Mángano *et al.*, 1998; Carmona *et al.*, 2010) (see Section 1.2.7). Schäfer (1972) also regarded the locomotion of brittle stars as a variant of a push-and-pull mechanism, although it strongly differs from the archetypal double anchor mechanism of bivalves (Box 3.2).

Bolting consists of the forward ejection of a frontal organ. This is performed either rapidly as a bolt or slowly pressing into the sediment to form a cavity. Bolting is employed by various infaunal soft-bodied organisms, such as siphunculids, priapulids, and polychaetes, the latter usually in conjunction with peristaltic or undulatory movements. Although biogenic structures produced by bolting have been observed in modern environments, their recognition in the fossil record is not straightforward. However, recent neoichnological experiments suggested that the burrow system *Treptichnus pedum* may be the product of priapulids employing a bolting mechanism (Vannier *et al.*, 2010).

Schäfer (1972) defined multiple circular shoveling as a mechanism consisting of the coordinated use of locomotory appendages in a circular fashion and associated it with spatangoids and some polychaetes. Multiple circular shoveling is essentially performed by organisms with rigidly armored bodies and appendages equipped with their own musculature. Interestingly, Trueman (1975) also affiliated this mechanism to arthropods, including echinoids and arthropods within the same group: organisms with a hard internal or external skeleton. A classic example is illustrated by the burrowing activities of the spatangoids *Echinocardium cordatum* and *E. mediterraneum* (Bromley and Asgaard, 1975; Kanazawa, 1995). Heart urchins have a calcareous thin test covered by delicate and highly specialized spines, perfectly adapted for different tasks during burrowing, sediment transport and maintenance of the structure. Spatangoids use the spatulate spines on the plastron to propel themselves forwards and the spines on the ambitus and aboral part of the test are used for digging down and transporting the sediment (mixed with mucus) from the frontal part backwards around the body (Bromley and Asgaard, 1975). Metachronal waves seem to run over the armor from the front and below backward and upward. The burrowing activities and feeding habits of *E. cordatum* and *E. mediterraneum* have been thoroughly investigated by Bromley *et al.* (1995), who convincingly proposed that chemosynthesis is a common strategy in some deep-tier burrowing spatangoids. In the ichnological record, this mechanism is illustrated by the spatangoid echinoids ichnogenera *Scolicia* and *Bichordites* (Smith and Crimes, 1983; Uchman, 1995). Some of these structures are constructed in relatively deep, partially dewatered firm substrate, completely impregnated with mucus and can preserve scratch marks produced by the work of the spines.

Pacing or stepping results in walking or running. Pacing involves the use of mobile supports (i.e. locomotory appendages) to allow the body to be carried above and ideally not touching the

Box 3.2 The trace-fossil record of ophiuroid movement

Modern ophiuroid locomotion is quite versatile, the animal being able to move in many possible ways. Flexible arms are a key evolutionary innovation of brittle stars, providing freedom of movement exploited in diverse modes of life and feeding strategies (Fig. 3.4a–e). Contrary to asteroids (Fig. 3.5a), ophiuroid locomotion is mainly performed by horizontal and vertical undulatory movements of the long, flexible arms; the tube feet, protruding from the underside of the arms, playing a subordinate role. Four, strong longitudinal muscles press the calcareous vertebra-like segments together achieving joint-like mobile connections between them. Freedom of movement is illustrated in feeding strategies (e.g. coiling) and in the rowing action of the muscular arms during horizontal locomotion, swimming, and digging. One of the most common locomotion strategies, the so-called walking gait, involves four arms organized in two pairs, the two arms of a pair working symmetrically. The odd arm is located at the front or is trailed behind, and does not participate in locomotion, although may serve as a sensor. Whip-like movements of the arms performed in a rowing mode are generated by contraction of longitudinal muscles. When the anterior pair of arms swings forwards, the angle between them decreases, they are laid down and grip the substrate with their tips providing an anterior anchor. As the arms are arched, the body is slightly dragged forward. Then, the posterior pair performs a forward beat. These arms bend as soon as they touch the ground, lift the body, and push it forward. As the amplitude of the beat of the anterior arms is typically larger than the posterior ones, the front ones pull, and the posterior ones push and lift. In a faster gait, only the anterior pair of arms is used in propulsion producing a series of leaps. In *Arcichnus saltatus*, described from the Devonian Hunsrück Slate of Germany, horseshoe trace fossils of the anterior arms are arched forwards and those of the posterior arms are lacking, suggesting “ophiuroid jumping”. The distance between consecutive horseshoe imprints suggests that the action of the current most likely allowed the producer to be carried further than it could normally leap. Yet another curious biogenic structure, recording another variant of ophiuroid locomotion, is the hook-shaped or sinuous trace fossil *Ophioichnus aysenensis* from the Lower Cretaceous Apeleg Formation of Chile. These structures are associated with *Asteriacites lumbricalis*. These ophiuroid trackways were produced by the sculling action of the flexible, long arms while the body was held clear off the ground. Ophiuroids are also active burrowers in soft substrates; some of them resting shallowly within the sediment, whereas others can inhabit semipermanent structures up to 10 cm deep, extending their arm tips above the sediment–water interface (Fig. 3.5f). When digging, the animal is fully extended; arms perform lateral undulations while the tips remain mostly stationary, anchored to the surface. As a result, the central disc rotates penetrating into the sediment, aided by the sweeping action of the disc tube feet. Resting and burrowing activities of brittle stars, mostly in marginal- to shallow-marine deposits, are commonly preserved in the trace-fossil record (Fig. 3.4a–e). Specimens of the resting trace *Asteriacites lumbricalis* with a distinct central disc impression or slender vermiform arms, or both, clearly point to an ophiuroid producer. However, irrespective of the asteroid appearance, morphotypes displaying proximal expansion of the arms, arm branching, or opened or curling arm tips are most likely the work of brittle stars (Figs. 3.4a–e, 3.5b–e). According to this view, the different morphological variants of *Asteriacites lumbricalis* are regarded as “snapshots” of burrowing ophiuroids moving up, down, or laterally as they interacted with the sediment. Proximal expansion of the arms and lanceolate shape result from the back and forth rotation of the central disc generated by the undulatory movement of the arms, while the tips remained mostly stationary on the surface. Specimens with a deep central impression and shallower short arms record a life position in which the disc and proximal arms were completely hidden in the sand, with the arm tips extended upwards. Some shallowly impressed structures with transverse delicate ornamentation on the arms or chevron-like ornamentation in the central disc-like structure reveal the sweeping action of the tube feet. Evidence of brittle star burrowing behavior is also displayed by deep, plug-shaped structures showing pentameral symmetry, assigned to the ichnogenus *Pentichnus*. These structures, described from the Carboniferous of Kansas, are interpreted as ophiuroid dwelling burrows (Fig. 3.5f).

References: Seilacher (1953b); Fell (1966); Reese (1966); Maerz *et al.* (1976); Heddle (1967); Schäfer (1972); Sutcliffe (1997); Mángano *et al.* (1999, 2002a); Bell (2004).

substrate. Appendages capable of pacing are arranged in pairs. If substrate conditions are appropriate, appendages imprint tracks on the sediment, which are in turn, organized in trackways (e.g. Davis *et al.*, 2007). Pacing is mostly employed by terrestrial organisms rather than aquatic ones, although limulids and many marine crustaceans (e.g. benthic decapods, isopods, notostracans) may also use this mechanism if moving on the sediment–water interface. In arthropods, the basic limb movements employed in pacing consist of combining promotor–remotor swing and levator–depressor movements (Trueman, 1975; Manton, 1977). While the promotor–remotor swing is implemented by muscles from the proximal part of the leg, which pass into the trunk, the levator–depressor movements are mostly controlled by intrinsic muscles within the leg. In most arthropods, the swing movement takes place at the proximal end of the limb (i.e. at the coxa–body junction) around an axis lying in the transverse plane of the body (Manton, 1977). The levator–depressor movement takes place at right angles to the promotor–remotor swing and distal to the coxa, using one or two pivot articulations situated between leg segments. During the forward swing, the leg is outstretched with its tip on the substrate at the beginning of the backstroke, halfway through the backstroke the leg flexes (if the limb tip is not to slip on the ground), and finally it is extended again during the latter part of the backstroke (Manton, 1977, Fig. 2.3b). The

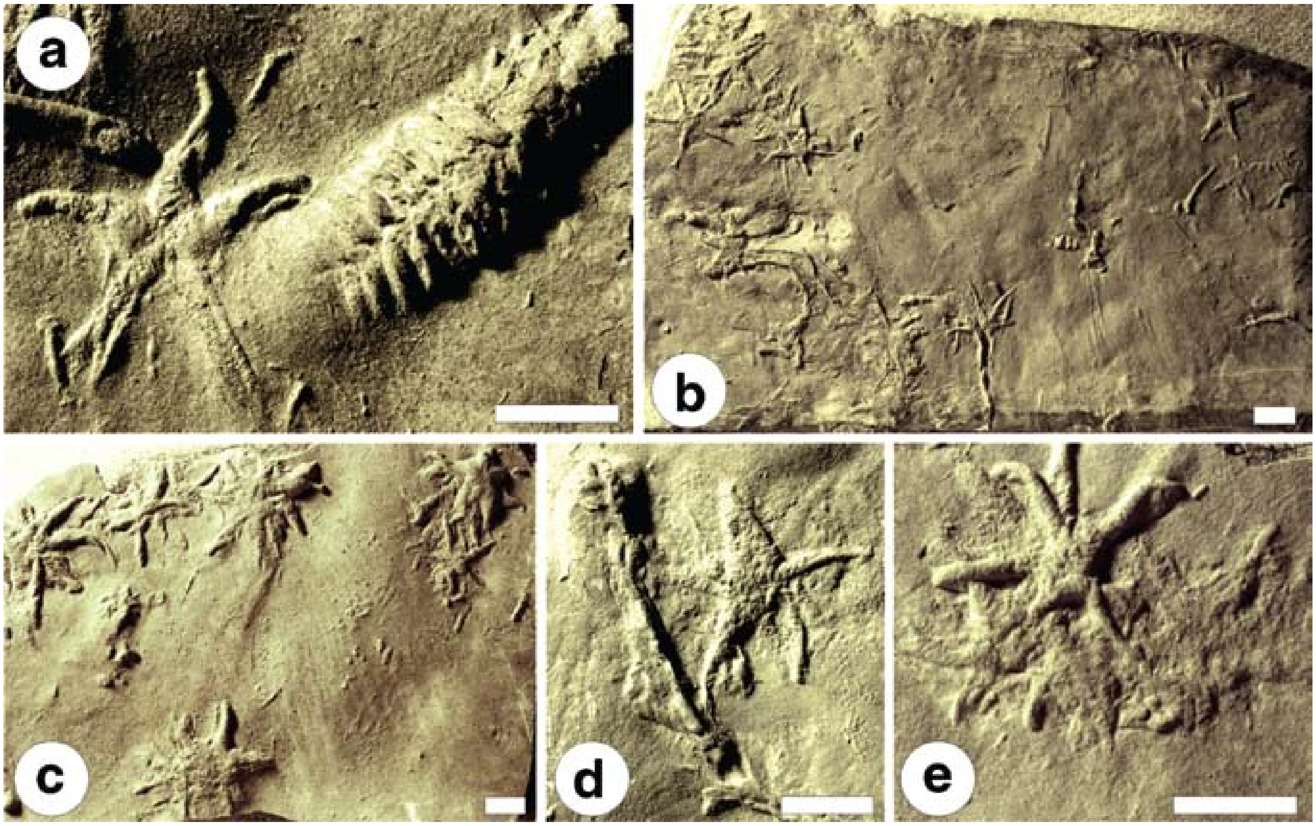

Figure 3.4 The ophiuroid resting trace *Asteriacites lumbricalis* from the Upper Carboniferous Rock Lake Shale Member, Stanton Formation, Lansing Group. Site south of the Kansas City International Airport, Missouri, central United States. All scale bars are 1 cm. (a) Arm proximal expansion recording the burrowing action of the tube feet in the disk area. (b) Assemblage consisting of multiple specimens displaying lateral and vertical repetition, resulting from animals trying to escape a sedimentation event. Note asteroid-like specimen (upper right) and structure reminiscent of an ophiuroid with well-defined polygonal disk (upper left). (c) Specimens displaying irregular morphology and multiple arms, produced by the superposition of successive impressions due to slight lateral shifting and repositioning. (d) Specimen displaying arms with variable morphology resulting from modification during burrowing: some arms are asteroid-like in appearance (upper and lower left arms), but others clearly reveal the ophiuroid origin (upper right). (e) Specimen exhibiting a double arm (upper) as result of passive rotation of the disk during arm rowing. The hook-like tip also reveals the flexible nature of the ophiuroid arm.

levator–depressor actions involve the flexure and extension of the limb, the limb being firmly pressed on the ground during the propulsive backstroke. This results in the forward movement of the body. In principle, large angles of swing and long legs can result in long strides and fast running. In Onychophora, the shortening and extension of the soft, non-articulated limbs during stepping is only performed by muscles without joints.

In a multi-legged organism steady locomotion is most commonly achieved by the existence of a phase difference between one leg and the next creating a metachronal rhythm. Successive limbs are coordinated so when some swing forward off the ground (forward recovery swing), others are pressing backward performing the propulsive backstroke. This results in cycles of limb movement or metachronal waves. The fields of movement of successive legs may overlap considerably, but legs themselves do not touch one another. The phase difference between one leg (n) and the next (n + 1) can range between 0 (both legs are moved synchronously) and 1 (phase difference is one complete cycle). The swing angle, limb length, and phase difference between successive legs (or groups of legs) together with the relative duration of the forward and backstroke are critical to gait pattern and speed of movement. Pacing or stepping represents a slow kind of walking. Increased speed turns into running, which involves a more rapid succession of paces. The slowest method of walking in arthropods and polychaetes involves stepping by the limbs or parapodia, respectively, while the trunk remains straight (Fig. 3.6a). In polychaetes, an increase in speed of pacing is accompanied by horizontal undulations of the trunk, which as they increase in amplitude lead to a swimming-like motion (Manton, 1977). However, in arthropods, trunk undulations tend to be inhibited. If undulatory movements are present, they do not contribute to locomotion or to an increase in speed of walking or running. The appearance of body undulations in centipedes and chilopods during their fastest gaits reduces the effective angles of swing of the propulsive legs, and, therefore, reduces the speed potential of the fastest gaits, wasting energy in lateral movements (Fig. 3.6b). Typically, as the relative duration of the backstroke decreases, the points of support of the body against the substrate also decrease (and are located further apart), and the distance between successive propulsive legs increases (compare Fig. 3.6c with Fig. 3.6d).

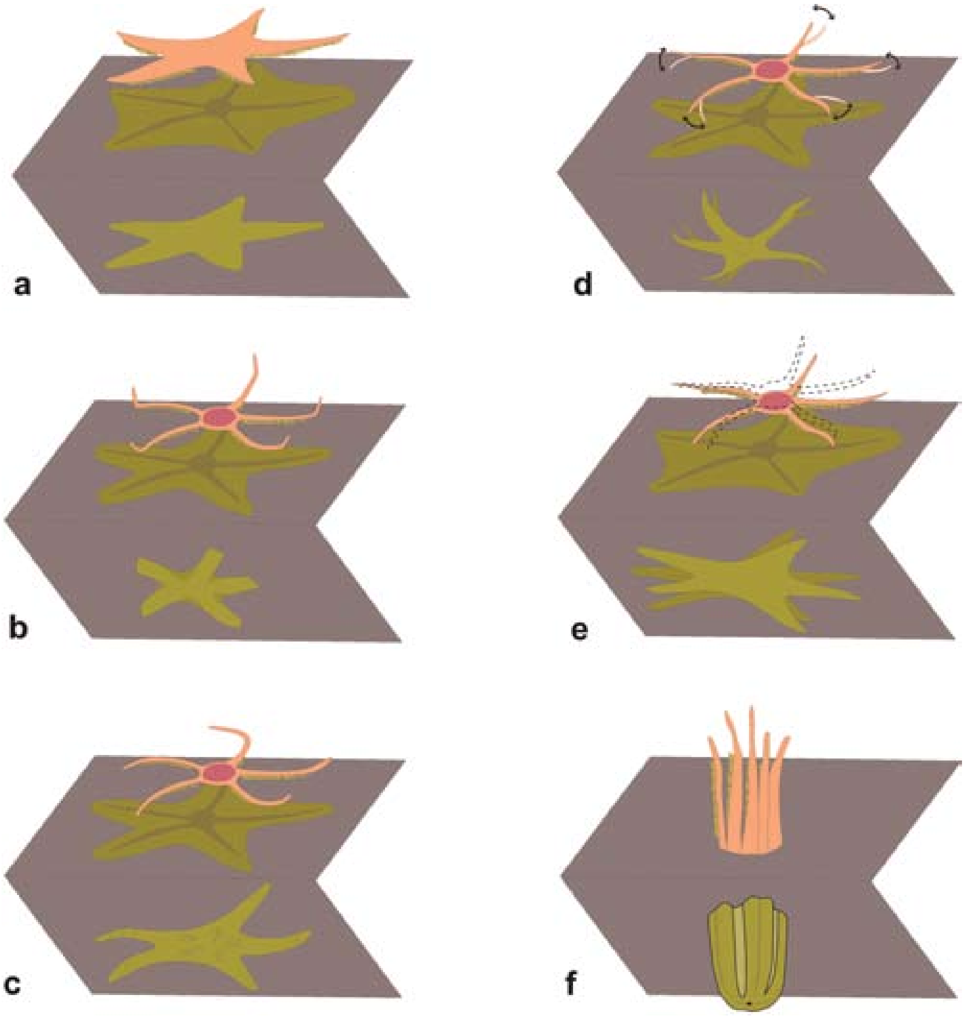

Figure 3.5 Asteroid and ophiuroid burrowing mechanisms and resulting biogenic sedimentary structures. (a) Asteroids stay still on the substrate with their arms extended and their tube feet projecting from the underside of the arms; arms perform a sweeping action that creates a shallow, inflated, five-rayed hypichnial structure (*Asteriacites quinquefolis*). (b–f) Wide range of behaviors recorded by extant burrowing ophiuroids. (b) Ophiuroid is resting with central disk deeper into the sediment and the tips projected upward. The resulting *A. lumbricalis* specimen displays a deeper central part and short truncated arms. (c) Ophiuroid is undulating its flexible arms in a horizontal plane at the same time as the tube feet of the disk area perform a sweeping action. The resulting *A. lumbricalis* specimen may display curved arm impressions and delicate chevron-like ornamentation in the disk area. (d) If the rowing action of the arms continues, the central part is buried into the sediment, the tips moving sideways on the sediment. The resulting *A. lumbricalis* specimen displays a deeper central area and arms with bifurcated tips. (e) Ophiuroid is migrating upwards escaping a rapid sedimentation event. The rowing action of the arms may result in rotation. The resulting *A. lumbricalis* specimen displays multiple superimposed impressions with slight lateral movement. (f) The disk of some burrowing ophiuroids can penetrate more than 10 cm into the sediment, generating a plug-shaped structure with pentameral symmetry (*Pentichnus gugelhupf*).

In high-speed variants, not only secondary undulations, but also abdominal marks indicating unsteady movement, may be present (Fig. 3.6b, d). Gait pattern is highly variable, and controlled by intrinsic (e.g. limb number and morphology) and extrinsic factors (e.g. substrate consistency, slope, temperature). Brady (1947) documented variations in arthropod gait patterns in trackways preserved in eolian-dune deposits, and related them to variations in slope, temperature of the environment, and sand moisture. The trace-fossil record hosts abundant evidence of structures produced by pacing, including a wide variety of arthropod and vertebrate trackways. The list of erected arthropod trackways documenting walking and running is impressive. Many of the available names, however, require further taxonomic revision, including some very common ichnotaxa such as *Diplichnites* (e.g. Buatois *et al.*, 1998b; Minter and Braddy, 2009). Many trackway names have been based on poorly preserved material or a poor evaluation of the locomotion mechanism and taphonomic controls (e.g. substrate consistency). Well-established, distinct ichnogenera include: *Paleohelcura* and *Octopodichnus*, attributed to the work of scorpions or spiders, respectively (Brady, 1947; Braddy, 1995; Minter and Braddy, 2009); *Palmichnium*, assigned to the walking of eurypterids (Braddy and Almond, 1999); *Dendroidichnites*, related to locomotion by myriapods on very soft surfaces (Demathieu *et al.*, 1992; Buatois *et al.*, 1998a;

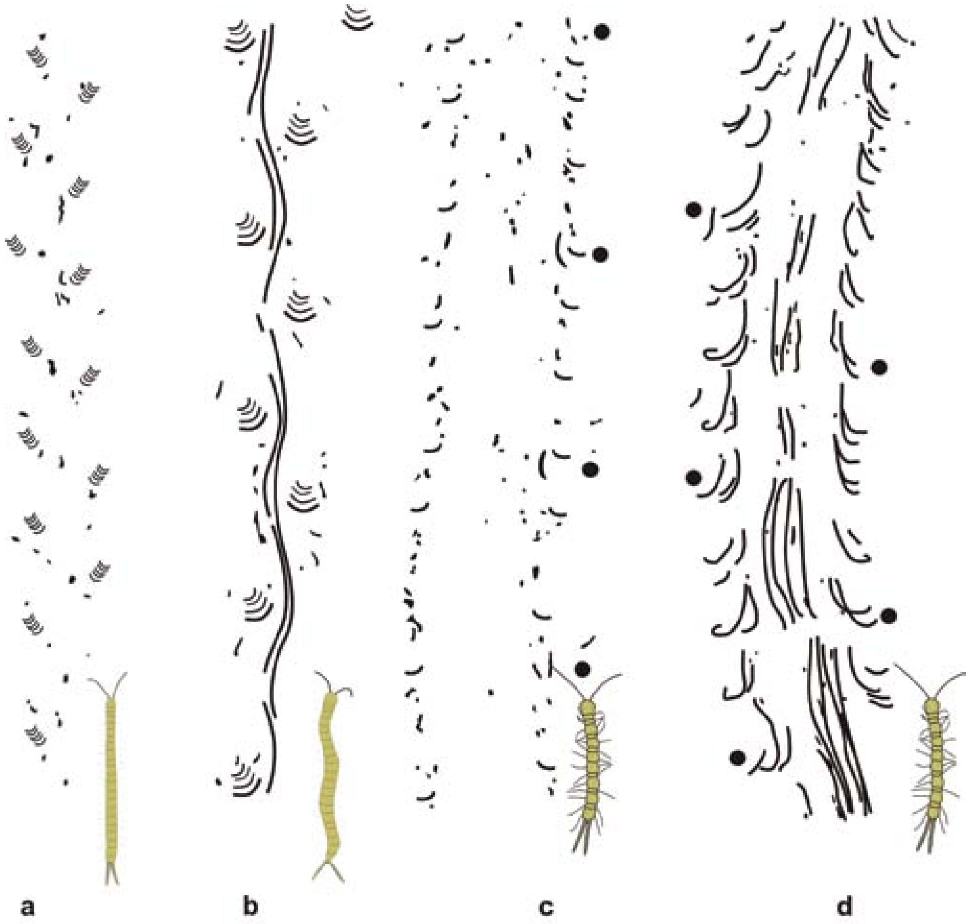

Figure 3.6 Extant centipede running trackways. Centipedes running over smoked paper (printed in reverse). All tracks 50 mm long. (a–b) Tracks of the centipede *Cormocephalus pseudopunctatus*. (a) Running at a slow gait. Tracks form oblique forwardly directed groups, no axial mark. (b) Running at a fast gait. Tracks fall on almost the same spot, and the stride is so long that the animal is unable to hold the body off the ground, resulting in an axial drag mark. (c–d) Tracks of the centipede *Lithobius forticatus*. Black spots are one stride length apart. (c) Running at a slow gait, stride length 14 mm, approximate speed 80 mm/s. Tracks look scattered, but in fact form a regular series. Legs of a pair are in phase. (d) Running at a fast gait, stride length 21 mm, approximate speed 280 mm/s. Tracks are grouped into four rows per stride length. Legs of a pair are in opposite phase (notice staggered black spots). Icons of the producers on lower right. Based on Manton (1977).

Minter and Braddy, 2009); *Lithographus*, attributed to trackways of pterygote insects (Minter and Braddy 2009); and *Stiallia*, interpreted as the feeding activities of an arthropod (Walker, 1985; Buatois *et al*., 1998a; Minter and Braddy, 2009). However, a cautious approach in interpreting the producers from trackways is needed as emphasized by recent experimental neoichnological studies. Davis *et al*. (2007) demonstrated that a wide range of morphologies can produce very similar trackways and, in contrast, one producer can generate trackways potentially attributable to different ichnotaxa.

Using what is essentially a modification of the mechanism for walking on the substrate, some arthropods are able to burrow within the sediment producing structures of variable complexity. An excellent example displaying ample representation in the trace-fossil record is the ichnogenus *Cruziana*, commonly, although not exclusively, attributable to the combined locomotion and feeding activities of trilobites in Lower Paleozoic rocks (Box 3.3).

Moving into hard substrates, drilling involves penetration in a cemented substrate (laterally persistent hardground or isolated wood logs or shells). This mechanism is typically associated with protection in the case of dwelling structures of boring bivalves such as *Petricola* and *Zirphaea*, or predation in the case of drill holes produced by carnivorous gastropods such as *Murex*, *Natica*, and *Thais*. The most general term "bioerosion" is preferred today because it includes every form of biological penetration into a hard substrate, such as etching, rasping, scraping, and drilling (Bromley, 1992). A wide variety of morphologies and ethological types are the product of bioerosion at all scales (see Section 1.1). Many groups of animals are able to interact with a hard substrate producing biogenic structures, including sponges, siphunculids, polychaetes, phoronids, acrothoracican cirripedians, patelled gastropods; holothurians, regular echinoids and cephalopods (Trueman, 1975; Bromley, 1992; Taylor and Wilson, 2003). Bioerosion can be performed by mechanical abrasion, chemical means, or a combination of both. In the first case, the animals use special tools to scrape off tiny particles. In the second case, a scar, tube, or cavity is generated by means of a corrosive secretion. As a generalization, mechanical bioerosion is mainly performed in calcareous substrates, and chemical bioerosion is performed in harder substrates. One of the best-known examples of mechanical drillers is that of pholadid bivalves. These borers employ cycles of successive contractions of the anterior and posterior adductor muscles, causing the movement of the valves in various directions, with consequent abrasion of the walls (Nair and Ansell, 1968; Trueman, 1975; Röder, 1977; Carmona *et al*., 2007). The valves of rock-boring bivalves have two axes around which they can pivot, in such a way that their marginal spines form a series of scratch ornaments arranged as if they were a row of chisels (Seilacher, 1985). In the ichnological record, structures of boring bivalves are represented by the ichnogenus *Gastrochaenolites*

Box 3.3 Trilobite burrowing: the trunk-limb feeding mechanism

Ichnological and functional-morphological evidence suggest that trilobites display a peculiar locomotion and burrowing strategy, which is herein referred to as the trunk-limb feeding mechanism. In fact, trilobites fed as they moved sweeping the sediment with their appendages in an inward direction (as opposed to most extant arthropods, such as insects). This mode involved moving sediment inward and backward towards the ventral midline. Scratch-mark ornamented bilobate trace fossils, typically preserved as hypichnial ridges on sandstone soles, provide excellent examples in Lower Paleozoic marine rocks. These ribbon-like bilobate structures ornamented by V-shaped striations are commonly assigned to the ichnogenus *Cruziana* and attributed, although not exclusively, to the combined locomotion and feeding activities of trilobites (Fig. 3.7a–e). *Rusophycus* is a short bilobate structure similar to, and in many cases forming compound structures with, *Cruziana* but recording stationary burrowing for resting, hiding, laying eggs, or feeding purposes. Functional analysis of the fine ornamentation of *Cruziana* and *Rusophycus* reveals details of the ventral morphology of trilobites and its peculiar feeding strategy. Contrary to the excavating strategy of many arthropods that move sediment away from under their body in a centrifugal fashion, the delicate scratch marks covering the lobes indicate that trilobites swept the sediment *towards* the ventral midline. Each walking (endopodal) leg describes a trajectory from the marginal-external area towards the mid-ventral surface where food is passed, close to the body towards the backwardly opening mouth. As multi-legged animals, trilobites use metachronal waves passing from the rear to the front of the organism to efficiently coordinate appendage movement. In trackways resulting from steady walking, series of imprints commonly overlap as each metachronal wave only advances the body a fraction of its length. In plunging structures or excavations, the coordinated action of the walking appendages (endopodites) on the substrate is responsible for the classic V-shaped ornamentation, the "V" opening being in the direction of movement. Trilobites lack specialized appendages able to manipulate large food items. In the absence of mandibles and chelipods, trilobites must have only been able to collect small food particles from the sediment (i.e. deposit feeders), using the inward sweeping action of their limbs. According to ichnological and anatomical evidence, a microphagous mode of feeding was most likely the primary habit, although the close association of some conspicuous *Rusophycus* with worm structures and the hypostome morphology suggest that a macrophagous feeding habit was attainable by some large trilobites. Filter feeding can also be inferred as a secondary feeding habit in trilobites based on ichnological evidence. Trilobites possessed biramous undifferentiated limbs only varying in size along the body, typically with the cephalic appendages being the most robust ones. The inner rami, the endopodite (also endite or telopodite), had the primary function of locomotion and assisted in feeding. The function of the outer rami, the exopodite (also exite), has been the subject of discussion. In principle, these feathered appendages primarily served for respiration purposes and swimming. Dolf Seilacher considered that the feathered exopodites were involved in straining the sediment while feeding and occasionally used in swimming. However, Jan Bergström proposed that exopodites could have played a dominant role in burrowing, with respiration being performed by other soft, non-preserved structures. In his interpretation, exopodites were provided with strong lamellar spines rather than soft gill filaments. According to this view, spines are the main tools recorded in some well-known *Cruziana* (e.g. the *rugosa* group) characterized by multiple (8 to 12) sets of parallel scratches. Behind the cephalon, a series of segments articulated with one another permitted dorso-ventral, but not lateral bending of the body. Posteriorly, the pygidium was formed by fused segments, each of which carried a pair of biramous legs. These posterior legs are typically the smallest in size. This basic body plan allowed trilobites to burrow in different positions, resulting in what has been called "segmental variation". The dorsally flexed attitude records the isoclinal burrowing position, the front and rear ends being slightly arched to promote the formation of a flushing current. Head down (prosocline) burrowing resulted in cruzianids characterized by conspicuous endopodal scratch marks performed by a few pairs of strong cephalic appendages. In this position, scratch marks are wide angled and are transverse to the midline; genal spines, being upwardly directed, are not recorded in biogenic structures. Some trilobites may have used the cephalon margin as a shovel in a way similar to modern xiphosurans. Deep prosocline rusophycid structures may show anterior crescentic ridges or exceptionally the impression of the anteriormost antennae (Fig. 3.8). In contrast, tail down (opisthocline) burrowing involved smaller pygidial endopodites and the brushing of the outer rami of the leg (exopodites). Exopodal scratch marks are commonly much more delicate than endopodal scratch marks, present at a more external position in relation to the axis (in many cases forming an external lobe, such as in *Cruziana semiplicata*), and tend to be more or less subparallel to the median line. In this position, the backward bend of genal and pleural spines may favor the formation of marginal ridges in the biogenic structure produced (Fig. 3.8).

References: Seilacher (1970, 1985); Eldredge (1970); Bergström (1973, 1976).

(Kelly and Bromley, 1984; Carmona *et al.*, 2007). Carmona *et al.* (2007) demonstrated that boring bivalves perform the same patterned behavior to penetrate firm- and hardgrounds, putting a cautionary note on recognizing hardgrounds based on the presence of the boring *Gastrochaenolithes* and restricting the distribution of this ichnogenus to hard substrates (see Section 2.7). Other bivalves (e.g. *Teredo*) are adapted to bore exclusively in xylic substrates. They do so by using the valves as boring tools, rather than employing them to enclose the soft body. Each valve consists of a beak-like front section, a protruding middle section

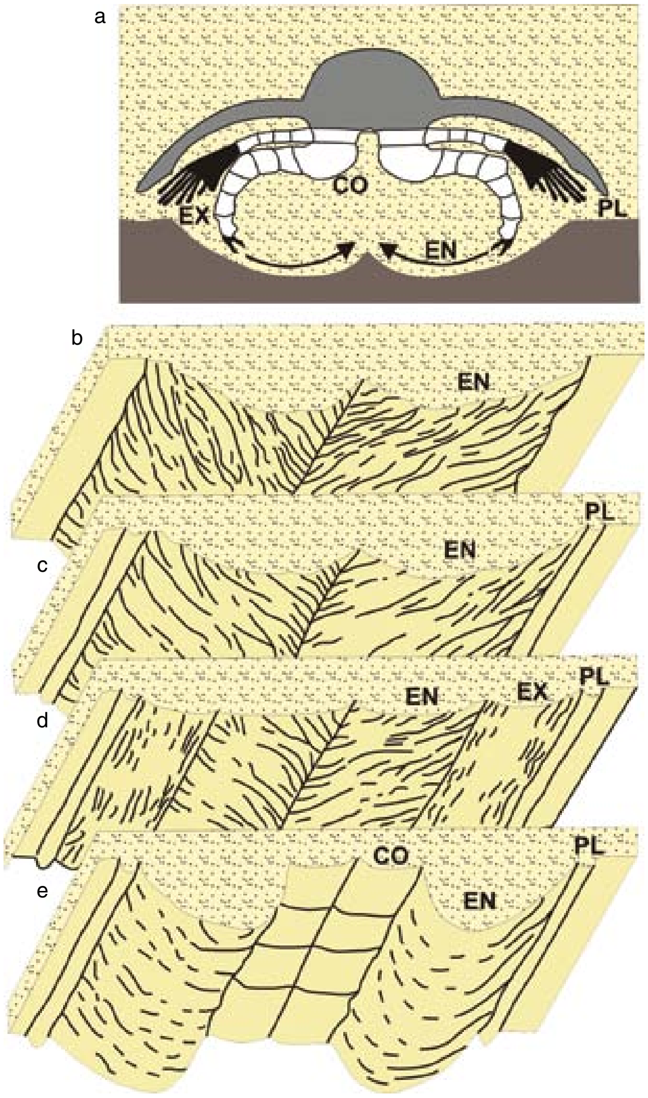

Figure 3.7 Trilobite burrowing and variability in the morphology of *Cruziana*. (a) Cross-sectional view of a trilobite showing first appendage segment (CO, coxae) and biramous appendages characterized by a strong inner branch (EN, endopodite) and feather-like outer branch (EX, exopodite). Some parts of the exoskeleton (gray), such as pleural/genal spines (PL), may also be recorded in some *Cruziana* and *Rusophycus*. (b) *Cruziana* displaying only endopodal lobes excavated by the endopodites (EN). (c) *Cruziana* exhibiting endopodal lobes (EN) and a marginal pleura/genal spine mark (PL). (d) *Cruziana* displaying a four-lobe geometry with two internal endopodal lobes (EN) adjacent to two external exopodal lobes (EX); pleural spine marginal mark may be present. (e) *Cruziana* displaying prominent axial coxal impression, two convex endopodal lobes and a marginal pleural/genal spine mark. Based on Seilacher (1970).

with rows of double pointed teeth, and a back section consisting of a smooth end. The activity of wood-boring bivalves is represented in the trace-fossil record by the ichnogenus *Teredolites* (Bromley *et al*., 1984). The well-known ichnogenus *Oichnus* is recorded by circular to oval holes produced by the predatory activity of carnivorous gastropods, although small holes, also included in the same ichnogenus, can be generated by octopodes to inject poison into their prey (Bromley, 1981, 1993). In addition to these classic examples, a large number of borings displaying diverse morphologies are known in the ichnological record (Bromley, 1992, 1994, 2004; Taylor and Wilson, 2003).

Schäfer (1972) included chimney climbing as a distinctive mechanism involved in the ascending and descending movement within vertical burrows with mucus-lined or constructed walls, although the same behavior should be expected on unlined vertical structures in firmgrounds. However, in the case of crustaceans or some polychaetes (e.g. *Sabellaria*), the use of appendages or parapodia during climbing is analogous to pacing or “walking on the walls”. Animals build their burrows with the right inner diameter (not too small, not too large) to allow for chimney climbing. The construction of sand tubes by the polychaete *Sabellaria* is one of the best-documented examples. *Sabellaria spinulosa* lives freely suspended in its tube, held only by three pairs of thoracic parapodia, which are used in locomotion up and down the tube. The worms settle in colonies forming large constructions referred to as sand-coral reefs (Ekdale and Lewis, 1993). If the internal diameter of the tube is too large, contact with the internal surface is insufficient to push effectively against the wall and move the body upward. On the other hand, if the body fits too tightly within the burrow, climbing is impossible and usually peristalsis, in the case of worms, is used to move up and down the tube (Schäfer, 1972). In other cases, organisms find an appropriate burrow built by another animal, and may occupy it either for protection or to hunt. In the trace-fossil record, *Skolithos* may illustrate strategies such as chimney climbing, as well as the crustacean burrow shafts of *Ophiomorpha* and *Spongeliomorpha*.

Jumping is a mechanism that requires large amounts of energy and is commonly used combined with swimming, walking, or running. It is exclusive of vertebrates and arthropods. The adaptations and dynamics involved in jumping are specific to different taxa. Most multi-legged animals cannot achieve steady locomotion by moving all of their legs or all legs of one side of the body in unison (Manton, 1977). Large flat thoracic legs of copepods are an exception; they move synchronously resulting in intermittent jumping through the water (Manton, 1977). However, the trace-fossil record suggests that several marine benthic arthropods were able to achieve jumping by multiple legs performing a backstroke in unison (Seilacher *et al*., 2005; Seilacher, 2007a). The oldest record of this jumping mechanism is recorded in the Cambrian by *Tasmanadia cachii* in which subsequent series of imprints do not overlap. Instead, they form individualized patterns that probably correspond to the general outline of the tracemaker (Seilacher *et al*., 2005). This means that the animal was not continuously supported; rather it must have moved in jumps, driven by the simultaneous action of all appendages (and most likely help by the current). The distinctive Carboniferous trackway *Orchesteropus atavus* also records a similar mechanism, most likely produced by “galloping” xiphosuran (Seilacher, 2007a). Based on functional morphology analysis, Manton (1977) concluded that some trilobites (e.g. *Olenoides*) were able to perform multiple-leg jumping. In marginal-marine and terrestrial settings, examples of jumping structures attributed to monuran apterygote insects have been included in the ichnogenus *Tonganoxichnus*

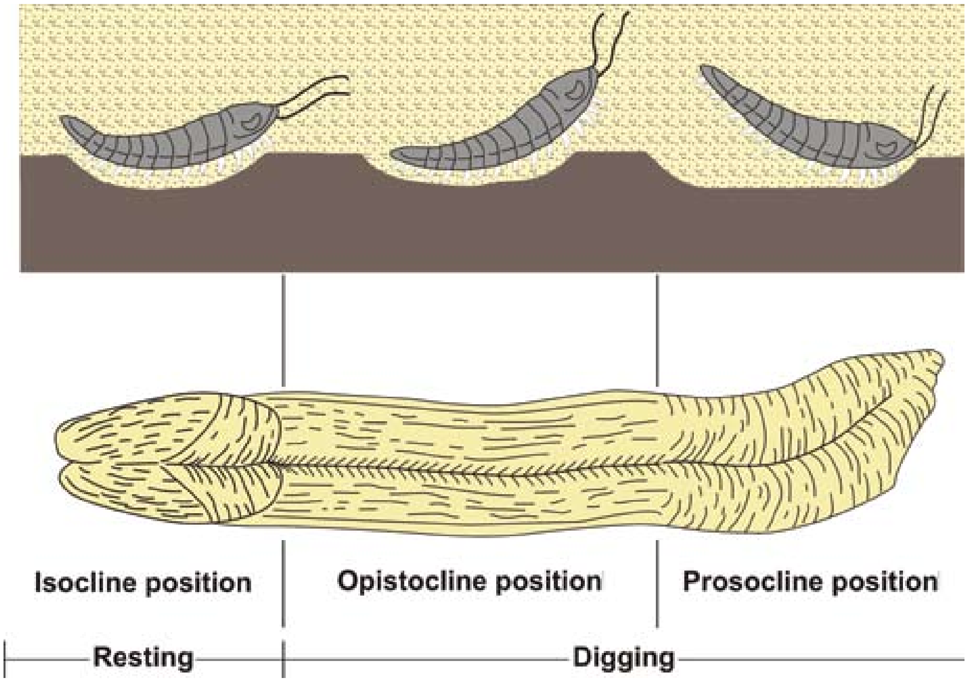

Figure 3.8 Trilobite burrowing position and the resulting biogenic structure. From left to right. Isocline resting position, *Rusophycus* displaying dorsoventral morphology; coxal and pleural/genal-spine marginal ridge may be present in some *Rusophycus* ichnospecies. Opisthocline (tail-down) burrowing position. Exopodal lobes get better representation; pleural or genal marginal ridge typically present. Prosocline burrowing position, endopodal lobes get full representation, exopodal markings uncommon, head-shield mark may be present in some rusophysid versions. Based on Seilacher (1970).

Box 3.4 The jumping of monuran insects

Superbly preserved trace fossils attributed to monuran insects (an extinct group of archaeognathan apterygote insects) occur in late Paleozoic paralic deposits in the United States. In particular, detailed study of specimens from Kansas and New Mexico allows the reconstruction of the functional morphology and behavior of their producers. These trace fossils, assigned to the ichnogenus *Tonganoxichnus*, provide evidence of monuran jumping behavior, favoring comparisons with modern machilid archaognathans, as illustrated by the genus *Petrobius*. The ichnospecies *T. ottawensis* (Fig. 3.9a) is characterized by a fan-like arrangement of mostly bifid scratch marks at the anterior area that records the head- and thoracic-appendage backstrokes against the sediment. The posterior area displays chevron-like markings or small subcircular impressions recording the abdominal appendages of the animal, ending in a thin straight terminal extension. Specimens display lateral repetition, and are commonly grouped into twos or threes with a fixed point at the posteriormost tail-like structure. *Tonganoxichnus ottawensis* is thought to record the ability of these apterygote insects to perform successive lateral jumps with a pivot point at the posterior tail-like extension. This ichnospecies most likely represents jumping in connection with a defensive strategy or feeding purposes (i.e. raking the microbial mat). The ichnospecies *Tonganoxichnus robledoensis* (Fig. 3.9b) has an anterior region characterized by the presence of a frontal pair of linear imprints, three pairs of lateral linear imprints, a middle medial oval imprint, and a posterior elongate axial imprint. Specimens are aligned, suggesting a forward progression via a linear succession of jumps. Jump distances were up to eight times body length. Monuran trackways, assigned to the ichnospecies *Stiaria intermedia*, are closely associated with the jumping structures. Ichnological evidence indicates that jumping was a common strategy in apterygote Paleozoic insects and developed very early in the evolutionary history of insects.

References: Mángano *et al.* (1997, 2001a); Braddy and Briggs, 2002; Minter and Braddy (2006a, 2009).

(Mángano *et al.*, 1997; Braddy and Briggs, 2002; Minter and Braddy, 2006a, 2009) (Box 3.4). Interestingly, monuran jumping trace fossils display similarities with modern archaeognathan takeoff structures documented by Sturm (1955).

3.3.2 BURROWING PRE-ADAPTATIONS: THE MORPHO-STRUCTURAL APPROACH

Another approach to the problem of burrowing mechanisms is to look at particular morphological adaptations to burrowing displayed by the different organisms (Carney, 1981). This approach assumes that burrowing is primarily constrained by organism morphology. Based on this assumption, Carney (1981) recognized five main morphologies: (1) completely soft bodied-lacking significant lateral appendages (e.g. some annelids and most worm-like organisms, almost all coelenterates, some holothurians, shell-less mollusks); (2) completely soft bodied with significant lateral appendages (e.g. annelids with large parapodia, most holothurians); (3) soft bodied with partial rigid external covering (e.g. most benthic mollusks,

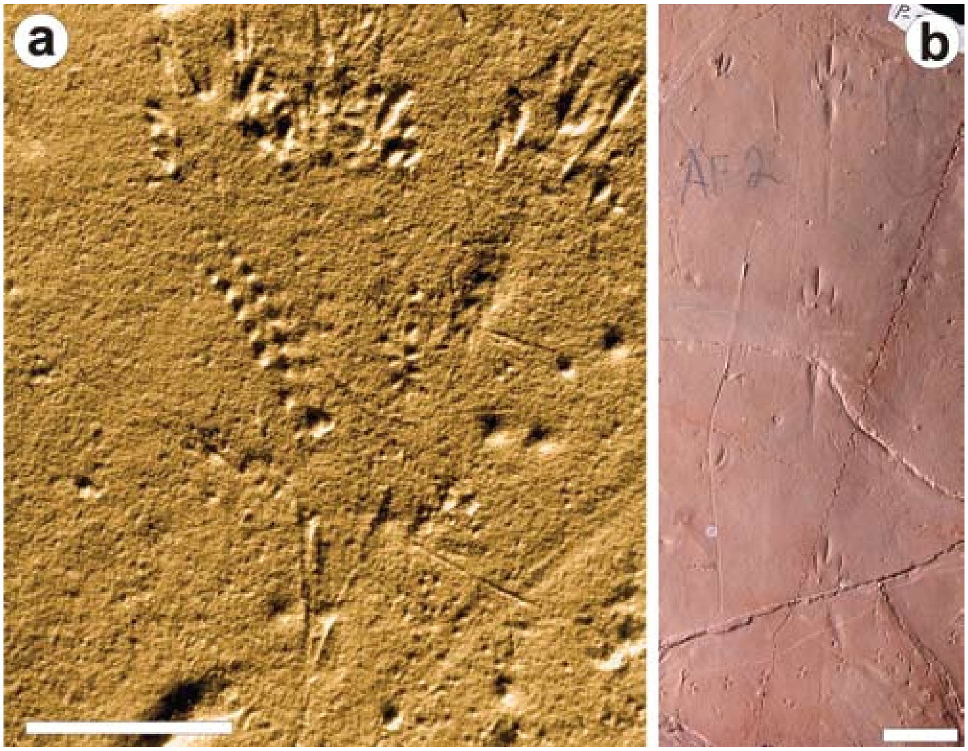

Figure 3.9 The ichnogenus *Tonganoxichnus* as evidence of jumping behavior in late Paleozoic monuran insects. (a) *Tonganoxichnus ottawensis*. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, central United States. See Mángano *et al.* (1997). Scale bar is 1 cm. (b) *Tonganoxichnus robledoensis*. Upper Permian, Robledo Mountains, Robledo Mountains Formation, southern New Mexico, southern United States. See Minter and Braddy (2006). Scale bar is 2 cm.

inarticulate brachiopods); (4) completely rigid external covering with numerous flexible appendages (e.g. most arthropods, echinoids), and (5) externally soft animals with some rigid internal structure (e.g. vertebrates, pennatulid coelenterates).

From an ichnological and functional standpoint, this morpho-structural classification is hard to adopt. For example, although large parapodia may be involved in locomotion, their presence or absence is not generally a determinant of the primary mechanism of locomotion involved. Also, the presence of a shell implies an additional cost of energy for locomotion, but does not itself determine the adopted burrowing mechanism. Regardless of the presence of the shell, the burrowing mechanism is controlled by the deformable body of the mollusk, resulting in the double anchor mechanism. In fact, this mechanism is employed by many animals lacking a shell (e.g. polychaetes). Finally, although both echinoids and arthropod exhibit multiple appendages coordinated in metachronal waves, the burrowing mechanisms are remarkably different, as clearly evidenced by the biogenic structures produced.

3.3.3 IN SEARCH OF A UNIVERSAL MECHANISM: THE RATIONALIST APPROACH

A different approach to the problem of locomotion is to search for a universal mechanism that essentially results from very basic mechanical principles. This has been the approach undertaken by Trueman (1975) and, although it may be termed a "rationalistic approach" (in the sense of being a major generalization based on inferential reasoning), it is firmly rooted in a well-founded experimental tradition (e.g. Ansell and Trueman, 1968; Trueman, 1966, 1967, 1968a, b, 1971; Trueman and Ansell, 1969). The underlying hypothesis to this approach is that despite the many morphological plans and particular locomotion techniques used by invertebrates, there are just a few basic principles involved in animal locomotion. These first principles are explained in terms of basic physical laws, such as the Newtonian laws of movement and the principles of hydraulics (Trueman, 1975; Barnes *et al.*, 1993). For example, Newton's third law established that for any action there is a reaction of the same magnitude but in the opposite direction. In ichnological terms, this means that, for example, when an organism attempts to penetrate the substrate by a propeller force (action), this is balanced by the substrate frictional resistance (reaction). The organism will only be able to move if an efficient anchoring system is created (e.g. the penetration and terminal anchors) to overcome substrate resistance.

According to Trueman (1975), the animal locomotory system can be subdivided into three main components, engine, transmission, and propeller. In the engine, the chemical energy is converted into mechanical energy due to contraction of the muscles. This energy is transmitted to the propeller by means of a system of levers in the case of organisms with hard parts (mechanic transmission) or through the fluids of a hydrostatic system in soft-bodied organisms (hydraulic transmission). The propeller is the part of the organism that is in contact with the substrate and, therefore, becomes the visible element acting in animal–substrate interaction. In vertebrates and arthropods, the propeller is commonly a specialized structure (rigid propeller), while in soft-bodied invertebrates or invertebrates that use soft processes of the body in locomotion, the propeller is generally represented by part of the corporal mass, such as the proboscis of a polychaete or muscular foot of a bivalve (deformable propeller).

Based on these elements, Trueman (1975) identified one universal mechanism: the double-anchor or push-and-pull mechanism (see Section 3.3.1), involving all soft-bodied invertebrates with a hydrostatic or fluid skeleton; in other words, all invertebrates with a body cavity containing incompressible fluid that functions as a hydraulic system. In such a system, a force generated by muscle contraction is transmitted to another region of the body where it may be used in locomotion. This soft-bodied group includes animals that are completely soft, such as most worms and sea anemones, and animals that utilize soft processes of the body to burrow, such as bivalves. A circular cross-section is ideally suited to penetrate and move through the substrate using the double-anchor mechanisms as the body wall is in contact with the substrate in all directions and muscles may contribute in locomotion without loss of anchorage. The body cavity used differs according to the phylum: coelenteron in Cnidaria, coelom in Annelida, and haemacoel in Mollusca (e.g. bivalves). Organisms with some rigid skeletal support (e.g. sea urchins, arthropods, and vertebrates) constitute a second group or organisms. Members of this functional group require an exo- or endoskeleton to allow muscular antagonism (e.g. flexor–extensor). These invertebrates with rigid skeleton, are unable to attain deformation of any soft part of the body and the propeller force is applied directly by muscles incepted in the inner zone of the exoskeleton.

3.4 MOVEMENT ECOLOGY

In recent years, movement ecology has been introduced in an attempt to generate a unifying paradigm for studying movement of all types of organisms within a broader framework (Nathan *et al.*, 2008). The approach undertaken consists of the formulation of basic principles to link empirical and theoretical movement studies. The four principles proposed aim to address the internal state (why move?), motion (how to move?), and navigation (when and where to move?) capacities of the individual, as well as the influence of external factors (Nathan *et al.*, 2008; Holyoak *et al.*, 2008). The internal state accounts for physiological and/or psychological motivations that determine why to move. This implies proximate (i.e. ecological), such as searching for food, avoiding a predator, and finding a mate, and ultimate (i.e. evolutionary), such as minimizing energy cost and surviving payoffs. Motion capacities reflect the biomechanical abilities to move, embracing the multiple modes of locomotion (e.g. push-and-pull, pacing) that determine how to move (see Section 3.3). Navigation capacities are displayed by mobile animals using their sensory and cognitive traits to obtain and process information about the environment, and to determine when and where to move. In doing so, animal movement includes interaction with the external environment, encompassing biotic factors (e.g. presence of resources, competitors, mates, predators) and abiotic factors (e.g. flow of water or air, presence of obstacles, light, oxygen).

Many of the previous proposals analyzed (see Sections 3.3.1 and 3.3.3) focused on the biomechanics of movement. The movement ecology paradigm complements other approaches to movement, such as those of the biomechanical, cognitive, random, and optimality paradigms. Of these, the optimality paradigm has a relatively strong tradition in ichnology (e.g. Raup and Seilacher, 1969; Papentin, 1973; Hammer, 1998; Hayes, 2003; Plotnick and Koy, 2005; Koy and Plotnick, 2007, 2010), while a few studies have adopted the perspective of the random paradigm (Kitchell *et al.*, 1978a; Kitchell, 1979; Hofmann, 1990). Ichnological studies are commonly framed within optimal foraging theory, which assumes that organisms are driven by a tendency to maximize net energy gained per unit of time feeding (e.g. Schoener, 1987). While foraging, animals are guided by a set of basic reactions, namely strophotaxis, phobotaxis, and thigmotaxis (Richter, 1928; Raup and Seilacher, 1969). Strophotaxis is a proclivity to make U-turns so that the animal turns around 180° at intervals. The length of the animal determines the geometry of the turn. Phobotaxis keeps the organism from crossing its own and other trails. Thigmotaxis makes the animal stay in close contact with a former trail. Based on these principles, computer simulations have been developed to reproduce foraging patterns (e.g. Raup and Seilacher, 1969; Hammer, 1998). Meandering and spiral trails can be understood as paths resulting from an organism's response to the perceived spatial distribution of resources (Koy and Plotnick, 2010). Neoichnological experiments have been recently designed to evaluate animal movements as a response to the location, shape, and density gradient of food patches (Koy and Plotnick, 2010). Optimal foraging theory considers that foraging patterns are intrinsically controlled by a series of commands written in the genetic code of the organism. However, more recent studies have emphasized that patchiness in resource distribution is a strong control on foraging movement and path morphology. Organisms interact with the environment using their sensory and cognitive traits (navigation capabilities) to explore the landscape and detect spatial heterogeneity (see Section 6.8).

More recently, there have been attempts to apply ideas derived from movement ecology to the study of the fossil record by introducing so-called "movement paleoecology" (Dornbos *et al.*, 2009; Plotnick, 2009). This approach may help to place ichnological studies into a broader theoretical framework, including both internal and external determinants of movement. Although the extrapolation of ecological frameworks to the fossil record always represents a challenge, adapting conceptual tools from ecology (e.g. the guild) has historically expanded the explanatory potential of ichnology. As in the case of the notion of complex trace fossils and extended organisms, movement paleoecology represents an approach that is worth exploring. Further work is needed in order to realize its potential, and to demonstrate how it can illuminate our understanding of the trace-fossil record.

4 The ichnofacies model

> Anyone can make the simple complicated. Creativity is making the complicated simple.
>
> Charles Mingus
>
> *Unsourced quote*

> Ichnofacies stand today as one of the most elegant but widely misunderstood concepts in ichnology.
>
> Robert Frey, George Pemberton, and Thomas Saunders
>
> "Ichnofacies and bathymetry: a passive relationship" (1990)

The ichnofacies model was introduced in a series of papers originally published in German by Seilacher (1954, 1955b, 1958, 1963b), and later expanded into English (Seilacher, 1964a, 1967b). In doing so, he created from a series of apparently disparate worldwide observations an elegant and coherent conceptual model. This body of work resulted in the first paradigm in ichnology, and transformed this field of research from a parochial discipline practiced by a few into a mainstream paleontological and geological science with a rich conceptual framework and multiple fruitful applications. Subsequently, the model was refined and expanded in a series of papers (e.g. Frey and Seilacher, 1980; Bromley *et al.*, 1984; Frey and Pemberton, 1984, 1985, 1987; Bromley, 1990, 1996; Pemberton *et al.*, 1992b; Bromley and Asgaard, 1993a; Lockley *et al.*, 1994; Buatois and Mángano, 1995b, 2009; Gibert *et al.*, 1998, 2007; Genise *et al.*, 2000, 2010a; Ekdale *et al.*, 2007; Hunt and Lucas, 2007; Minter and Braddy, 2009), remaining at the core of ichnology, both as a theoretical framework and as a tool. The aim of this chapter is to provide an updated review of the ichnofacies model, addressing not only marine softground and substrate-controlled ichnofacies, but also invertebrate and vertebrate continental ichnofacies. Vertebrate ichnofacies are still in flux and what is presented herein should be understood as a preliminary "state-of-the-art" rather than a consensus view on the matter.

4.1 THE ICHNOFACIES CONCEPT

In our definition (Box 1.1), Seilacherian or archetypal ichnofacies are conceptual constructs based on the identification of key features shared by different ichnocoenoses of a wide range of ages formed under a similar set of environmental conditions. A key component of any ichnofacies is their archetypal nature, being both individual ichnofacies and, at a different scale, the ichnofacies model, conceptual constructs. Ichnofacies is not simply a concept. The notion of ichnofacies itself involves a group of concepts that are linked and interrelated providing a new meaning. The elaboration of an ichnofacies involves two steps: (1) the distillation process or selection of key features (e.g. dominant ethologies, ichnodiversity levels, feeding strategies) within a representative sample of ichnocoenoses of different ages, and (2) the articulation of these key features with ecologic factors and depositional processes. Any potential ichnofacies should be based on a series of examples carefully selected from the ichnological record, rather than a mere list of theoretical assemblages or documentation of local examples.

Seilacherian archetypal ichnofacies should not be confused with and should not be replaced by ichnocoenoses (see Box 1.1). An ichnocoenosis refers to a group of biogenic structures that results from the work of a single community and, therefore, is a very different concept than ichnofacies, and is applicable to different scale analysis (Bromley, 1990, 1996). Occasionally, the term "ichnofacies" has been used at a different scale. For example, Lockley *et al.* (1987) introduced the *Curvolithus* ichnofacies, but specified that this may be better understood as a subdivision of the *Cruziana* ichnofacies (see also Bromley, 1990, 1996). Another related concept is ichnosubfacies, which has been used mostly in the context of deep-marine ichnofaunas (e.g. Uchman, 2009).

As noted by Pemberton *et al.* (1992b), the ichnofacies model is analogous to facies models and, accordingly, archetypal ichnofacies are produced through a "distillation" process that concentrates the diagnostic features of various ichnofaunas and eliminates the local peculiarities or the "noise" of the particular examples (Walker, 1984). As in the case of facies models, an ichnofacies serves as a norm for purposes of comparison, framework, and guide for future observations, predictor in new situations, and basis for interpretation. Of course, at a local scale, discrete ichnofacies may be subdivided into different assemblages with paleoecological and paleoenvironmental implications, integrating sedimentological and ichnological datasets (MacEachern *et al.*, 1999a; McIlroy, 2004a). In

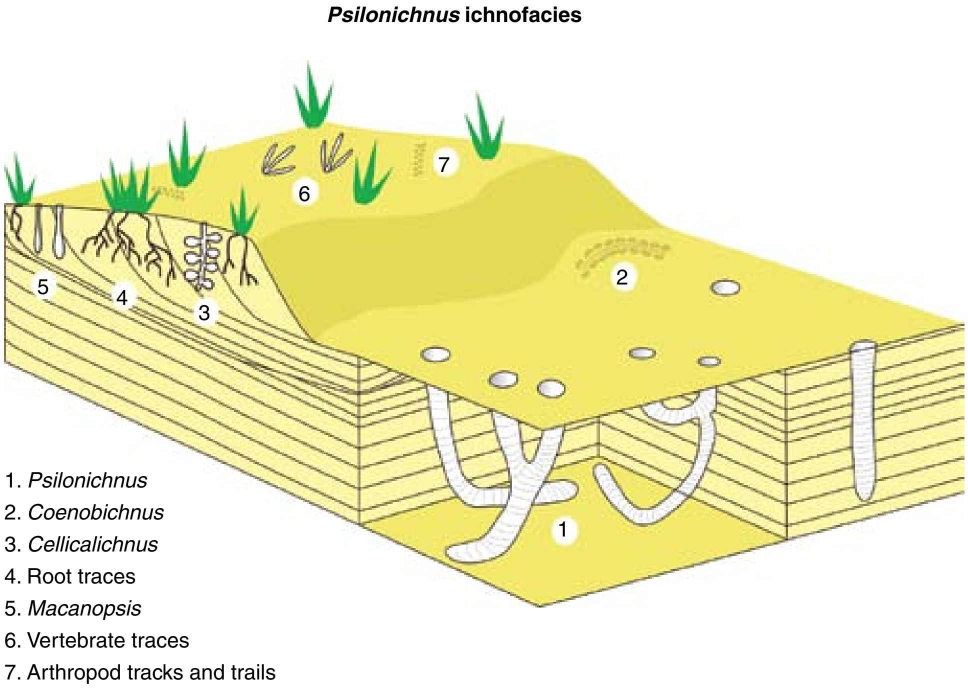

Figure 4.1 Schematic reconstruction of the *Psilonichnus* ichnofacies.

shallow-marine clastic successions, this approach has resulted in models of onshore–offshore ichnofacies gradients that have been extremely useful in refining environmental zonations (e.g. MacEachern *et al.*, 1999a). Similar subdivisions have been suggested for tide-dominated shorelines (Mángano and Buatois, 2004a). Additionally, the incorporation of concepts and methods derived from the ichnofabric approach, such as the recognition of the taphonomic factors involved in the shaping of particular ichnofacies (Bromley and Asgaard, 1991), should be taken into account to produce more robust models. Based on these ideas, Bromley and Asgaard (1991) noted that some ichnofacies are closely related to biofacies, while others are more akin to taphofacies.

Ichnofacies has been historically established based on invertebrate ichnotaxa. Exceptionally, vertebrate trace fossils, such as the fish trail *Undichna*, were noted as common in the freshwater *Mermia* ichnofacies (Buatois and Mángano, 1995b), and various vertebrate trackways are documented in the *Psilonichnus* and *Scoyenia* ichnofacies (e.g. Frey and Pemberton, 1986). More recently, attempts have been made to establish ichnofacies based on vertebrate trace fossils (Lockley *et al.*, 1994; Hunt and Lucas, 2007). Hunt and Lucas (2007) noted the existence of two traditions in ichnology, the ethological and the biotaxonomic. Invertebrate ichnologists mostly use an ethological approach characterized by naming structures based on the behavior represented. This is the most standard practice in ichnology. However, vertebrate ichnologists commonly apply a biotaxonomic approach, attempting to relate trackways to the taxonomy of the producer. Ichnologists working with insect trace fossils in paleosols represent a departure from this dichotomy because they commonly employ a taxonomic approach (e.g. Genise, 2004). Accordingly, Hunt and Lucas (2007) noted that invertebrate ichnofacies are ethoichnofacies, while vertebrate ichnofacies are biotaxonichnofacies. Ichnofacies fall broadly into four main categories: softground marine ichnofacies, substrate-controlled ichnofacies, continental invertebrate ichnofacies, and vertebrate ichnofacies. The rest of this chapter is mainly devoted to analyzing each of these ichnofacies.

4.2 SOFTGROUND MARINE ICHNOFACIES

Softground marine ichnofacies are probably the most traditional ichnofacies, and have been the focus of the majority of ichnological research until the recognition of the sequence-stratigraphic significance of substrate-controlled ichnofacies (Pemberton *et al.*, 1992b). Five archetypal softground marine ichnofacies are recognized at present: *Psilonichnus*, *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites*.

4.2.1 *PSILONICHNUS* ICHNOFACIES

The *Psilonichnus* ichnofacies is a subsequent addition to the set of Seilacherian ichnofacies, and was introduced by Frey and Pemberton (1987). This ichnofacies has been further explored in more recent papers (e.g. Nesbitt and Campbell, 2006; Netto and Grangeiro, 2009). It characterized by: (1) dominance of vertical J-, Y-, or U-shaped dwelling burrows produced by ghost crabs; (2) presence of small, unlined vertical dwelling burrows with bulbous basal cells produced by arachnids and insects; (3) local presence of vertebrate trackways and invertebrate trails and trackways; (4) root traces; (5) coprolites; (6) low ichnodiversity; and (7) low abundance (Fig. 4.1).

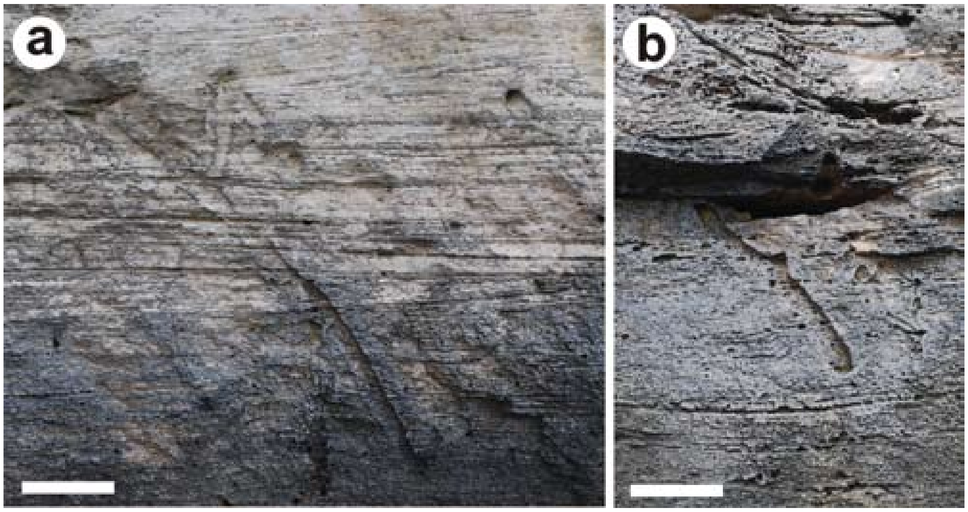

Figure 4.2 *Psilonichnus upsilon* in eolian calcarenites. Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay, San Salvador Island, Bahamas. (a) Holotype preserved. (b) Inclined shaft with partially preserved branching. All scale bars are 20 cm. See Curran (2007).

The most common component of this ichnofacies is, by far, the ichnogenus *Psilonichnus* (Fig. 4.2a–b), which is produced by ghost crabs of the family Ocypodidae and includes several ichnospecies (Frey *et al.*, 1984a; Frey and Pemberton, 1987; Mynt, 2001, 2007; Nesbitt and Campbell, 2002; Netto and Grangeiro, 2009). Arachnid and insect burrows are currently assigned to *Cylindricum* or *Skolithos*. Stellate nests of halictid bees (*Cellicalichnus*) may also occur (Curran and White, 2001; Curran, 2007). More rarely, trackways of land hermit crabs (*Coenobichnus*) are present (Walker *et al.*, 2003). There is a remarkable disparity between the relatively rich assemblages observed in modern environments, and the poorly diverse ichnofaunas preserved in the fossil record. Modern examples of the *Psilonichnus* ichnofacies contain incipient *Archaeonassa*, *Protovirgularia*, *Lockeia*, *Gordia*, and various trackways. Invertebrate tracemakers include gastropods, bivalves, worms and arthropods. Vertebrate structures include rodent and reptile burrows, and reptile, mammal, and avian trackways. All these invertebrate and vertebrate traces are rarely preserved in the fossil examples, clearly revealing very low preservation potential (MacEachern *et al.*, 2007a). Trophic types mostly include scavengers, deposit feeders, predators, and herbivores (Frey and Pemberton, 1987). Halophyte plants may occur in these coastal settings and are represented in the ichnological record by abundant root traces (Curran, 2007).

The *Psilonichnus* ichnofacies is linked to remarkable variations in energy, grain size, and salinity. In addition, it is associated with subaerial exposure, periodic influx of freshwater due to precipitation, and storm surges (Frey and Pemberton 1987). This ichnofacies indicates transitional conditions between marine and continental settings. According to MacEachern *et al.* (2007a), marine conditions usually prevail during spring tides and storms, while continental processes (mostly eolian) are dominant during neap tides and non-storm periods. In terms of specific depositional environments, the *Psilonichnus* ichnofacies is typical of coastal environments, both carbonate and clastic, including barrier islands, strand plains, delta plains, estuaries, lagoons, and bays. Within these settings it may be present in backshore areas, washover fans, coastal dunes and supratidal flats (Frey and Pemberton, 1987) (see Sections 7.1.1 and 11.1.1). Low diversity and abundance of trace fossils is related to the stressful conditions dominant in these environments, and to a taphonomic overprint resulting from low fossilization potential. Stressful conditions also promote the presence of opportunistic organisms, rather than climax faunas.

The *Psilonichnus* ichnofacies can be subdivided in landward and seaward associations. The landward association tends to be dominated by insect and arachnid burrows and nests, while the marine association is commonly monospecific and composed of *Psilonichnus* (Curran, 2007). The landward association grades towards the continent into freshwater and terrestrial ichnofacies, namely the *Scoyenia* ichnofacies and the *Coprinisphaera* or *Termitichnus* ichnofacies, depending on the nature of the plant formations in the coastal plain. In carbonate shorelines, the *Psilonichnus* ichnofacies grades into the *Celliforma* ichnofacies. The seaward association is replaced by the *Skolithos* ichnofacies in a seaward direction, this transition being relatively abrupt, at least as encountered in modern environments (Frey and Pemberton, 1987).

Due to its low diversity, recognition of the *Psilonichnus* ichnofacies is in practice, unfortunately, closely linked to the identification of the eponymous ichnogenus. This is complicated by the fact that ghost crabs and their burrows are unknown in pre-Cretaceous rocks. Therefore, recurrence of the *Psilonichnus* ichnofacies is much lower than that of the other marine softground ichnofacies and even of that of the freshwater ichnofacies.

4.2.2 *SKOLITHOS* ICHNOFACIES

The *Skolithos* ichnofacies is one of the original ichnofacies introduced by Seilacher (1963b, 1967b) as the *Skolithos* facies, and subsequently systematized in a series of papers (e.g. Frey and Seilacher, 1980; Frey and Pemberton, 1984, 1985). It is characterized by: (1) dominance of vertical, cylindrical, simple

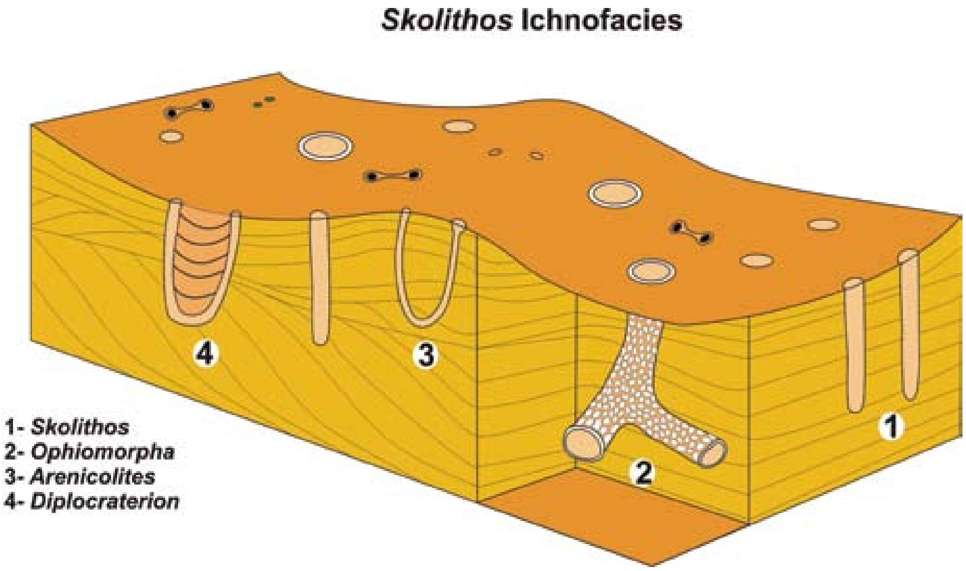

Figure 4.3 Schematic reconstruction of the *Skolithos* ichnofacies.

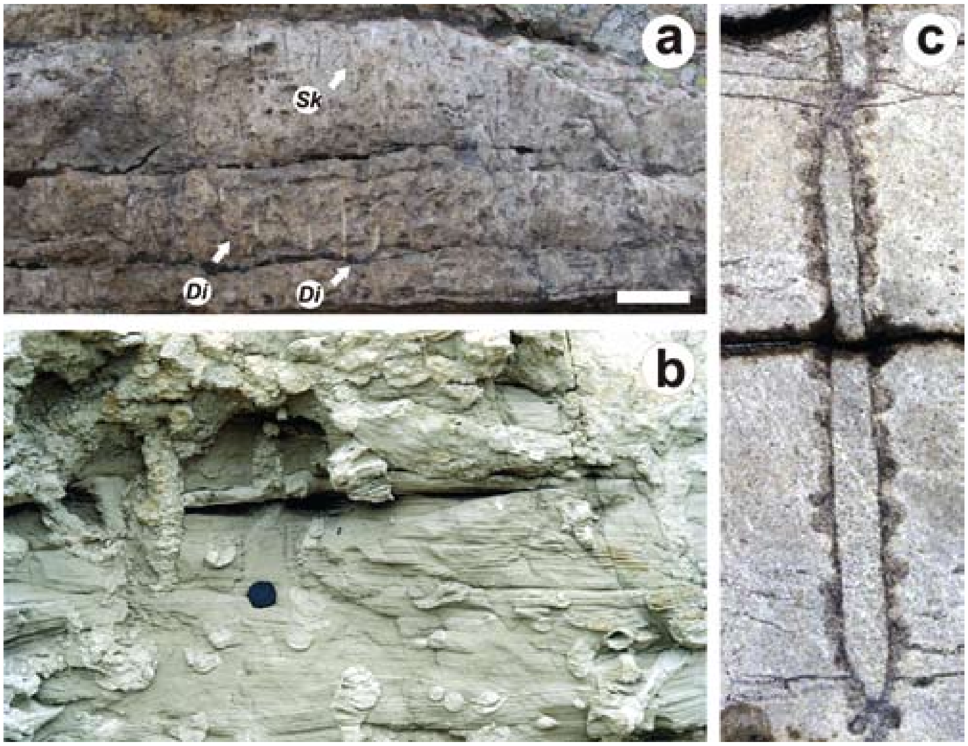

Figure 4.4 Examples of typical components of the *Skolithos* ichnofacies. Note dominance of vertical burrows and very low ichnodiversity. (a) Outcrop expression. *Skolithos linearis* (*Sk*) and *Diplocraterion parallelum* (*Di*). Lower Cambrian, Lake O'Hara Member, St. Piran Formation, Gog Group, Fairview Mountain, southern Canadian Rocky Mountains. Scale bar is 10 cm. See Desjardins *et al.* (2010a). (b) Outcrop expression. *Ophiomorpha borneensis*. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Scasso and Bellosi (2004). (c) Core expression. *Ophiomorpha nodosa*. Middle Eocene, Pauji Formation, Motatán Field, Maracaibo Basin, western Venezuela. Core width is 6 cm. See Delgado *et al.* (2001).

or U-shaped dwelling burrows of suspension feeders and passive predators; (2) presence of spreiten U-shaped equilibrium burrows and escape traces; (3) abundance of three-dimensional burrow systems dominated by vertical components; (4) scarcity of horizontal traces produced by a mobile fauna; (5) low ichnodiversity; and (6) variable abundance (Figs. 4.3 and 4.4a–c).

The most common ichnogenera of the *Skolithos* ichnofacies are *Skolithos*, *Ophiomorpha*, *Arenicolites*, and *Diplocraterion*. *Conichnus* and *Bergaueria* may occur locally. Typical producers are polychaetes, siphunculids, crustaceans, and sea anemones. Horizontal traces, although common in modern occurrences, are not preserved in fossil examples of the *Skolithos* ichnofacies, due to intense erosion that only allows preservation of deeper vertical burrows. Preservational bias reveals the importance of taphonomic factors in the final shaping of the ichnofacies (Bromley and Asgaard, 1991).

Dominance of vertical burrows of suspension feeders reveals high abundance of organic particles that are kept in suspension in the well-oxygenated water column by waves and currents. However, some U-shaped burrows commonly lacking spreite may be produced by a deposit-feeding infauna (Bromley, 1990, 1996). Other animals clearly display passive predation strategies seeking refuge within the burrow and preying on other organisms that are caught by the tentacles and carried to the mouth (Ruppert *et al*., 2004). Deep emplacement of most of these burrows suggests relatively high energy and intense erosion. Erosion is also revealed by the common presence of truncated burrows. Spreite in U-shaped burrows may be either protrusive or retrusive, and develop in response to substrate aggradation or degradation, representing equilibrium structures. Under conditions of episodic sedimentation, escape traces develop. The predominance of vertical components over horizontal components indicates relatively high energy (Howard and Frey, 1984; Anderson and Droser, 1998). Burrows are permanent domiciles, which are lined to preclude collapse in shifting and soft sandy substrates that serve mainly as anchoring media (MacEachern *et al*., 2007a). Low ichnodiversity, typically monospecific occurrences, reflects stressful conditions related to relatively high energy. Trace-fossil abundance is highly variable. Some deposits containing the *Skolithos* ichnofacies are sparsely bioturbated revealing short-term colonization windows. In contrast, other deposits are pervasively bioturbated forming *Skolithos* pipe rock (Droser, 1991; Desjardins *et al*., 2010a).

In terms of depositional settings, the *Skolithos* ichnofacies is typical of foreshore to upper- and middle-shoreface environments of wave-dominated shorelines. In these wave-dominated systems, the *Skolithos* ichnofacies grades seawards into the *Cruziana* ichnofacies (see Section 7.1). However, similar conditions to that of nearshore settings also occur in a wide variety of sedimentary environments. Also in wave-dominated clastic environments, the *Skolithos* ichnofacies may be present displaying post-depositional suites in tempestites emplaced in deeper positions, typically lower shoreface to lower offshore, where they record opportunistic colonization of sandy substrates (e.g. Vossler and Pemberton, 1988). In the case of tide-dominated shorelines, the *Skolithos* ichnofacies typically occur in subtidal sandbars to lower-intertidal sand flats depending of the tidal regime and, therefore, grade landwards into the *Cruziana* ichnofacies (Mángano and Buatois, 1999b, 2004a) (see Section 7.2). The *Skolithos* ichnofacies may also occur in numerous marginal-marine environments, commonly in areas of moderately high energy, such as delta fronts, sandy bars and spits, tidal inlets, flood and ebb tidal deltas, sandy bay margins, estuary-mouth complexes, and bay-head deltas (MacEachern *et al*., 2007a). However, these settings are usually associated with additional stress conditions due to salinity fluctuations and water turbidity and, therefore, the *Skolithos* ichnofacies displays even lower diversity than in their fully marine counterparts (see Chapter 8). The *Skolithos* ichnofacies is also present in deep-marine turbidite systems, commonly in channels and lobes of proximal to middle areas which are characterized by high energy, shifting sandy substrates, rapid deposition, high erosion, and good oxygenation, therefore mimicking conditions in shallow-marine zones (Crimes, 1977) (see Section 9.2). However, typical shallow-water forms (e.g. *Ophiomorpha, Skolithos*) are not restricted to the most proximal zones of deep-sea systems, but also occur in distal zones, if these are affected by turbidity currents (Uchman, 1991a). The presence of simple and U-shaped burrows in high-energy sites of continental systems, such as fluvial channels and lacustrine deltaic mouth bars, may indicate that the *Skolithos* ichnofacies also occurs in freshwater settings (Buatois and Mángano, 1998, 2004a) (see Sections 10.2 and 10.3). The broad spectrum of depositional environments in which the *Skolithos* ichnofacies may occur reflects the opportunistic nature of this ichnofacies.

The *Skolithos* ichnofacies may be subdivided in order to refine paleoenvironmental zonations. Bromley and Asgaard (1991) have even suggested the possibility of distinguishing two different ichnofacies. In this scheme, the *Skolithos* ichnofacies characterizes fair-weather conditions in nearshore, continuously agitated waters, while the *Arenicolites* ichnofacies is typical of opportunistic colonization of episodic sandstone beds (tempestites and turbidites). However, it has been noted that the archetypal *Skolithos* ichnofacies can accommodate this variability (Pemberton *et al*., 1992d; 2001; Goldring, 1993). MacEachern *et al*. (2007a) suggested subdivisions of the *Skolithos* ichnofacies according to proximal–distal trends. These authors indicated that while the archetypal *Skolithos* ichnofacies characterizes proximal environments, a distal expression can also be recognized. Although still dominated by suspension burrows, the distal *Skolithos* ichnofacies includes some structures produced by detritus and deposit feeders (e.g. *Cylindrichnus*, *Rosselia*). Within this framework, the distal *Skolithos* ichnofacies is considered intergradational with proximal expressions of the *Cruziana* ichnofacies in wave-dominated settings. Under conditions of very high energy, such as those typical of the foreshore and upper shoreface in wave-agitated beaches, the archetypal *Skolithos* ichnofacies is replaced by an assemblage dominated by the ichnogenus *Macaronichnus* (Pemberton *et al*., 2001) (see Section 7.1.2). Furthermore, distinction between shallow and deep occurrences of the *Skolithos* ichnofacies may be possible. Ongoing studies suggest that taxonomic assignments at ichnospecific level may help to distinguish the composition of the *Skolithos* ichnofacies in shallow- and deep-marine environments.

The *Skolithos* ichnofacies is known since the Cambrian, although it is not present in earliest Cambrian rocks (Mángano and Buatois, 2007). This ichnofacies has experienced variations in taxonomic composition through the Phanerozoic. The most notable one is the common replacement of *Skolithos* by *Ophiomorpha* as the dominant form in post-Paleozoic occurrences, probably reflecting the Mesozoic radiation of decapod crustaceans (Carmona *et al*., 2004).

4.2.3 *CRUZIANA* ICHNOFACIES

The *Cruziana* ichnofacies originated from recurrent trace-fossil assemblages observed by Seilacher (1954, 1955b, 1958) in what were called molasse deposits, and was subsequently referred to as the *Cruziana* facies of the original ichnofacies model (e.g. Seilacher, 1963b, 1964a, 1967b). More formal definitions were provided by Frey and Seilacher (1980), and Frey and Pemberton (1984, 1985). It is characterized by: (1) dominance of horizontal

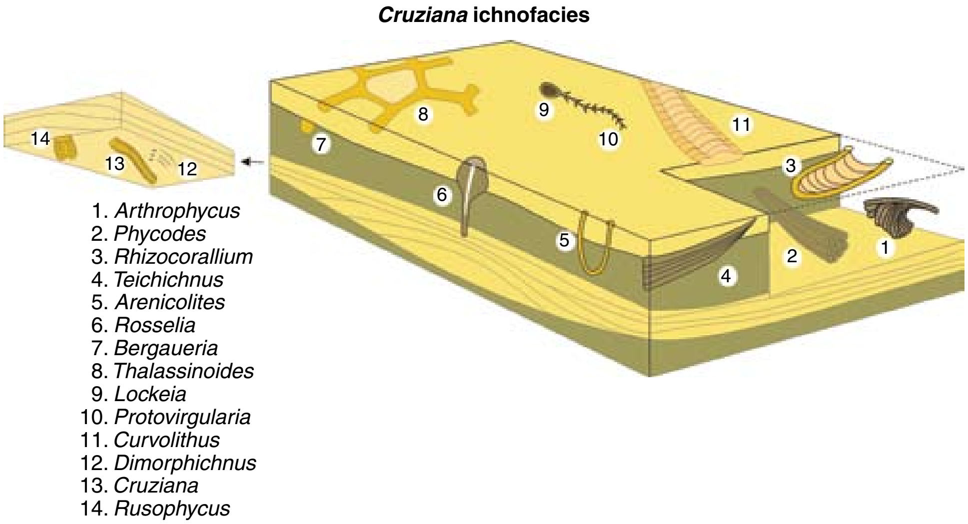

Figure 4.5 Schematic reconstruction of the *Cruziana* ichnofacies.

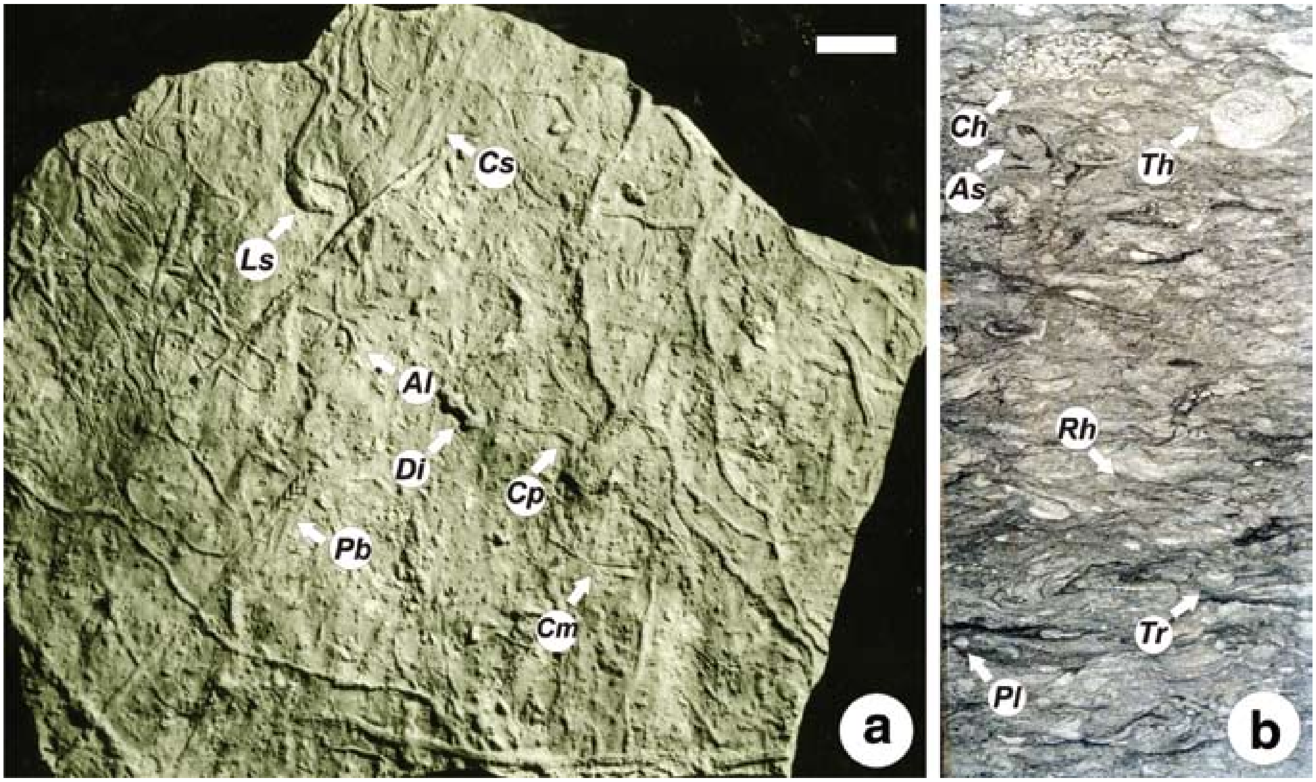

Figure 4.6 Examples of the *Cruziana* ichnofacies. Note dominance of horizontal structures and high ichnodiversity. (a) Outcrop expression. Base of sandstone slab containing *Curvolithus simplex* (*Cs*), *Curvolithus multiplex* (*Cm*), *Lockeia siliquaria* (*Ls*), *Diplocraterion* isp. (*Di*), *Asteriacites lumbricalis* (*Al*), *Cruziana problematica* (*Cp*), *Protovirgularia bidirectionalis* (*Pb*). Upper Pennsylvanian, Stull Shale Member, Kanwaka Shale Formation, Shawnee Group, Waverly, eastern Kansas, United States. Scale bar is 5 cm. See Mángano and Buatois (2004b). (b) Core expression. *Chondrites* isp. (*Ch*), *Thalassinoides* isp. (*Th*), *Teichichnus rectus* (*Tr*), *Planolites* isp. (*Pl*), *Asterosoma* isp. (*As*) and *Rhizocorallium* isp. (*Rh*). *Chondrites* is locally reworking *Thalassinoides* burrow fills. Upper Cretaceous, Napo Formation, Auca Field, Oriente Basin, northeast Ecuador. Core width is 8 cm.

traces and subordinate presence of vertical and inclined structures; (2) a wide variety of ethological categories, including locomotion, feeding, resting, dwelling, and grazing traces; (3) dominance of deposit and detritus feeding traces, although suspension feeding and predation are also involved; (4) dominance of traces produced by a mobile fauna and subordinate presence of permanent domiciles; (5) high ichnodiversity; and (6) high abundance (Figs. 4.5 and 4.6a–b).

The most common elements of the *Cruziana* ichnofacies are various types of locomotion, resting, feeding, dwelling, and grazing traces. Locomotion trails include *Cruziana*, *Didymaulichnus*, *Protovirgularia*, *Archaeonassa*, *Gyrochorte*, and *Curvolithus*, while *Diplichnites*, *Dimorphichnus*, and *Monomorphichnus* represent examples of trackways. Resting traces are illustrated by *Rusophycus*, *Asteriacites*, and *Lockeia*. Feeding structures may include inclined to horizontal U-shaped traces, such as *Rhizocorallium*, and other structures of variable complexity, such as *Phycodes*, *Heimdallia*, *Arthrophycus*, *Teichichnus*, *Phoebichnus, Phycosiphon*, and *Asterosoma*. Dwelling-burrow systems are mostly represented by the facies-crossing ichnogenus *Palaeophycus* and by *Ophiomorpha* and *Thalassinoides* displaying dominance of horizontal to inclined components. Vertical cylindrical burrows, such as *Rosselia*, *Cylindrichnus*, and *Schaubcylindrichnus*, may be present but are rarely dominant. Nonspecialized simple grazing trails (e.g. *Helminthoidichnites*, *Gordia*, *Helminthopsis*) may occur also.

Producers are extremely variable, reflecting the abundance and diversity of benthic fauna, and include arthropods, mollusks (mostly bivalves and gastropods), echinoderms (ophiuroids and echinoids), and many different types of worm-like animals (e.g. polychaetes). The *Cruziana* ichnofacies not only includes deep-tier structures but traces emplaced close to the sediment–water interface. The overall aspect of the assemblage varies according to the degree of maturity reached by the community that controls the degree of bioturbation and burrowing depth (Bromley and Asgaard, 1991; Bromley, 1990, 1996).

Dominance of horizontal structures produced by a mobile fauna reflects accumulation of organic detritus in the sediment under moderate- to low-energy conditions. Associated substrates vary from silty to sandy, and are represented by interbedded layers of sandstone and siltstone forming heterolithic successions. Preservation of horizontal trace fossils is favored by the presence of these sandstone–mudstone interfaces. Lack of lithological contrast usually inhibits preservation and visibility of biogenic structures. The variable ethologies and trophic types represented, and the high diversity and abundance of biogenic structures commonly reflect overall environmental stability and low to moderate sedimentation rates. However, episodic sedimentation (i.e. storms) may punctuate fair-weather conditions, leading to ichnofaunal turnovers.

Environmentally, this ichnofacies occurs from slightly above the fair-weather wave base to the storm wave base, in a zone ranging from the lower shoreface to the lower offshore in wave-dominated seas (MacEachern and Pemberton, 1992; MacEachern *et al*., 1999a) (see Section 7.1). Conversely, in tide-dominated shorelines the *Cruziana* ichnofacies occurs landward of the *Skolithos* ichnofacies, broadly between high and low tide, albeit depending on tidal regime (Mángano and Buatois, 2004a) (see Section 7.2). The *Cruziana* ichnofacies also occurs in protected areas of marginal-marine, brackish-water environments, such as estuarine basins, bays, and lagoons. However, stressful conditions in these restricted settings dramatically reduced overall diversity, resulting in impoverished assemblages (MacEachern and Pemberton, 1994) (see Chapter 8).

Subdivisions of the *Cruziana* ichnofacies have been proposed in a series of studies by MacEachern *et al*. (1999a, 2007a). While the archetypal *Cruziana* ichnofacies characterizes the upper offshore to offshore transition, proximal and distal expressions are typical of the lower shoreface and the lower offshore, respectively. The proximal *Cruziana* ichnofacies is transitional with the *Skolithos* ichnofacies. Accordingly, although assemblages are dominated by deposit-feeding structures, they contain large numbers of dwelling traces of suspension feeders and passive predators. Distal expressions of the *Cruziana* ichnofacies are transitional with the *Zoophycos* ichnofacies. Assemblages of the distal *Cruziana* ichnofacies contain significant numbers of grazing trails and specialized feeding traces. *Phycosiphon*, *Helminthopsis*, *Chondrites*, *Zoophycos*, and *Planolites* tend to dominate.

The *Cruziana* ichnofacies is known since the Cambrian. However, an incipient *Cruziana* ichnofacies occurs in Ediacaran rocks, but is poorly diverse and dominated by grazing trails. The *Cruziana* ichnofacies has experienced remarkable evolutionary changes through the Phanerozoic, mostly reflecting faunal replacements and an increase in burrowing depth and extent of bioturbation (see Section 14.2.1).

4.2.4 *ZOOPHYCOS* ICHNOFACIES

The *Zoophycos* ichnofacies, one of the original ichnofacies proposed in the Seilacherian model, was formerly referred to as the *Zoophycos* facies. It has subsequently been systematized in different studies (e.g. Frey and Seilacher, 1980; Frey and Pemberton, 1984, 1985; Bromley, 1990, 1996). It is characterized by: (1) dominance of relatively simple to complex feeding structures with spreite; (2) subordinate occurrence of grazing traces; (3) dominance of deep-tier structures of deposit feeders or farmers; (4) low ichnodiversity; and (5) high abundance (Fig. 4.7).

Zoophycos is the typical ichnogenus, but *Phycosiphon*, *Chondrites*, and certain ichnospecies of *Nereites* (notably *N. missouriensis*, previously referred to as *Scalarituba*) are present also. In fact, Frey and Pemberton (1984) noted that replacement of *Zoophycos* by *Phycosiphon* as the dominant ichnogenus is common. In many instances, the presence of the *Zoophycos* ichnofacies is recorded by monospecific occurrences of the ichnogenus itself. The inferred producers of *Zoophycos* are echiuran worms (Kotake, 1992). Other tracemakers in this ichnofacies include different types of worm-like animals, such as enteropneusts and polychaetes. Ethologically, *Zoophycos* was originally considered the feeding trace of a deposit-feeding organism (Seilacher, 1967a). However, more recently it has been regarded as reflecting bacterial farming (Bromley, 1991; Fu and Werner, 1995).

The *Zoophycos* ichnofacies is in all probability the most problematic of all archetypal ichnofacies, and has been dubbed "the black sheep of the family of marine softground ichnofacies" by Bromley (1990, 1996). Most of the complications result from the fact that recognition of this ichnofacies is, in practice, too dependent on the identification of *Zoophycos* itself. Therefore, uncertainties in the ethological interpretation of *Zoophycos* complicate evaluation of the paleoecological significance of the ichnofacies. The classical interpretation is that the *Zoophycos*

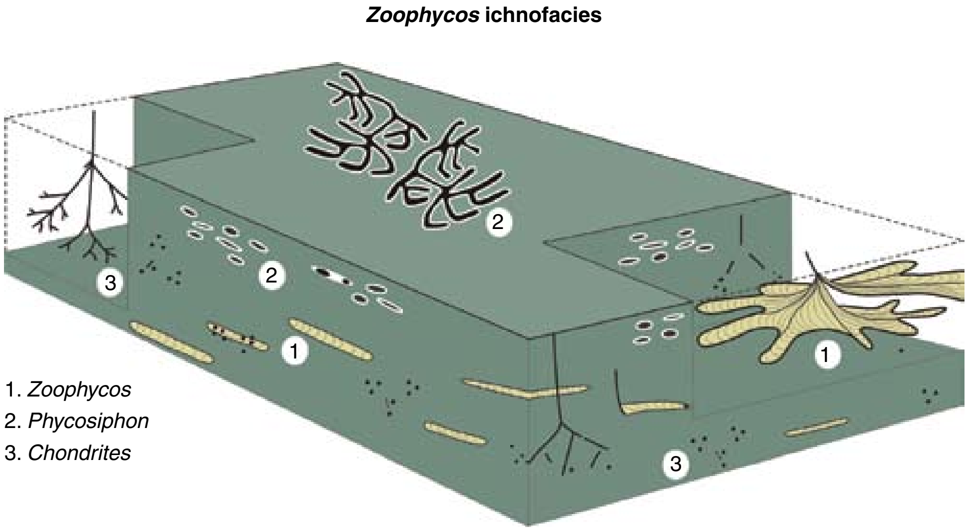

Figure 4.7 Schematic reconstruction of the *Zoophycos* ichnofacies.

ichnofacies is linked to poor oxygenation (e.g. Frey and Seilacher, 1980; Frey and Pemberton, 1984, 1985). According to this view, the ichnogenus *Zoophycos* and other members of the ichnofacies are seen as the product of opportunistic organisms (Ekdale, 1985; M. Miller, 1991). Subsequently, other authors noted that the *Zoophycos* ichnofacies is dominated by deep-tier structures in intensely bioturbated substrates that result from the activity of climax communities (Bromley and Asgaard, 1991; Bromley, 1990, 1996). Furthermore, complexity and downward increase in size of some specimens of *Zoophycos* seem to be inconsistent with its interpretation as the product of opportunistic organisms and, in contrast, indicate "once in a lifetime" construction (Bromley, 1990, 1996). *Zoophycos* and *Chondrites* penetrate deeply into the substrate in oxygen-depleted sediment, but this does not necessarily indicate poor oxygenation in bottom waters. Intense bioturbation also argues against oxygen depletion. Also, it was originally thought that the *Zoophycos* ichnofacies occurs in areas free of turbidity currents (Seilacher, 1967b). This is supported by the fact that typically the *Zoophycos* ichnofacies occurs in silt and clay substrates that slowly and continuously accumulate due to suspension fallout, allowing intense levels of bioturbation (MacEachern *et al.*, 2007a). However, it has been also recognized in sandy substrates deposited by turbidity currents and debris flows in slope environments, albeit with traces emplaced during times of background sedimentation (Buatois and Mángano, 1992). It has also been proposed that the *Zoophycos* ichnofacies is present in organic-rich substrates under conditions of abundant food supply that may have inhibited development of the *Nereites* ichnofacies (D'Alessandro *et al.*, 1986; Buatois and López Angriman, 1992b). However, this interpretation only seems to work if *Zoophycos* and the associated components of the ichnofacies represent the work of deposit feeders rather than microbial farmers.

Another problem derives from the fact that *Zoophycos* has a broad paleobathymetric range. MacEachern *et al.* (2007a) concluded that such a widespread environmental range suggests that the *Zoophycos* animal tolerates a considerable range of water depths, substrate types, food resources, energy levels, and oxygen content. To complicate matters further, *Zoophycos* experienced an onshore–offshore migration throughout the Phanerozoic (Bottjer *et al.*, 1988). Because *Zoophycos* is very common in Paleozoic shallow-marine rocks, recognition of the ichnofacies in deposits of this age may become problematic, and some authors have even suggested that the utility of this ichnofacies is very limited in Paleozoic strata (M. Miller, 1991).

In the original model proposed by Seilacher (1964a, 1967b), the *Zoophycos* ichnofacies occurs between the *Cruziana* and *Nereites* ichnofacies. Environmentally, it characterizes quiet-water settings below the storm wave base, particularly in shelfal to slope areas (see Sections 7.1.9 and 9.1). However, it may occur at shallower and deeper water. Shallow-water occurrences are common in Paleozoic epeiric seas (Marintsch and Finks 1982; Frey and Pemberton, 1984), while deep-marine examples are more typical of post-Paleozoic mudstone that characterizes interturbidite times (Wetzel, 1984). According to MacEachern *et al.* (2007a), the *Zoophycos* animal was able to compete successfully with the diverse benthic fauna associated with the *Cruziana* and *Nereites* ichnofacies, but few other organisms were able to compete with *Zoophycos* in oxygen-depleted environments. Therefore, *Zoophycos* tends to be dominant in shelf and slope environments. The *Zoophycos* ichnofacies is known since the Ordovician, although it is well established in shelf and slope areas by the Silurian (Bottjer *et al.*, 1988).

4.2.5 *NEREITES* ICHNOFACIES

The *Nereites* ichnofacies originated from recurrent trace-fossil assemblages that Seilacher (1954, 1958) documented from what were referred to as flysch deposits. These examples form the basis of what was subsequently named the *Nereites* facies (e.g. Seilacher, 1963b, 1964a, 1967b) of his original ichnofacies model. A more systematic treatment and formal definitions were subsequently provided by Frey and Seilacher (1980) and Frey and Pemberton (1984, 1985). It is characterized by: (1) dominance of complex graphoglyptids produced by animals that farm bacteria and trap microorganisms; (2) presence of sophisticated grazing trails and

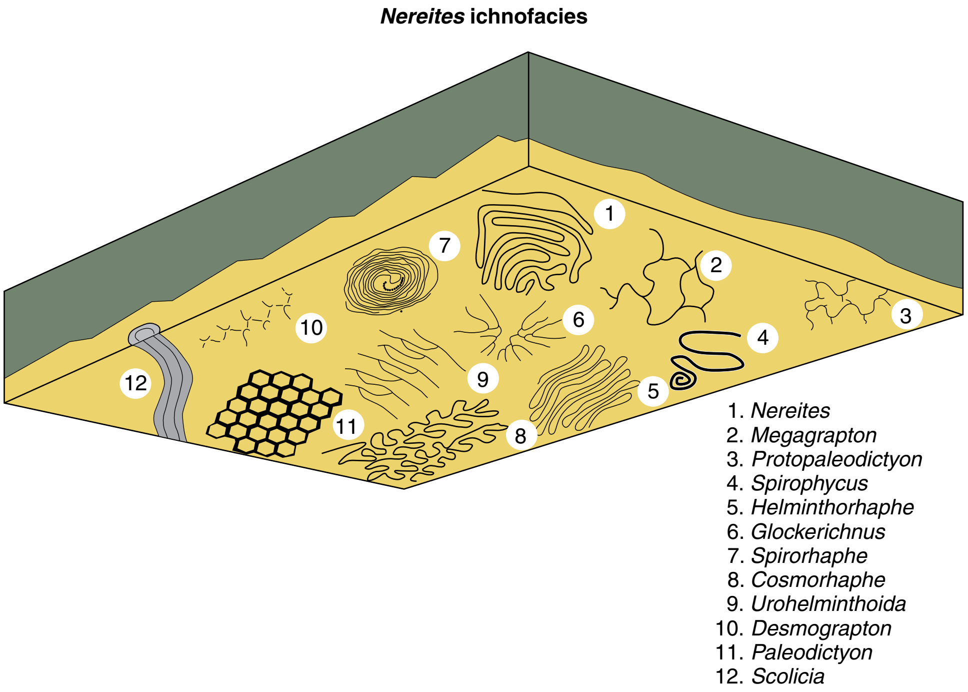

Figure 4.8 Schematic reconstruction of the *Nereites* ichnofacies.

feeding traces of detritus and deposit feeders; (3) dominance of shallow-tier trace fossils; (4) very high ichnodiversity; and (5) high abundance, but low density, of individual ichnotaxa (Fig. 4.8).

Graphoglyptids are arguably the diagnostic components of the ichnofacies. Typical graphoglyptid ichnogenera are *Paleodictyon*, *Protopaleodictyon*, *Spirorhaphe*, *Urohelminthoida*, *Desmograpton*, *Megagrapton, Acanthorhaphe, Helicolithus*, *Belorhaphe*, *Spirocosmorhaphe*, and *Paleomeandron*. Grazing trails are represented by guided meandering traces, such as highly specialized ichnospecies of *Nereites* and *Scolicia*. *Helminthorhaphe* and *Cosmorhaphe* may either represent grazing trails or graphoglyptids. Feeding traces include radial structures (*Glockerichnus*, *Lorenzinia*, *Capodistria*), branched systems (*Polykampton*, some ichnospecies of *Treptichnus*) and simpler forms (*Halopoa*, *Fustiglyphus*, *Circulichnis*). Resting traces are relatively rare and mostly represented by the ichnogenus *Cardioichnus*, which commonly intergrades with *Scolicia*.

Although the *Nereites* ichnofacies is clearly dominated by shallow-tier traces, the presence of complex structures and the high ichnodiversity indicate the activity of climax communities with enough time to develop specialized and varied behavioral patterns (Seilacher, 1977a; W. Miller, 1991a). This is only possible under very stable environmental conditions in an overall low-energy, well-oxygenated setting. In addition, the presence of sophisticated feeding strategies suggests scarce food resources. In the case of delta-fed turbidity systems, the *Nereites* ichnofacies has been reported to occur in organic-rich deposits (Fürsich *et al*., 2007; Olivero *et al*., 2010). These occurrences either reflect that oligotrophy is not a limited factor in graphoglyptid distribution (Fürsich *et al*., 2007) or that trophic resources fluctuate, with graphoglyptids colonizing the sea bottom during times of oligotrophy (Olivero *et al*., 2010).

The benthic community associated with the *Nereites* ichnofacies typically flourishes in environments characterized by slow, continuous suspension fallout deposition of silt and clay. However, distinctive elements of the *Nereites* ichnofacies are typically preserved as positive hyporeliefs on the base of sandstone turbidites. While graphoglyptids of the *Nereites* ichnofacies reflect the activity of a benthic fauna developed in muddy, low-energy substrates, their preservation is linked to turbidity currents that punctuate fallout of fine-grained sediment (Seilacher, 1962, 1977a). The standard explanation is that turbidity currents erode the uppermost millimeters of the substrate and cast with sand the shallowly emplaced biogenic structures. More recently, Seilacher (2007a) proposed that the excellent preservation of these delicate traces is due to a shock wave immediately prior to deposition that sucks the unconsolidated mud into suspension without significant erosion. In either case, preservation of graphoglyptids can only take place in zones affected by turbidity currents. In the absence of event sedimentation, the activity of the deep-tier bioturbators would have destroyed all the shallowly emplaced traces (Bromley and Asgaard, 1991). In fact, biogenic structures similar to those in the *Nereites* ichnofacies have been observed in modern abyssal plains in areas beyond the reach of turbidity currents (Hollister *et al*., 1975; Ekdale and Berger, 1978; Kitchell *et al*., 1978b; Ekdale, 1980; Gaillard, 1991). However, pelagic deposits are characterized in the fossil record by intensely mottled textures and a few discrete traces, such as *Zoophycos*, *Planolites*, and *Teichichnus* (Ekdale, 1977; Ekdale and Berger, 1978). Ekdale and Berger (1978) suggested the existence of an abyssal or deep-sea ichnofacies that occupies deeper settings than the *Nereites* ichnofacies, although the absence of discrete trace fossils in these sediments complicates further characterization of this potential ichnofacies (see Section 9.4).

The *Nereites* ichnofacies is arguably the one that displays the closest links with a certain bathymetry. It occurs in base-of-slope turbidity systems and is particularly common in thin-bedded turbidites that accumulate in the fringe of terminal splays, crevasse splays and levees (see Section 9.2.1). Potential occurrences in shallower settings await further documentation (Gierlowski-Kordesch and Ernst, 1987; Ernst and Gierlowski-Kordesch, 1989; Ting *et al*., 1991). However, the ichnogenus *Paleodictyon*, a typical component of the *Nereites* ichnofacies, has been documented in shallow-water prodelta turbidites (Fürsich *et al*., 2007). In addition, it has been demonstrated that the *Nereites* ichnofacies may extend into sub-neritic environments during rapid shallowing (Uchman *et al*., 2004a) and relatively shallow-water delta-fed turbidite systems (Olivero *et al*., 2010).

The *Nereites* ichnofacies was subdivided by Seilacher (1974) into the *Nereites* and *Paleodictyon* ichnosubfacies. The *Nereites* ichnosubfacies typifies the most distal parts of the turbidite systems characterized by very thin intercalations of turbidite sandstone and background mudstone. This ichnosubfacies is dominated by backfilled trace fossils of deposit feeders, such as *Nereites*, *Phycosiphon*, *Dictyodora*, and *Zoophycos*. According to Seilacher (1974), the *Paleodictyon* ichnosubfacies tends to occur in slightly more proximal settings where turbidite sandstones weather out as resistant beds with graphoglyptids (e.g. *Paleodictyon*, *Helicolithus*, *Urohelminthoida*, *Desmograpton*) preserved at the base. Although proximality trends may be established, local factors play a key role in controlling distribution of these two ichnosubfacies, with food supply probably being a limiting factor (Wetzel and Uchman, 1998). More recent research has suggested the existence of a third ichnosubfacies, the *Ophiomorpha rudis* ichnosubfacies, which consists of a few ichnotaxa, typically *Ophiomorpha rudis*, *O. annulata*, and *Scolicia*, and less commonly, *Nereites irregularis*, *Chondrites*, and a few graphoglyptids (Uchman, 2009). This ichnosubfacies occurs in channel and proximal-lobe deposits (see Section 9.2).

The *Nereites* ichnofacies is known since the Ordovician. Cambrian deep-marine ichnofaunas are remarkably different from their younger counterparts, and deviate from the basic features of the *Nereites* ichnofacies (Orr, 2001, Buatois and Mángano, 2003a). Furthermore, the *Nereites* ichnofacies has experienced numerous changes through the Phanerozoic, including progressive size decrease of its components, increase in diversity and increase in the degree of complexity of some of the trace fossils (Seilacher, 1974, 1977a; Uchman, 2003, 2004a) (see Section 14.2.2).

4.3 SUBSTRATE-CONTROLLED ICHNOFACIES

Substrate-controlled ichnofacies have received a lot of attention during the last two decades after the realization that they are very useful to delineate surfaces with sequence-stratigraphic implications (MacEachern *et al*., 1992; Pemberton *et al*., 1992b, 2004) (see Chapter 12). Four substrate-controlled ichnofacies are regarded here as valid: *Glossifungites*, *Trypanites*, *Gnathichnus*, and *Teredolites*.

4.3.1 *GLOSSIFUNGITES* ICHNOFACIES

The *Glossifungites* ichnofacies was originally proposed by Seilacher (1967b), subsequently redefined by Frey and Seilacher (1980) and, more recently, reviewed in a number of papers, mostly in the context of its sequence-stratigraphic implications (Pemberton and Frey, 1985; MacEachern *et al*., 1992, 2007a; Pemberton *et al*., 1992b, 2001, 2004). It is characterized by: (1) sharp-walled, unlined, passively filled, dwelling burrows of suspension feeders or passive predators; (2) dominance of robust, vertical to subvertical, simple and spreite U-shaped burrows; (3) presence of branched burrow systems; (4) presence of burrows with ornamented walls; (5) low ichnodiversity; and (6) high abundance (Figs. 4.9 and 4.10a–c).

The most common ichnotaxa in this ichnofacies correspond to the ichnogenera *Diplocraterion*, *Skolithos*, *Arenicolites*, *Gastrochaenolites*, *Thalassinoides*, *Spongeliomorpha*, and *Rhizocorallium*. More rarely, the ichnogenera *Fuersichnus* and *Zoophycos* have been recognized to occur in the *Glossifungites* ichnofacies (Buatois, 1995; MacEachern and Burton 2000). Ironically, the eponymous ichnogenus is a junior synonym of *Rhizocorallium* (Uchman *et al*., 2000). Firmground burrowers include various bivalves, crustaceans, nemerteans, and polychaetes (Pemberton and Frey, 1985; Gingras *et al*., 2001) (Box 4.1).

The *Glossifungites* ichnofacies develops in stable and cohesive substrates (firmgrounds), commonly dewatered muds, and, more rarely, highly compacted sands (MacEachern *et al*., 1992, 2007a; Pemberton *et al*., 1992b, 2004). The presence of vertical, unlined shafts penetrating into fine-grained intervals reflects the cohesiveness of the substrate. Additional evidence of substrate stability at the time of excavation is provided by the passive burrow fill and the presence of walls ornamented with striations, as commonly revealed by *Spongeliomorpha*, *Rhizocorallium*, *Fuersichnus*, *Diplocraterion*, and *Gastrochaenolites*. Passive burrow fills reflect colonization by suspension feeders or passive predators that construct open domiciles, which are subsequently filled by sedimentation. Other animals, such as crabs, may leave their burrows in search for food (Pemberton *et al*., 1992b). Trace fossils of deposit feeders are typically absent in this ichnofacies because nutritious particles are scarce in compacted muds. However, corkscrew burrows similar to *Gyrolithes* have been recorded (Netto *et al*., 2007). Although ichnodiversity is commonly relatively low, the abundance of trace fossils is high in the *Glossifungites* ichnofacies. In modern examples, densities of approximately 150 specimens/m^2 have been documented (Gingras *et al*., 2001). Even higher densities have been estimated in cores and outcrops (Pemberton *et al*., 2004; Buatois and Encinas, 2006).

In siliciclastic deposits, the *Glossifungites* ichnofacies is typically associated with erosional exhumation of previously buried sediments, more commonly linked to relative sea-level changes, although autogenic erosional processes may be also responsible (see Section 12.8; MacEachern *et al*., 1992, 2007a; Pemberton *et al*., 2004). Colonization of these firmground substrates occurs during a depositional hiatus that takes place between the erosional event and sedimentation of the overlying

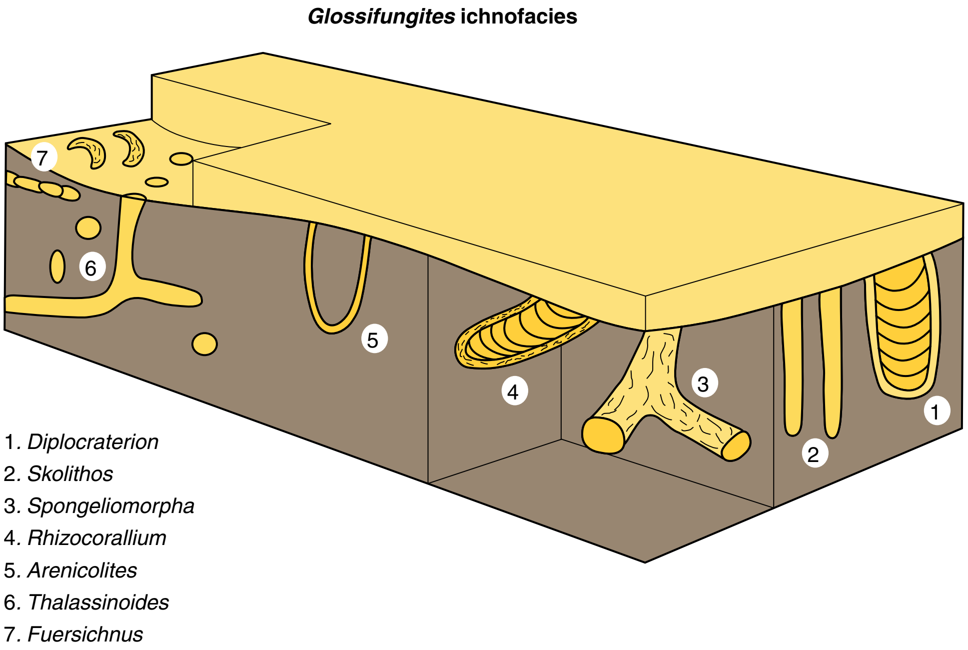

Figure 4.9 Schematic reconstruction of the *Glossifungites* ichnofacies.

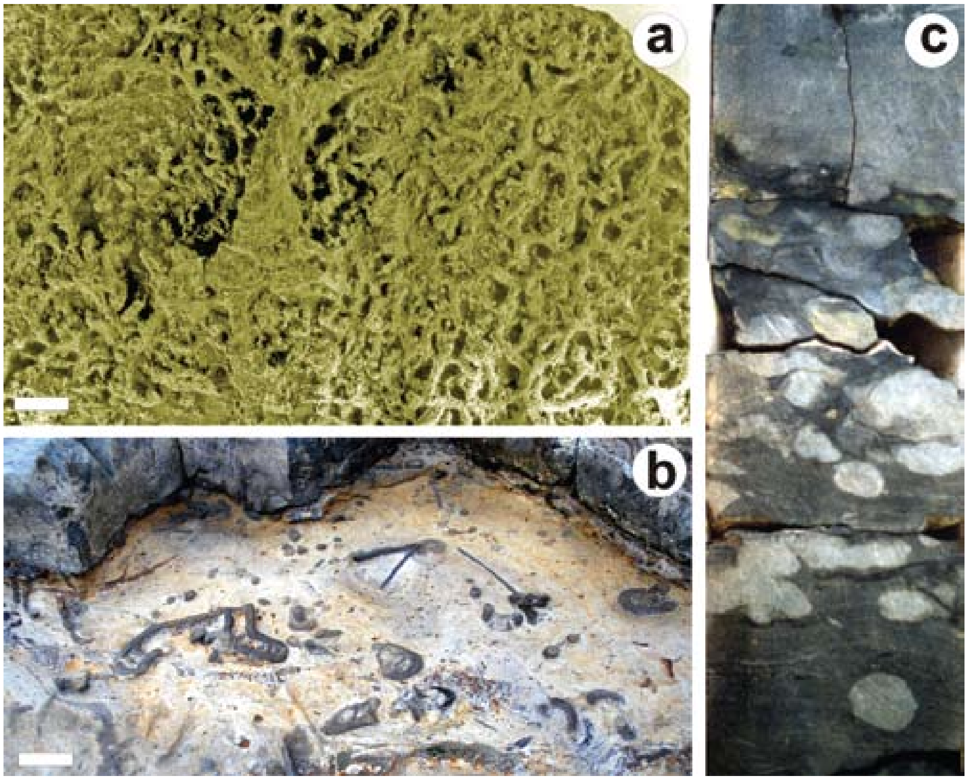

Figure 4.10 Examples of the *Glossifungites* ichnofacies. (a) Outcrop expression. High-density association of small *Thalassinoides suevicus* and large specimen of the same ichnotaxa. Upper Cretaceous, Hidden Lake Formation, Brandy Bay, James Ross Island, Antarctica. Scale bar is 1cm. (b) Outcrop expression. *Rhizocorallium* isp. penetrating from the overlying bed into a firmground. Upper Jurassic, Rodiles Formation, El Puntal Cliffs, San Martín del Mar, Villaviciosa, Asturias, northern Spain. Scale bar is 5 cm. (c) Core expression. *Thalassinoides* penetrating into mudstone and passively filled with sand from an overlying sandstone. Note circular to subcircular cross-sections and absence of lining. Upper Oligocene-Lower Miocene, Naricual Formation, Pirital Field, Eastern Venezuela Basin. Core width is 9 cm.

unit. The typical examples of the *Glossifungites* ichnofacies have been recorded in shallow- to marginal-marine environments. In these settings, it is associated with alostratigraphic surfaces, such as regressive surfaces of erosion formed during forced regressions (see Section 12.2.1), lowstand erosion surfaces due to relative sea level fall (see Section 12.2.2), ravinement surfaces formed during transgressions (see Section 12.2.3), and co-planar surfaces or amalgamated surfaces of lowstand and transgressive erosion (e.g. estuarine valley incision surfaces) (see Section 12.2.4; MacEachern *et al.*, 1992, 2007a; Pemberton *et al.*, 1992b, 2004). More rarely, the *Glossifungites* ichnofacies has been recorded in deep-marine environments associated to incised submarine canyons (see Section 12.2.1; Hayward, 1976). Firmground surfaces demarcated by the *Glossifungites* ichnofacies may be also formed

Box 4.1 A modern example of the *Glossifungites* ichnofacies along the Georgia coast of the United States

Information from modern environments, although commonly overlooked, may provide valuable information to characterize and understand ichnofacies. The Georgia coast of the eastern United States is a fascinating natural laboratory to elucidate the producers and mechanisms of formation of the *Glossifungites* ichnofacies. Here, the *Glossifungites* ichnofacies occurs in previously buried and dewatered muds of Holocene salt marshes that have been subsequently exhumed by beach or tidal-channel erosion. Three main intergradational ichnocoenoses have been recognized: (1) a petricolid ichnocoenose; (2) a petricolid–pholad–crustacean ichnocoenose; and (3) a petricolid-crustacean-polydoran ichnocoenose. Petricolid and pholad bivalves produce incipient *Gastrochaenolites*, the polychaete *Polydora* excavate small *Diplocraterion*-like burrows, various polychaetes produce incipient *Palaeophycus*, shrimps construct *Thalassinoides* galleries, and crabs produce *Psilonichnus*. Crustaceans tend to be dominant in more protected back-barrier settings influenced by low-energy tidal currents, while petricolid and pholad bivalves are more characteristic of high-energy foreshore areas affected by wave-induced currents. Other factors influencing the distribution of trace-making organisms are density of the relict *Spartina* root mats, substrate cohesiveness, sediment texture, duration of subaerial exposure, and sandblasting from nearshore areas. Neoichnological observations have been essential in furthering our understanding of the nature and significance of the *Glossifungites* ichnofacies.

Reference: Pemberton and Frey (1985).

due to autogenic sedimentary processes (see Section 12.8). In this case, erosion due to migrating tidal channels and tidal creeks represent a common environmental scenario conducive to the production and colonization of firmground substrates (Gingras *et al.*, 2000; MacEachern *et al.*, 2007a). MacEachern *et al.* (2007a) also noted that long periods of quiescence may be conducive to the formation of relatively firm mudstones, allowing the establishment of the *Glossifungites* ichnofacies. According to these authors, examples of the *Glossifungites* ichnofacies related to autogenic processes tend to show some evidence of burrow compaction, contain more deeply penetrating burrows due to minimal substrate stiffness, and include ichnogenera less typical of firmground settings.

Stratigraphic and environmental implications of the *Glossifungites* ichnofacies in carbonate rocks are rather different (see Section 12.6). Because carbonates commonly undergo rapid consolidation and cementation due to early diagenetic processes, firmgrounds are not necessarily related to erosional exhumation of the substrate as in siliciclastic rocks. On the contrary, endurated substrates in carbonate rocks are commonly related with omission surfaces representing reduced rates of sedimentation (Bromley, 1975). However, spectacular examples of the *Glossifungites* ichnofacies in ravinement surfaces, analogous to those formed in siliciclastic substrates may occur in carbonates (Rodríguez-Tovar *et al.*, 2007).

This ichnofacies can be very heterogeneous displaying remarkable spatial variations. Gingras *et al.* (2001) found that degree of substrate firmness, position within the intertidal zone, sediment texture, and presence of a sediment veneer rank were among the most important controlling factors of the nature and composition of modern examples the *Glossifungites* ichnofacies. Spatial heterogeneity revealed by changes in the proportion of their components has been documented also in ancient examples of this ichnofacies (Carmona *et al.*, 2006). MacEachern and Burton (2000) documented an unusual occurrence of the *Glossifungites* ichnofacies dominated by *Zoophycos*, and also having *Thalassinoides*, *Spongeliomorpha*, and *Rhizocorallium* in lower offshore deposits. Therefore, these authors suggested potential subdivisions of the *Glossifungites* ichnofacies corresponding to proximal–distal trends. According to this scheme, the archetypal *Glossifungites* ichnofacies occurs most commonly in high-energy shallow water, while the association with *Zoophycos* represents a distal expression of the *Glossifungites* ichnofacies. Although in its original definition the *Glossifungites* ichnofacies was not restricted to marine environments (Seilacher, 1967b), continental firmground ichnofaunas are dominated by the ichnogenus *Scoyenia* and related trace fossils, and seem to be remarkably different from their marine counterparts (e.g. Buatois *et al.*, 1996a) (see Section 12.7). However, an occurrence of firmground *Rhizocorallium* in Miocene fluvial deposits has been noted (Fürsich and Mayr, 1981). The *Glossifungites* ichnofacies is known since the Early Cambrian (Bromley and Hanken, 1991).

4.3.2 *TRYPANITES* ICHNOFACIES

The *Trypanites* ichnofacies was originally introduced by Frey and Seilacher (1980), and subsequently revised in a number of papers (e.g. Frey and Pemberton, 1984; Pemberton *et al.*, 1992b, 2001, 2004; Bromley and Asgaard, 1993a; Gibert *et al.*, 1998, 2007). Bromley and Asgaard (1993a) noted that the *Trypanites* ichnofacies includes two different associations: *Entobia* (dominated by deep-tier borings) and *Gnathichnus* (dominated by shallow- to very shallow-tier raspings and etchings). These two associations were regarded either as subdivisions of the *Trypanites* ichnofacies or as archetypal ichnofacies that replace the more general *Trypanites* ichnofacies. Subsequent work demonstrated the archetypal nature and recurrence of the *Entobia* association in cliffs and sediment-starved hardgrounds during most of the Mesozoic and Cenozoic (Gibert *et al.*, 1998, 2007). MacEachern *et al.* (2007a) stated that the *Entobia* and *Gnathichnus* associations are closely associated with tiers and, therefore, serve as expressions of the suites that characterize the

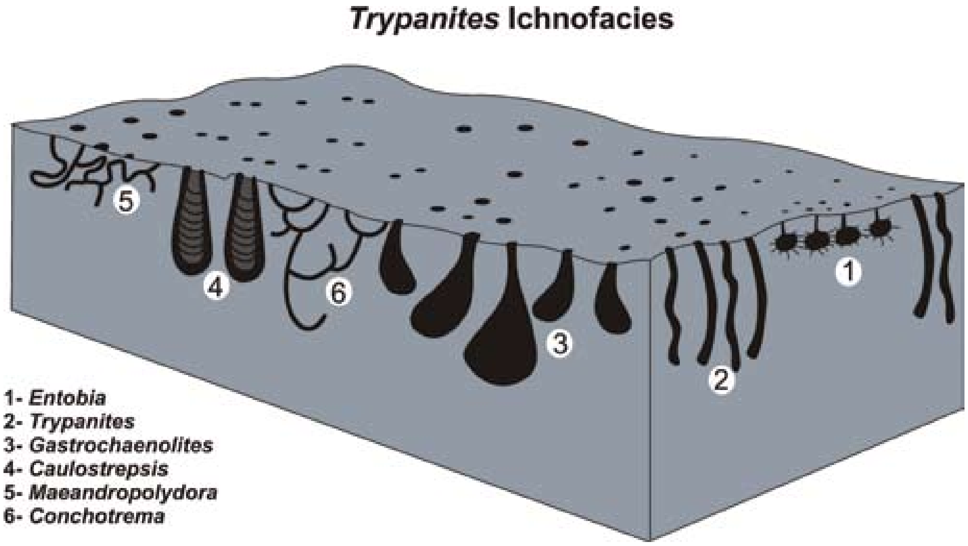

Figure 4.11 Schematic reconstruction of the *Trypanites* ichnofacies.

Trypanites ichnofacies as a whole. Interestingly, this is not really different from the distinction between the *Nereites* (shallow-tier structures preserved at the base of turbidites) and *Zoophycos* (deep-tier structures preserved in the fine-grained background mudstone) ichnofacies (Wetzel, 1984; Bromley, 1990, 1996). Also, it has been noted that the *Entobia* association is identical to the *Trypanites* ichnofacies on morpho-ethological grounds (MacEachern *et al.*, 2007a). Accordingly, the *Entobia* association is regarded here as an equivalent of the *Trypanites* ichnofacies (see Section 14.2.3).

The *Trypanites* ichnofacies is characterized by: (1) dominance of deep-tier borings; (2) dominance of sharp-walled, unlined, passively filled, vertical to subvertical, cylindrical, simple, tear-, vase- or U-shaped dwelling borings of suspension feeders or passive predators; (3) presence of branched and multi-chambered borings produced by suspension feeders; (4) low to moderate ichnodiversity; and (5) high abundance (Fig. 4.11).

The most common components of the *Trypanites* ichnofacies are *Trypanites* (simple vertical borings), *Gastrochaenolites* (tear-shaped borings), and *Entobia* (branched systems). Other elements are *Caulostrepsis* (U-shaped pouches), *Maeandropolydora* (multi-entrance networks), *Conchotrema* (branched, multi-apertured cylindrical borings) and *Ubiglobites* (vase-shaped borings). Typical producers include polychaetes (*Trypanites*), bivalves (*Gastrochaenolites*), and sponges (*Entobia*). Microborings are also elements of this ichnofacies (Glaub *et al.*, 2002; Glaub and Vogel, 2004).

The *Trypanites* ichnofacies is typical of cemented, fully lithified substrates, such as sediment-starved hardgrounds, cliffs, beachrock, and reefs (Frey and Pemberton, 1984; Pemberton *et al.*, 1992b, 2001, 2004). More rarely, this ichnofacies can occur in bone beds or coquinas. The *Trypanites* ichnofacies indicates long periods of bioerosion without any interruption by frequent depositional events. Continuous activity by deep bioeroders leads to destruction of shallow tiers (Bromley and Asgaard, 1993a). The *Trypanites* ichnofacies is directly associated with different types of unconformities forming either omission or erosive surfaces and, as such, is significant in sequence stratigraphy (see Sections 12.2, 12.3, and 12.6). Only bioerosion in laterally persistent substrates should be included in the *Trypanites* ichnofacies (Pemberton *et al.*, 1992b). Bored, isolated shells or clasts, although significant in terms of information potential (Gibert *et al.*, 1996; Siggerud and Steel, 1999), do not represent the *Trypanites* ichnofacies. Evidence of emplacement in lithified substrate is revealed by the fact that borings cut through shells or grains instead of avoiding them (Bromley, 1975). A high density of borings indicates major breaks in sedimentation and sediment starvation. In ancient examples, bioerosion densities of up to 1500 borings per m^2 have been measured (Gibert *et al.*, 1996; Domènech *et al.*, 2001). However, as noted by Bromley and Asgaard (1993b), overall boring density is highly dependent of boring size. As in the case of the *Glossifungites* ichnofacies, deposit-feeding trace fossils are typically absent in the *Trypanites* ichnofacies due to the absence of nutritious particles in lithified substrates.

The *Trypanites* ichnofacies may be intergradational with the *Glossifungites* ichnofacies. In this case, the *Trypanites* suite cross-cuts the *Glossifungites* suite, reflecting progressive cementation of the original substrate (Bromley, 1975). Hardground formation may occur in both siliciclastic and carbonate substrates, although it tends to be more common in the latter (MacEachern *et al.*, 2007a). In siliciclastic substrates most hardgrounds are associated with erosionally exhumed surfaces, which are typically formed during relative sea-level changes (Pemberton *et al.*, 1992b, 2004). MacEachern *et al.* (2007a) cautioned against assignment of sequence-stratigraphic significance of the *Trypanites* ichnofacies in carbonate sediments. Because carbonates commonly undergo rapid lithification due to early diagenesis, hardground formation is not necessarily related to erosional exhumation in this type of substrates (see Section 12.6). Occurrences of the *Trypanites* ichnofacies in connection to sediment-starved omission surfaces are probably the rule rather than the exception (e.g. Bromley, 1975; Mángano and Buatois, 1991). In

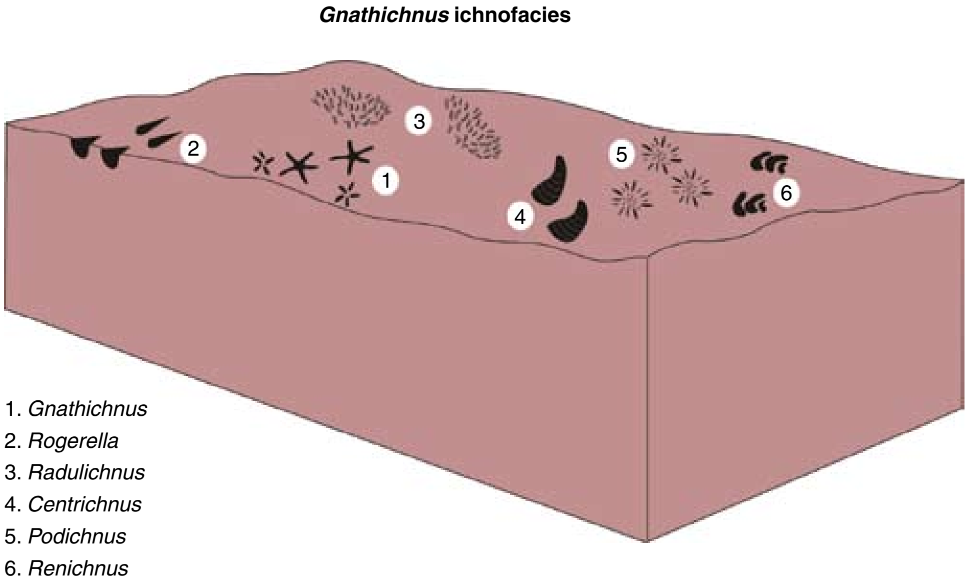

Figure 4.12 Schematic reconstruction of the *Gnathichnus* ichnofacies.

any case, the *Trypanites* ichnofacies has been recognized in erosionally exhumed carbonates associated with a regional unconformity (Pemberton *et al.*, 1980). A depauperate *Trypanites* ichnofacies has been introduced recently for non-carbonate substrates (Buatois and Encinas, 2011). Comparable bioeroded surfaces in continental environments are poorly known. Borings in modern lacustrine stromatolites from Lake Turkana (Kenya) have been documented by Ekdale *et al.* (1989). Embedment cavities have been recorded in Cenozoic lacustrine carbonates of Kenya and Wyoming by Lamond and Tapanila (2003). Artificial lakes in Kansas contain Recent U-shaped structures produced by chironomids penetrating into Carboniferous shale. The *Trypanites* ichnofacies is known since the Early Cambrian (James *et al.*, 1977).

4.3.3 *GNATHICHNUS* ICHNOFACIES

The *Gnathichnus* ichnofacies or association was introduced by Bromley and Asgaard (1993a) for bored shells and boulders. MacEachern *et al.* (2007a) noted that this example of the *Gnathichnus* association does not form continuous mappable surfaces, and therefore does not qualify as an ichnofacies. However, Bromley and Asgaard (1993a) suggested that the same suite may be present in rapidly buried laterally continuous substrates. In fact, the assemblage was subsequently recognized in the Miocene of Spain (Mayoral and Muñiz, 1996), and its archetypal nature and temporal recurrence during most of the Mesozoic and Cenozoic have been now demonstrated (Gibert *et al.*, 2007).

The *Gnathichnus* ichnofacies is characterized by: (1) dominance of shallow to very shallow-tier grazing structures; (2) presence of other ethological categories, such as domichnia, fixichnia, and praedichnia; (3) subordinate occurrence of deeper structures; (4) dominance of radulation and gnawing traces produced by algal grazers; (5) presence of etched attachment scars; (6) occurrence of sock-shaped borings; (7) low to moderate ichnodiversity; and (8) high abundance (Fig. 4.12).

The most common components of the *Gnathichnus* ichnofacies are *Gnathichnus* (stellate gnawing traces), *Radulichnus* (radulation traces), *Renichnus* (spiral- to arcuate-shaped etched attachment scars), *Podichnus* (radiating arcs of attachment pits), and *Centrichnus* (drop-shaped attachment pits). The deeper-tier *Maeandropolydora* (multi-entrance networks) may be present. Gastropods, chitons, regular echinoids, brachiopods, acrothoracican barnacles, and bryozoans are among the most common producers.

This association suggests short-term bioerosion interrupted by rapid sedimentation, allowing preservation of shallow-tier bioerosion in the absence of a mature deep-tier endolithic community (Bromley and Asgaard, 1993a). In contrast to the long-term colonization windows that typify the *Trypanites* ichnofacies, the *Gnathichnus* ichnofacies reflects short-term colonization windows. It commonly occurs in spatially restricted, mobile shellgrounds formed under moderate energy conditions (Gibert *et al.*, 2007). The *Gnathichnus* ichnofacies is known since the Jurassic (Gibert *et al.*, 2007).

4.3.4 *TEREDOLITES* ICHNOFACIES

The *Teredolites* ichnofacies was introduced by Bromley *et al.* (1984), and has been recently revised by Gingras *et al.* (2004). Additional work on the *Teredolites* ichnofacies focused on the implications of bored log-grounds in sequence stratigraphy (e.g. Savrda, 1991a; Savrda *et al.*, 1993, 2005). This ichnofacies is characterized by: (1) dominance of clavate borings; (2) boring walls ornamented with the texture of the host substrate; (3) very low ichnodiversity, most commonly monospecific suites; and (4) high density of borings, albeit with rare interpenetration (Fig. 4.13).

The ichnogenus *Teredolites* (Fig. 4.14a–b), a clavate boring produced by pholadid bivalves (e.g. *Teredo*, *Martesia*, *Lyrodus*, *Bankia*), is the typical component of this ichnofacies (Bromley *et al.*, 1984). However, analysis of a modern example reveals

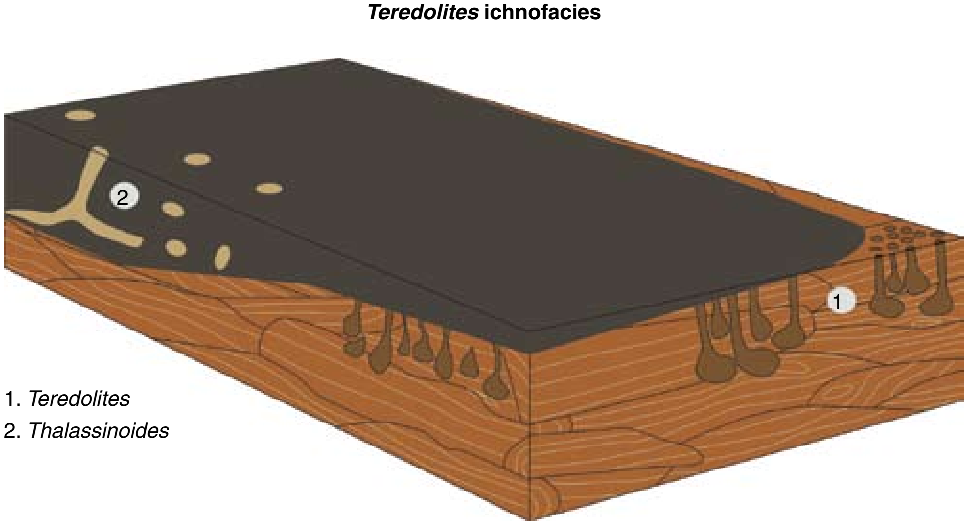

Figure 4.13 Schematic reconstruction of the *Teredolites* ichnofacies.

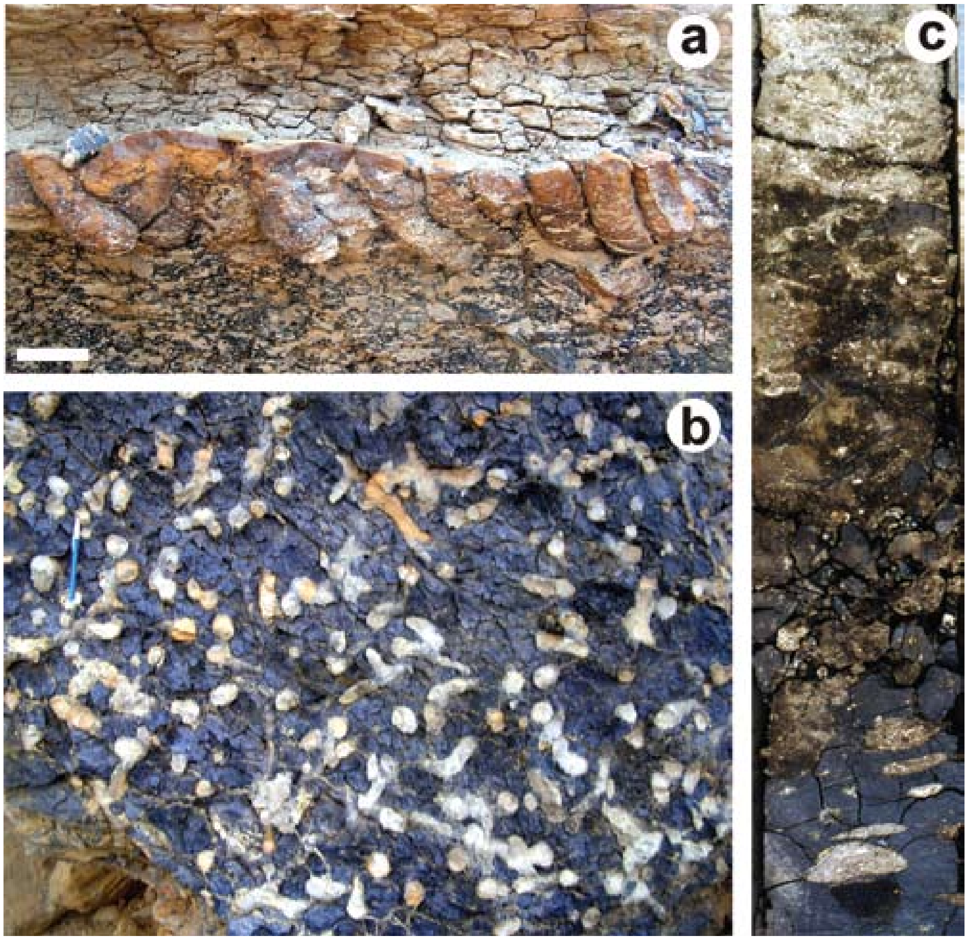

Figure 4.14 Examples of the *Teredolites* ichnofacies. (a) Type locality of the *Teredolites* ichnofacies showing high density of *Teredolites clavatus* in a coal layer. Upper Cretaceous, Horseshoe Canyon Formation, East Coule, Drumheller, Alberta, western Canada. Scale bar is 5 cm. See Bromley *et al.* (1984). (b) Bedding-plane view showing high density of *Thalassinoides suevicus* in coal layer. Middle to Upper Miocene, Urumaco Formation, Urumaco River, northwestern Venezuela. Pen is 15 cm. (c) *Thalassinoides* isp. in coal layer. Lower Miocene, Oficina Formation, Oritupano Field, Eastern Venezuela Basin. Core width is 8 cm.

the presence of borings similar to *Caulostrepsis*, *Entobia*, *Maeandropolydora*, *Psilonichnus*, *Rogerella*, *Thalassinoides*, and *Trypanites* emplaced in log-grounds (Gingras *et al.*, 2004). According to this study, other potential tracemakers for the *Teredolites* ichnofacies are spionid polychaetes (*Polydora proboscidea*) and isopods (*Limnoria lignorum*). While a variety of woodground borings are known from modern environments, fossil examples are almost invariably monospecific, containing only the ichnogenus *Teredolites*. Although the ichnospecies *Teredolites longissimus* is the most common ichnotaxa, *T. clavatus* may occur also (Bromley *et al.*, 1984). Occasionally, the ichnogenus *Thalassinoides* has been recognized in fossil woodgrounds both in outcrops (Gingras *et al.*, 2004) (Fig. 4.14b) and cores (Buatois *et al.*, 2002a) (Fig. 4.14c). Differences between modern and ancient examples of the *Teredolites* ichnofacies reveal taphonomic filters of the fossilization barrier. Deep-penetrating borings, such as *Teredolites*, have a higher preservation potential that shallowly emplaced structures, such as *Rogerella* or *Maeandropolydora* (Gingras *et al.*, 2002).

The *Teredolites* ichnofacies characterizes resistant xylic (woody and coaly) substrates, such as drifted log pavements and peat deposits that may be preserved as coal or lignite in the rock record (Pemberton *et al.*, 2001). In contrast to lithic substrates, xylic substrates are flexible, consist of organic matter, and are rapidly biodegradable (Bromley *et al.*, 1984). Ecologically, while hardground borings are commonly produced for protection, woodground borings are related with the quest for food (Bromley *et al.*, 1984). Boring walls are commonly ornamented with the host substrate texture, and xenoglyphs of tree growth rings may be present. Size-class variations are commonly present in *Teredolites* suites, suggesting animals at different stages of maturity (Bromley *et al.*, 1984; Savrda *et al.*, 1993; Gingras *et al.*, 2004). Bimodal size distributions probably reveal successive colonization events (Gingras *et al.*, 2004). Only occurrences associated with a laterally persistent substrate should be included in the *Teredolites* ichnofacies; bored, isolated log fragments do not represent the ichnofacies (Pemberton *et al.* 1992b). The term "log-ground" may be used for high concentrations of allochthonous wood (Savrda *et al.*, 1993). As noted by MacEachern *et al.* (2007a), these concentrations may form useful mapping surfaces, particularly where associated with stratigraphic discontinuities (e.g. Savrda, 1991a; Savrda *et al.*, 1993, 2005) (see Box 12.1).

Typically, the *Teredolites* ichnofacies is associated with omission surfaces formed in shallow-marine and marginal-marine environments, commonly bays, estuaries, lagoons, and deltas (Bromley *et al.*, 1984; Pemberton *et al.*, 1992b; MacEachern *et al.*, 2007a). The ichnogenus *Teredolites* is confined to environments with salinities ranging from brackish to fully marine, and apparently cannot tolerate freshwater. This is consistent with almost all the examples documented in the stratigraphic record (e.g. Bromley *et al.*, 1984; Savrda, 1991a; Savrda *et al.*, 1993, 2005). Two occurrences in Cretaceous and Eocene supposed fluvial environments (Plint and Pickerill, 1985) are in rocks now regarded as formed in marginal-marine, brackish-water settings (Plint, 2000; MacEachern *et al.*, 2007a). However, a freshwater example was documented by Bertling and Hermanns (1996) in Neogene fluvial deposits. Wood borings are also present in continental settings, and are mostly produced by isopods (Genise, 1995; Genise and Hazeldine, 1995; Mikuláš and Cílek, 1998; Mikuláš, 2008). Further research is still necessary in order to erect a continental equivalent of the *Teredolites* ichnofacies; recognition of laterally extensive substrates will be critical. The *Teredolites* ichnofacies is known since the Cretaceous (Bromley *et al.*, 1984).

4.4 INVERTEBRATE CONTINENTAL ICHNOFACIES

The ichnofacies model has been expanded into the continental realm in recent years, and efforts have been made to recognize archetypal invertebrate ichnofacies (Buatois and Mángano, 1995b, 2007; Genise *et al.*, 2000, 2010a; Hunt and Lucas, 2007; Ekdale *et al.*, 2007; Minter and Braddy, 2009). In his original model, Seilacher (1967b) recognized only one ichnofacies for continental environments, the *Scoyenia* ichnofacies. The fact that the *Scoyenia* ichnofacies was only one of the many potential recurrent trace-fossil assemblages of continental environments, and that these settings are as diverse as marine environments was acknowledged by ichnologists long ago and illustrated by Bromley and Asgaard (1979) in a seminal paper. However, it is only in the last 15 years that studies addressing the problem of recognizing additional continental ichnofacies have been published (Smith *et al.*, 1993; Buatois and Mángano, 1995b; Bromley, 1996; Genise *et al.*, 2000, 2010a; Ekdale *et al.*, 2007; Hunt and Lucas, 2007). At present, six continental archetypal ichnofacies have been proposed: the *Scoyenia*, *Mermia*, *Coprinisphaera*, *Termitichnus*, *Celliforma*, and *Octopodichnus–Entradichnus* ichnofacies. Part of this scheme has received quantitative support by recently performed cluster analysis (Minter and Braddy, 2009). The continental invertebrate ichnofacies model has reached a level of resolution similar to that of marine environments. While the *Scoyenia* and *Mermia* ichnofacies are mostly controlled by the position of the water table (Buatois and Mángano, 1995b, 2002, 2009a), terrestrial ichnofacies show a close correspondence with the plant formations identified by Mueller-Dombois and Ellenberg (1980). In fact, Genise *et al.* (2010a) noted that of the seven global plant formations recognized by these authors, four display correlation with terrestrial ichnofacies.

4.4.1 *SCOYENIA* ICHNOFACIES

Seilacher (1967b) proposed the *Scoyenia* ichnofacies for "nonmarine sands and shales, often red beds, with a distinctive association of trace fossils", and referred to a previous schematic illustration (Seilacher 1963b, Fig. 7), which included meniscate traces, arthropod trackways, and bilobed traces, as well as several physical sedimentary structures (e.g. desiccation cracks). Frey *et al.* (1984b) noted that the *Scoyenia* ichnofacies subsequently was used as a catchall for all occurrences of continental trace fossils, and proposed a refined definition in order to retain its ecological and environmental significance. Further refinements were suggested by Buatois and Mángano (1995b), who noted the abundance of arthropod trackways in the *Scoyenia* ichnofacies. The *Scoyenia* ichnofacies is characterized by: (1) abundance of horizontal meniscate backfilled traces produced by mobile deposit feeders; (2) abundance of locomotion traces, including both trackways and bilobate trails; (3) presence of vertical domiciles; (4) a mixture of invertebrate (mostly arthropod), vertebrate and plant traces; (5) low to moderate ichnodiversity; and (6) localized high abundance (Fig. 4.15).

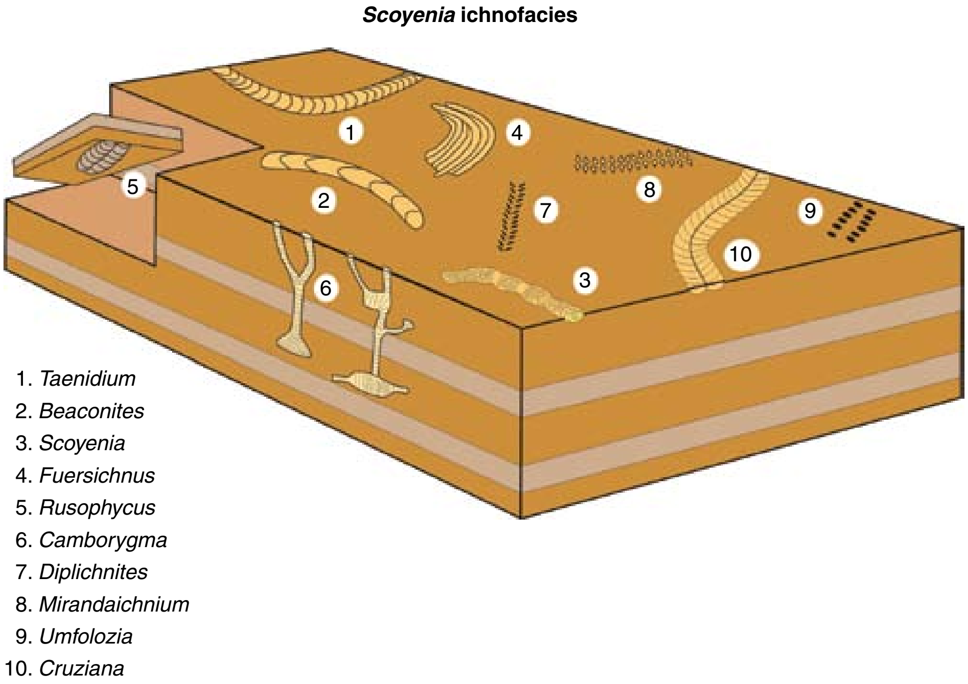

Figure 4.15 Schematic reconstruction of the *Scoyenia* ichnofacies.

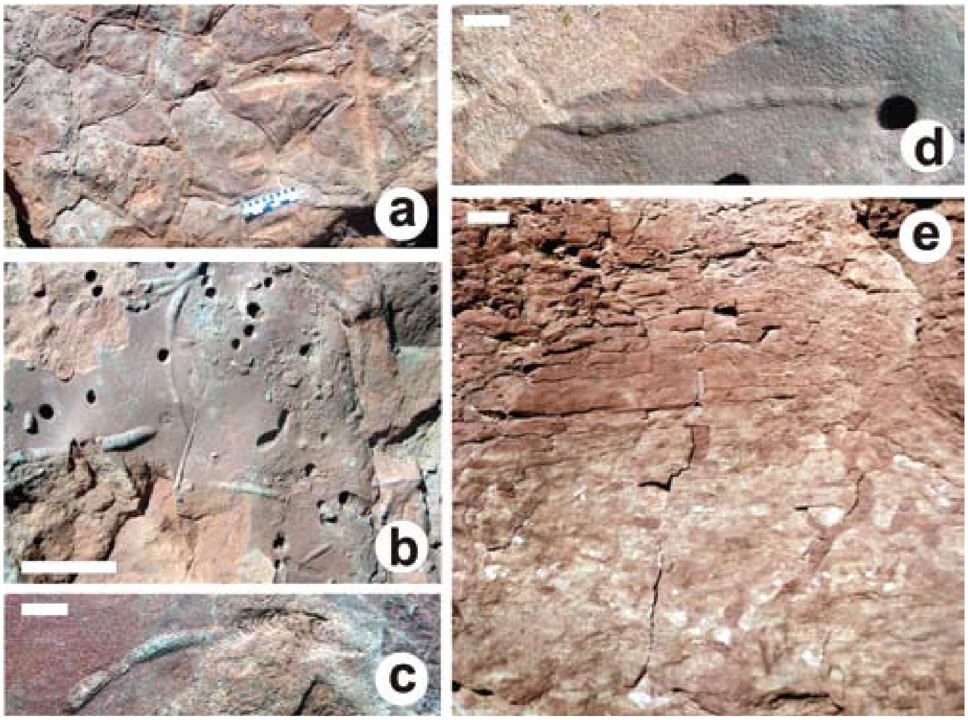

Figure 4.16 Examples of the *Scoyenia* ichnofacies, illustrating the typical dominance by meniscate trace fossils. (a) General view of a bedding plane with several specimens of *Scoyenia gracilis* associated with desiccation cracks. Lower Jurassic, Kayenta Formation, Grandview Point, Canyonland National Park, Utah, United States. Scale bar is 10 cm. (b) Close-up showing burrow sculpture and presence of raindrop imprints. Scale bar is 5 cm. (c) Close-up showing meniscate fill and wall with parallel striations. Scale bar is 1 cm. (d) Close-up of wall striations. Scale bar is 1 cm. (e) Vertical cross-section showing intense bioturbation by *Taenidium* isp. Middle Triassic, Youfangzhuang Formation, Nanshan Forest Park, Jiyuan City, Henan Province, central China. Scale bar is 1 cm. See M. Wang *et al.* (2009).

Meniscate trace fossils include *Scoyenia* (Fig. 4.16a–d), *Beaconites*, and *Taenidium* (Fig. 4.15e). Adhesive meniscate burrows of Hasiotis (2004), recently referred to the new ichnogenus *Naktodemasis* by Smith *et al.* (2008a), actually belong in *Taenidium* (Krapovickas *et al.*, 2009). Arthropod trackways are represented by a wide variety of ichnotaxa, including *Umfolozia*, *Merostomichnites*, *Diplichnites*, *Hexapodichnus*, *Permichnium*, and *Acripes*. Bilobate traces include locomotion (*Cruziana*) and associated resting structures (*Rusophycus*). Simple facies-crossing ichnotaxa, such as *Planolites*, *Palaeophycus*, and *Cochlichnus*, are common. Vertical burrows are currently assigned to *Skolithos* and *Cylindricum*. Some examples of the ichnofacies may include crayfish burrows (*Camborygma*) and banana-shaped feeding traces (*Fuersichnus*). Vertebrate tracks may be abundant and varied (Hunt and Lucas, 2007).

The *Scoyenia* ichnofacies is characterized by very low-diversity assemblages, mostly monospecific occurrences of meniscate trace fossils (Frey *et al.*, 1984b). However, moderately diverse assemblages of arthropod trackways may occur (Buatois and Mángano, 1995b). The dominance of horizontal traces of deposit feeders suggests low-energy settings. Furthermore, the abundance of meniscate traces and arthropod trackways is typical of sediments periodically exposed to air or periodically inundated, and intermediate between aquatic and terrestrial environments (Frey *et al.*, 1984b; Frey and Pemberton, 1984, 1987). This environmental scenario is consistent with the associated physical structures, which are indicative of periodic subaerial exposure (e.g. desiccation cracks, raindrop imprints) (Fig. 4.16a).

The *Scoyenia* ichnofacies is typical of fluvial and lacustrine systems, although it may also occur in certain eolian subenvironments. In fluvial settings, it is present in floodplain deposits, covering a wide variety of subenvironments, such as ponds, levees, and crevasse splays (Frey *et al.*, 1984b; Frey and Pemberton, 1984, 1987; Buatois and Mángano, 1995b, 2002, 2004a) (see Section 10.2). In lacustrine environments, the *Scoyenia* ichnofacies typically characterizes lake-margin areas, being present in both open and closed lacustrine basins, and in both ephemeral and perennial lakes (Buatois and Mángano, 1998, 2004a) (see Section 10.3). It is not restricted to siliciclastic systems, but is also present along the margins of carbonate lakes (Genise *et al.*, 2010a). In eolian systems, it may occur in wet interdunes (Buatois and Mángano, 2004a) (see Section 10.4).

Bromley (1996) proposed a more restricted definition of the *Scoyenia* ichnofacies as a continental equivalent of the firmground *Glossifungites* ichnofacies of the marine realm. In fact, the *Scoyenia* ichnofacies may be subdivided into two distinct suites: one characterized by meniscate structures without ornamentation (*Taenidium*, *Beaconites*) developed in a soft substrate, and the second typified by striated traces (*Scoyenia*, *Spongeliomorpha*), cross-cutting the former and developed in a firm substrate (Buatois *et al.*, 1996a; Savrda *et al.*, 2000; Buatois and Mángano, 2002, 2004a). The resulting palimpsest surfaces reflect progressive desiccation of sediment.

Bromley (1996) also tentatively proposed the *Rusophycus* ichnofacies for fluvial to shallow-lacustrine environments, and the *Fuersichnus* ichnofacies for lake settings below the fair-weather wave base. The *Rusophycus* ichnofacies is dominated by arthropod locomotion and resting trace fossils, and cannot be distinguished at present from the *Scoyenia* ichnofacies (Buatois and Mángano, 2004a). The *Fuersichnus* ichnofacies is based on examples in which the eponymous ichnogenus occurs in continental environments. However, the "type" examples suggested are from fluvial (MacNaughton and Pickerill, 1995) and ephemeral alluvial plain and sand-flat deposits (Gierlowski-Kordesch, 1991) rather than relatively deep lakes. As presently defined, the *Fuersichnus* ichnofacies cannot be distinguished from the *Scoyenia* ichnofacies (Buatois and Mángano, 2004a). However, further research in these two types of ichnofaunas may hold the potential to distinguish trace-fossil associations with a lower degree of recurrence than archetypal ichnofacies, but of paleoenvironmental utility in basin-by-basin studies.

The *Scoyenia* ichnofacies is known since the Ordovician (Johnson *et al.*, 1994). Paleozoic occurrences of this ichnofacies tend to be dominated by arthropod trackways, while meniscate trace fossils seem to be more common since the Permian and particularly the Triassic (Buatois *et al.*, 1998c) (see Section 14.2.6). The crayfish burrow *Camborygma* is a common addition to the ichnofacies since the Triassic (Hasiotis and Dubiel, 1993).

4.4.2 *MERMIA* ICHNOFACIES

The *Mermia* ichnofacies was introduced by Buatois and Mángano (1995b) to fill some of the gaps in continental ichnofacies. It is characterized by: (1) dominance of horizontal to subhorizontal grazing and feeding traces produced by mobile deposit feeders; (2) subordinate occurrence of locomotion traces; (3) relatively high to moderate ichnodiversity; (4) high abundance; and (5) low degree of specialization of grazing and feeding patterns (Fig. 4.17).

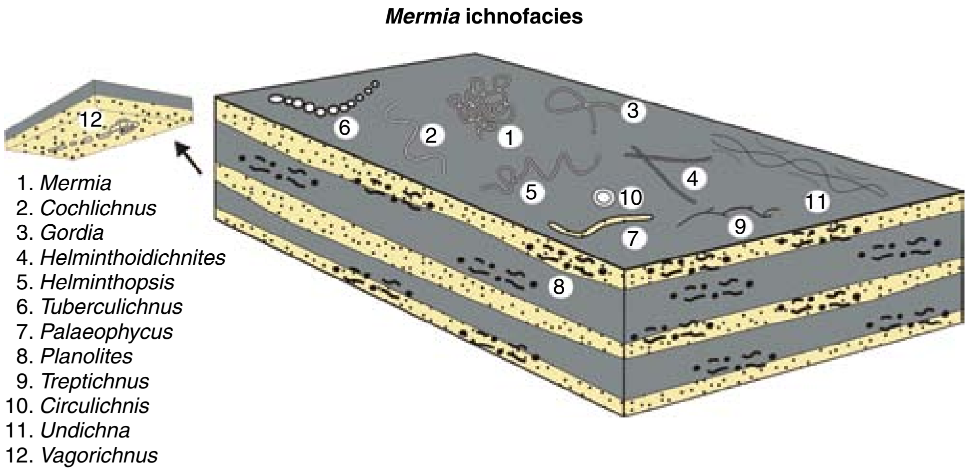

Figure 4.17 Schematic reconstruction of the *Mermia* ichnofacies.

The most typical components of the *Mermia* ichnofacies are a variety of unspecialized grazing traces, such as *Mermia*, *Gordia*, *Helminthopsis*, and *Helminthoidichnites*. The sinusoidal trail *Cochlichnus*, that may represent either locomotion or grazing, is also common. Simple feeding structures include very shallow-tier trace fossils, such as *Treptichnus* and *Circulichnis*. Locomotion traces are typically represented by the fish trail *Undichna* or by the invertebrate trail *Diplopodichnus*. However, arthropod trackways (e.g. *Maculichna*, *Diplichnites*) may occur also, although they are rarely the dominant elements.

Although some examples of the *Mermia* ichnofacies may attain relatively high ichnodiversity, the diversity of trace fossils does not necessarily equate with species richness (Buatois and Mángano, 1998). The various ichnogenera recorded in the *Mermia* ichnofacies may result from minor behavioral variations of a very simple, unspecialized grazing pattern developed by a single tracemaker (e.g. *Helminthopsis*, *Helminthoidichnites*, *Gordia*, *Mermia*). The simple patterns revealed by grazing and feeding traces mark a clear difference with respect to assemblages preserved in deep-marine turbidites. The dominance of horizontal grazing traces of deposit and detritus feeders suggests low-energy environments. Substrates are fine-grained, mostly unconsolidated silts and very fine- to fine-grained sands. Absence of scratch marks and common poor preservation of trace-fossil morphology suggest very soft, submerged substrates. Moderate ichnodiversity indicates relatively stable and well-oxygenated settings. Under anoxic conditions the *Mermia* ichnofacies is suppressed.

The *Mermia* ichnofacies typifies permanently subaqueous zones of lacustrine systems, extending from shallow to deep bathymetric zones (Buatois and Mángano, 1995b) (see Section 10.3). This ichnofacies is commonly present in open perennial siliciclastic lacustrine systems, but may occur in carbonate lakes also (Gibert *et al*., 2000; Buatois *et al*., 2000; Genise *et al*., 2010a). However, the ichnofacies may be present in floodplain water bodies under subaqueous conditions (Buatois and Mángano, 2002; Mikuláš, 2003) (see Section 10.2.2). The lower ichnodiversity of these floodplain assemblages in comparison with their lacustrine counterparts probably reflects less stable conditions and the temporary nature of floodplain ponds. Also, the *Mermia* ichnofacies may occur in fjord settings under freshwater conditions due to glacial melting (Buatois and Mángano, 1995b, 2003b; Buatois *et al*., 2006a, 2010a).

There are no archetypal trace-fossil associations that clearly distinguish shallow- and deep-lacustrine environments, probably because of the wide variability of lakes. Accordingly, Buatois and Mángano (1998) considered the *Mermia* ichnofacies as a continental equivalent of the *Cruziana*, *Zoophycos*, and *Nereites* ichnofacies in the classical Seilacherian scheme. Trace-fossil assemblages typically recorded from relatively deep-lacustrine areas may also occur in shallower zones (e.g. Pickerill, 1992).

The *Mermia* ichnofacies is known since the Carboniferous. In contrast to Paleozoic permanent subaqueous assemblages typified by surface trails, Mesozoic and Cenozoic assemblages tend to contain a higher proportion of infaunal burrows (Buatois *et al*., 1996b).

4.4.3 *COPRINISPHAERA* ICHNOFACIES

The *Coprinisphaera* ichnofacies was introduced by Genise *et al*. (2000) in an attempt to detect recurrent trace-fossil assemblages in paleosols. This ichnofacies is characterized by: (1) dominance of trace fossils of bees, wasps, ants, and beetles; (2) subordinate presence of termite ichnofossils; (3) dominance of nesting traces or calichnia; (4) tiering structures that result from variable depths of emplacement of hymenopterous, termite, and dung-beetle nests; (5) moderate to relatively high ichnodiversity; and (6) high abundance (Fig. 4.18).

The typical component of this ichnofacies is the dung beetle nest *Coprinisphaera*, which is present in most recorded occurrences of the ichnofacies. Other beetle traces include *Pallichnus*,

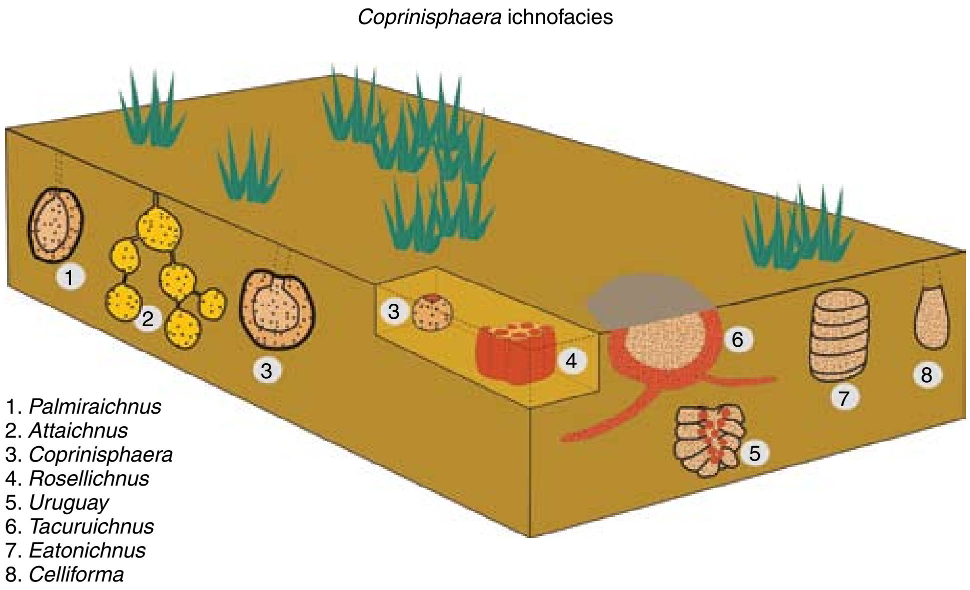

Figure 4.18 Schematic reconstruction of the *Coprinisphaera* ichnofacies.

Eatonichnus, Monesichnus, *Fontanai*, and *Teisseirei*. Common elements also include several bee trace fossils, such as *Celliforma*, *Uruguay*, *Ellipsoideichnus*, *Palmiraichnus*, and *Rosellichnus*. Other hymenopterous trace fossils belong to wasps (*Chubutolithes*, wasp cocoons), and ants (e.g. *Attaichnus, Parowanichnus*). Termite nests, mostly *Syntermesichnus*, *Coatonichnus*, *Tacuruichnus*, or even some ichnospecies of *Termitichnus* (*T. schneideri*) and *Vondrichnus* (*V. planoglobus*) may be locally present (Duringer *et al*., 2007). In addition, Genise *et al*. (2000) noted that other components still await formal taxonomic documentation. Root trace fossils are also present.

The *Coprinisphaera* ichnofacies strongly correlates with occurrences of herbaceous plant communities, mostly savannas, grasslands, prairies, and steppes (Genise *et al*., 2000). This correlation reflects the fact that dung beetles provision their nests with excrement of vertebrate herbivores. Hymenopterous insects seek bare, dry soil exposed to sun and, therefore, display similar environmental preferences to dung-beetles. On the other hand, termites display different environmental tolerances, and are strongly dependent on atmospheric and soil moisture, mostly inhabiting tropical rain forests (Grassé, 1986). Accordingly, termite nests are only occasionally present in the *Coprinisphaera* ichnofacies (Genise *et al*., 2000; Duringer *et al*., 2007).

The *Coprinisphaera* ichnofacies is typical of paleosols developed in paleoecosystems of herbaceous communities (*sensu* Mueller-Dombois and Ellenberg, 1980), climatically ranging from dry and cold to humid and warm conditions (Genise *et al*., 2000) (see Section 10.5). Evaluation of the relative abundance of the different trace fossils within the assemblage allows more refined paleoclimatological inferences. Hymenopterous traces tend to be dominant under drier conditions, whereas termite nests are linked to more humid environments (Genise *et al*., 2000; Duringer *et al*., 2007). The *Coprinisphaera* ichnofacies occurs in paleosols that have developed in various depositional systems subject to subaerial exposure, including alluvial plains, overbank, and eolian settings. Undoubtedly, this reflects the capacity of insects to nest in many different sedimentary environments. The emerging pattern suggests that paleosol ichnofaunas, and the *Coprinisphaera* ichnofacies, in particular, are controlled by ecological parameters, such as vegetation, climate, and soil, rather than by depositional processes (Genise *et al*., 2000).

The presence of the *Coprinisphaera* ichnofacies is well documented since the Paleocene (Genise *et al*., 2000). Although some Late Cretaceous assemblages contain fossil bee cells, coleopteran pupal chambers, wasp nests, and undetermined insect nests (e.g. Johnston *et al*., 1996; Elliott and Nations, 1998), assignation to the *Coprinisphaera* ichnofacies is doubtful. Further research in Mesozoic terrestrial ichnofaunas may yield valuable insights into the evolution of paleosol ichnofacies.

4.4.4 *TERMITICHNUS* ICHNOFACIES

The *Termitichnus* ichnofacies has a convoluted history. It was originally proposed by Smith *et al*. (1993) as a subset of the *Scoyenia* ichnofacies to include all paleosol trace-fossil assemblages. Subsequently, it was regarded as an ichnofacies for all paleosol assemblages, but at the same hierarchical level of the *Scoyenia* ichnofacies (Buatois and Mángano, 1995b). However, Genise *et al*. (2000) suggested that the *Termitichnus* ichnofacies as originally defined be abandoned, because it does not reflect the diversity of paleosol settings and, therefore, fails to reveal significant paleoecological information. A definition of a *Termitichnus* ichnofacies *sensu strictu* that includes assemblages dominated by termite nests in paleosols of closed forest ecosystems was suggested pending recognition of its temporal and spatial recurrence (Genise *et al*., 2000, 2004a, 2010a).

This ichnofacies is characterized by: (1) dominance of trace fossils of termites; (2) low ichnodiversity; and (3) high abundance (Fig. 4.19). Typical components are *Termitichnus*, *Vondrichnus*, *Fleaglellius*, and *Krausichnus* (Genise and Bown, 1994b). Root trace fossils are abundant, including ichnofossils of flank-buttressed trees (Wing *et al*., 1995). Other associated trace fossils, such as *Masrichnus* (Bown, 1982), are of uncertain affinities (Genise and Cladera, 2004).

The *Termitichnus* ichnofacies characterizes paleosols formed in closed forests (*sensu* Mueller-Dombois and Ellenberg, 1980) with plant growth under warm and humid conditions (Genise *et al*., 2000, 2004a, 2010a) (see Section 10.5). A high water table is indicated by the presence of trace fossils of flank-buttressed tress (Wing *et al*., 1995). The best-documented example of this ichnofacies was recorded in the Eocene-Oligocene Jebel Qatrani Formation of Egypt, which includes *Termitichnus* and other ichnotaxa attributable to fossil termite nests (Genise and Bown, 1994b). Additional examples are necessary to further document the stratigraphic recurrence of this ichnofacies, as well as its significance.

4.4.5 *CELLIFORMA* ICHNOFACIES

In a study dealing with the definition of paleosol ichnofacies, Genise *et al*. (2000) noticed the presence of a potentially recurrent association in carbonate-rich paleosols (see also Genise *et al*., 2004a). More recently, Genise *et al*. (2010a) introduced the *Celliforma* ichnofacies to account for this specific type of ichnofauna. This ichnofacies is characterized by: (1) dominance of halictid bee nests; (2) association with hackberry endocarps and freshwater and terrestrial snail shells; (3) dominance of callichnia; (4) presence of pupichnia; (5) moderate ichnodiversity; and (6) high abundance (Fig. 4.20). Typical components are *Celliforma*, *Rosselichnus*, *Pallichnus*, *Rebuffoichnus*, *Palmiraichnus*, and *Teisseirei*. Meniscate trace fossils (*Taenidium*) and root structures are also common.

The *Celliforma* ichnofacies characterizes carbonate-rich paleosols (Genise *et al*., 2010a). Most examples correspond to palustrine conditions, but occurrences in calcretes have been also documented (see Section 10.5). In the former case, the time of subaerial exposure was enough to allow the formation of well-aerated and bare soils required for hymenopteran nesting (Genise *et al*., 2010a). In the case of shorter subaerial exposure,

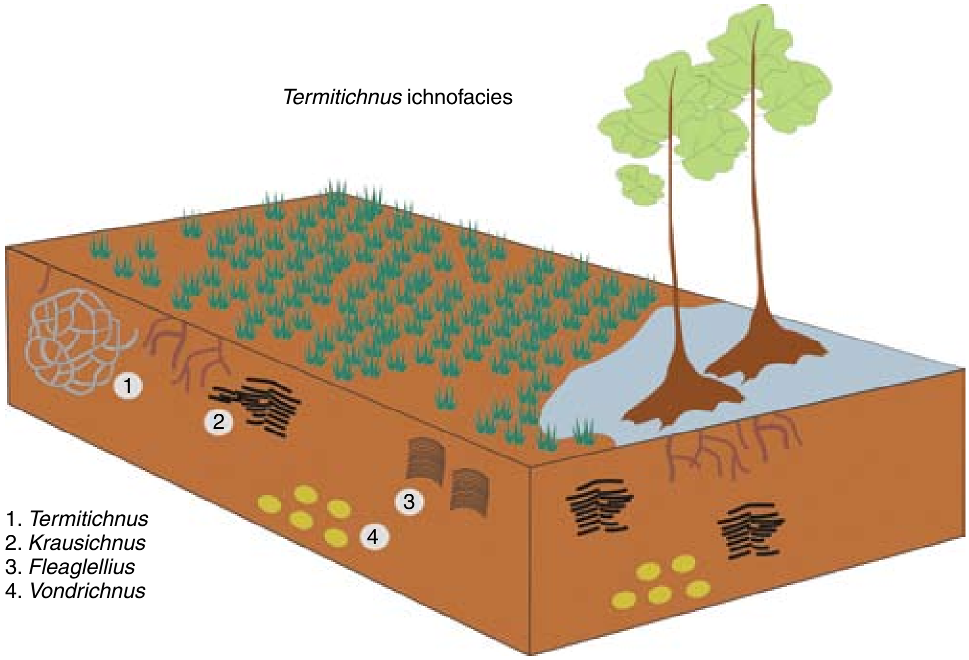

Figure 4.19 Schematic reconstruction of the *Termitichnus* ichnofacies.

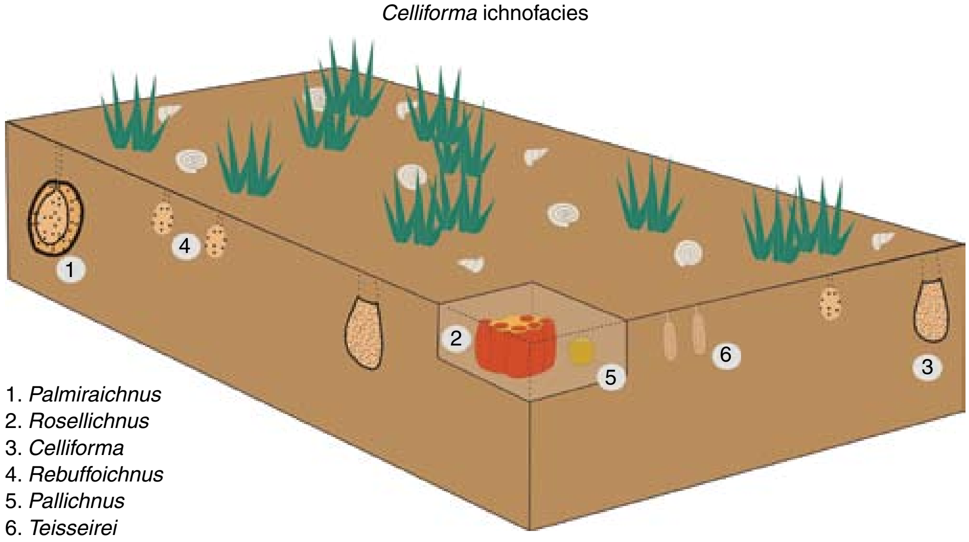

Figure 4.20 Schematic reconstruction of the *Celliforma* ichnofacies.

the *Scoyenia* ichnofacies develops. Under continuous and progressive desiccation of the substrate, the *Scoyenia* ichnofacies may be replaced by the *Celliforma* ichnofacies. Under terrestrial conditions, the *Celliforma* ichnofacies characterizes a drier climate than the *Coprinisphaera* ichnofacies (Genise *et al.*, 2010a). In terms of the global plant formations of Mueller-Dombois and Ellenberg (1980), the *Celliforma* ichnofacies characterizes scrubs and woodlands. In the case of palustrine environments, it ranges from subhumid to subarid settings (Alonso-Zarza, 2003).

The *Celliforma* ichnofacies is known since the Eocene (e.g. Melchor *et al.*, 2002). A potential older occurrence may be represented by the Calizas de Queguay, Uruguay, which may range into the Cretaceous, although more conclusive data on the age of this unit are necessary (Alonso-Zarza *et al.*, 2010; Genise *et al.*, 2010a).

4.4.6 *OCTOPODICHNUS–ENTRADICHNUS* ICHNOFACIES

Eolian ichnofaunas have received increasing attention in recent years, resulting in the proposal of archetypal ichnofacies in two independent studies (Fig. 4.21). Hunt and Lucas (2007) introduced the *Octopodichnus* ichnofacies, and Ekdale *et al.* (2007) the *Entradichnus* ichnofacies, both for eolian dune environments (see Section 10.4). The *Octopodichnus* ichnofacies of Hunt and Lucas (2007) consists of low diversity assemblages of arthropod trackways, mostly spiders and scorpions. The *Entradichnus* ichnofacies of Ekdale *et al.* (2007) consists of shallow traces of desert-dwelling arthropods, including vertical domiciles and meniscate traces. Diverging characterization of both eolian

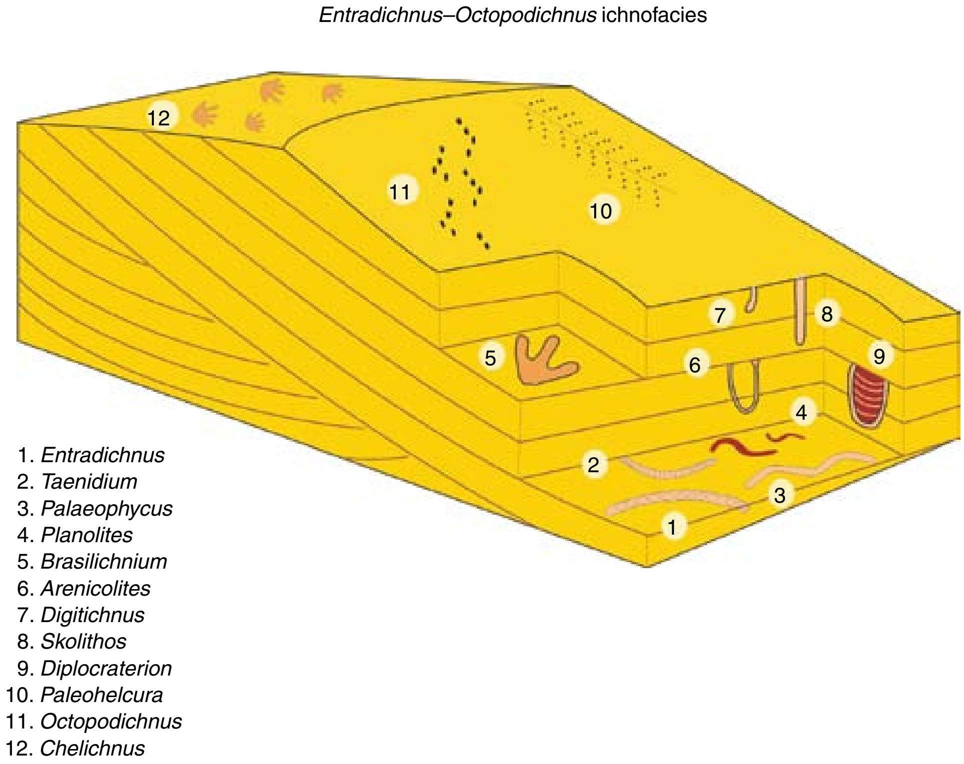

Figure 4.21 Schematic reconstruction of the *Octopodichnus–Entradichnus* ichnofacies.

ichnofacies undoubtedly results from disparate databases. Hunt and Lucas (2007) based the *Octopodichnus* ichnofacies essentially on Permian eolian dunes, the Coconino Sandstone of Arizona being the classic example. In contrast, the *Entradichnus* ichnofacies of Ekdale *et al*. (2007) is mostly based on the study of Jurassic examples, more specifically the Navajo Sandstone of Utah. Differences may result from the fact that a change in eolian ichnofaunas seems to have occurred by the Permian–Triassic transition with the appearance of more varied behavioral patterns, and an increase in infaunal bioturbators (Gradzinski and Uchman, 1994; Buatois *et al*., 1998c) (see Section 14.2.6). Both datasets are integrated and combined here in a single ichnofacies, referred to as the *Octopodichnus–Entradichnus* ichnofacies (Buatois and Mángano, 2008b). Further studies in eolian ichnofaunas should be undertaken in order to refine the characterization of this ichnofacies.

4.5 VERTEBRATE ICHNOFACIES

Lockley *et al*. (1994) first proposed a series of vertebrate ichnofacies. However, subsequent work by Hunt and Lucas (2007) demonstrated that those tetrapod ichnofacies should be considered ichnocoenoses because they represent the traces of specific communities that lack the recurrence that would warrant their consideration as archetypal ichnofacies. Accordingly, these authors re-evaluated vertebrate ichnofacies and defined five archetypal tetrapod ichnofacies for continental and coastal-plain environments: *Chelichnus, Grallator, Brontopodus, Batrachichnus*, and *Characichichnos* ichnofacies. In turn, they subdivided these ichnofacies into stratigraphically restricted, age-controlled ichnocoenoses. Vertebrate ichnofacies commonly have less temporal recurrence than their invertebrate counterparts. Hunt and Lucas (2007) suggested that vertebrate ichnofacies may provide greater resolution in terrestrial environments and that invertebrate ichnofacies may be of greater precision in subaqueous freshwater environments. However, recent developments in terrestrial invertebrate ichnology suggest increasing refinement of the paleosol ichnofacies model (Genise *et al*., 2010a). Some of the vertebrate ichnofacies directly correlate with invertebrate ichnofacies (e.g. *Chelichnus* and *Octopodichnus–Entradichnus* ichnofacies), while others may encompass more than one invertebrate ichnofacies (e.g. *Characichichnos* ichnofacies covering both the *Mermia* and *Skolithos* ichnofacies), or may represent a subdivision of an invertebrate ichnofacies (*Grallator*, *Brontopodus*, and *Batrachichnus* ichnofacies as subdivisions of the *Scoyenia* ichnofacies) (see Hunt and Lucas, 2007, Fig. 1). Freshwater invertebrate ichnofacies are controlled by the position of the water table and terrestrial invertebrate ichnofacies essentially by climate and plant formation. However, elucidation of the controlling factors in delineation and distribution of vertebrate ichnofacies requires further research. Recent work seems to indicate that the distribution of tetrapod trace fossils is more related to regional factors, such as climate and resource availability, than to local environmental factors at the scale of subenvironments (Krapovickas, 2010).

4.5.1 *CHELICHNUS* ICHNOFACIES

The *Chelichnus* ichnofacies was defined by Hunt and Lucas (2007) to replace the *Laoporus* ichnofacies formerly introduced by Lockley *et al*. (1994). It is characterized by: (1) dominance of tetrapod trackways whose manual and pedal tracks are equant in shape, subequal in size, and have short digit impressions; and (2) low ichnodiversity. *Chelichnus* and *Brasilichnium* are common elements. This ichnofacies occurs in dune faces of eolian environments (see Section 10.4). The *Chelichnus* ichnofacies encompasses two ichnocoenoses: the *Chelichnus* and the *Brasilichnium* ichnocoenoses (Hunt and Lucas, 2007). The former is common in the Permian, while the latter occurs in the Triassic and Jurassic. Overall the *Chelichnus* ichnofacies ranges in age from the Permian to the Jurassic. It correlates with the *Octopodichnus*–*Entradichnus* ichnofacies in the invertebrate realm.

4.5.2 *GRALLATOR* ICHNOFACIES

The *Grallator* ichnofacies was defined by Hunt and Lucas (2007) and represents a refinement of several ichnofacies formerly introduced by Lockley *et al*. (1994) and Lockley (2007) that are now regarded as ichnocoenoses. It is characterized by: (1) dominance of trackways of trydactil avian and non-avian theropods or other bipeds; and (2) moderate ichnodiversity. Typical components are *Grallator*, *Jindongornipes*, *Koreanoformis*, *Avipeda*, *Brachychirotherium*, *Rhychosauroides*, and *Eubrontes*. Environmentally, this ichnofacies typifies lacustrine shorelines (see Section 10.3). The *Grallator* ichnofacies includes four ichnocoenoses: the *Grallator*, *Eubrontes*, *Jindongornipes*, and *Avipeda* ichnocoenoses (Hunt and Lucas, 2007). The *Grallator* ichnocoenosis is typical of Late Triassic, the *Eubrontes* ichnocoenosis occurs in the Early Jurassic, the *Jindongornipes* ichnocoenosis is present in Early Cretaceous rocks, and the *Avipeda* ichnocoenosis (shorebird ichnofacies of Lockley *et al*., 1994) characterizes Cenozoic assemblages. Overall the *Grallator* ichnofacies ranges in age from the Triassic to the Recent.

4.5.3 *BRONTOPODUS* ICHNOFACIES

The *Brontopodus* ichnofacies was introduced by Hunt and Lucas (2007). As in the case of the *Grallator* ichnofacies, the *Brontopodus* ichnofacies encompasses several ichnofacies formerly introduced by Lockley *et al*. (1994) that are considered to be ichnocoenoses by Hunt and Lucas (2007). The *Brontopodus* ichnofacies is characterized by: (1) dominance of trackways of terrestrial herbivores; (2) subordinate presence of trackways of terrestrial carnivores; and (3) moderate ichnodiversity. Typical components of this ichnofacies are *Caririchnium*, *Ceratopsipes*, *Amblydactylus*, and *Brontopodus*. The *Brontopodus* ichnofacies tends to occur in coastal-plain to shoreline environments, including lacustrine margins (see Section 10.3). Therefore, there is some environmental overlap between the *Grallator* and *Brontopodus* ichnofacies, the latter encompassing, in addition, marine shorelines. Additional work is required to evaluate which specific controlling factors are involved in both ichnofacies (Krapovickas, 2010). The *Brontopodus* ichnofacies encompasses five ichnocoenoses: the *Parabrontopus*, *Caririchnium*, *Ceratopsipes*, *Amblydactylus*, and *Brontopodus* ichnocoenoses (Hunt and Lucas, 2007). The *Parabrontopus* ichnocoenosis occurs in Late Jurassic lacustrine shorelines, the *Caririchnium* ichnocoenosis is typical of Early Cretaceous clastic marine shorelines, the *Ceratopsipes* ichnocoenosis is present in Late Cretaceous coastal plains, the *Amblydactylus* ichnocoenosis characterizes Early to Late Cretaceous clastic marine shorelines, and the *Brontopodus* ichnocoenosis typifies Early Cretaceous carbonate marine shorelines. The *Brontopodus* ichnofacies ranges in age from the Jurassic to the Cretaceous.

4.5.4 *BATRACHICHNUS* ICHNOFACIES

The *Batrachichnus* ichnofacies was introduced by Hunt and Lucas (2007). This ichnofacies is characterized by: (1) dominance of trackways of quadrupedal carnivores; and (2) moderate ichnodiversity. Typical components are *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Dromopus, Dimetropus*, *Gilmoreichnus*, and *Chirotherium*. This ichnofacies represents a wide variety of environments ranging from distal alluvial fans, and fluvial plains to tidal flats (see Sections 10.2 and 7.2). Two ichnocoenoses are recognized within the *Batrachichnus* ichnofacies: the *Batrachichnus* and *Chirotherium* ichnocoenoses (Hunt and Lucas, 2007). The former is typically Early Carboniferous–Early Permian while the latter is Triassic. Overall the ichnofacies ranges from the Devonian to the Triassic.

4.5.5 *CHARACICHICHNOS* ICHNOFACIES

Hunt and Lucas (2007) proposed the *Characichichnos* ichnofacies. This ichnofacies is characterized by (1) dominance of swimming tracks and trails; and (2) moderate ichnodiversity. Typical components are *Characichichnos*, *Undichna*, *Lunichnium*, *Puertollanopus*, *Serpentichnus, Batrachichnus*, and *Hatcherichnus*. This ichnofacies represents lacustrine settings and inner zones of tide-dominated estuaries (see Sections 10.3 and 8.1.2). Three named ichnocoenoses have been recognized: *Serpentichnus*, *Characichichnos*, and *Hatcherichnus* (Hunt and Lucas, 2007). The *Serpentichnus* ichnocoenosis occurs in the late Paleozoic, the *Characichichnos* ichnocoenosis is of Middle Jurassic age, and the *Hatcherichnus* is present in Upper Jurassic strata. In terms of correlation with invertebrate ichnofacies, the *Characichichnos* ichnofacies commonly overlap with the *Mermia* ichnofacies in lacustrine settings. In the case of late Paleozoic inner-estuarine deposits (*Serpentichnus* ichnocoenosis), it is typically associated with a mixed *Scoyenia*–*Mermia* ichnofacies.

4.6 PITFALLS AND CONFUSIONS IN ICHNOFACIES ANALYSIS

Despite the efforts of many workers in addressing the ichnofacies model (e.g. Frey and Pemberton, 1984; Pemberton *et al*.,

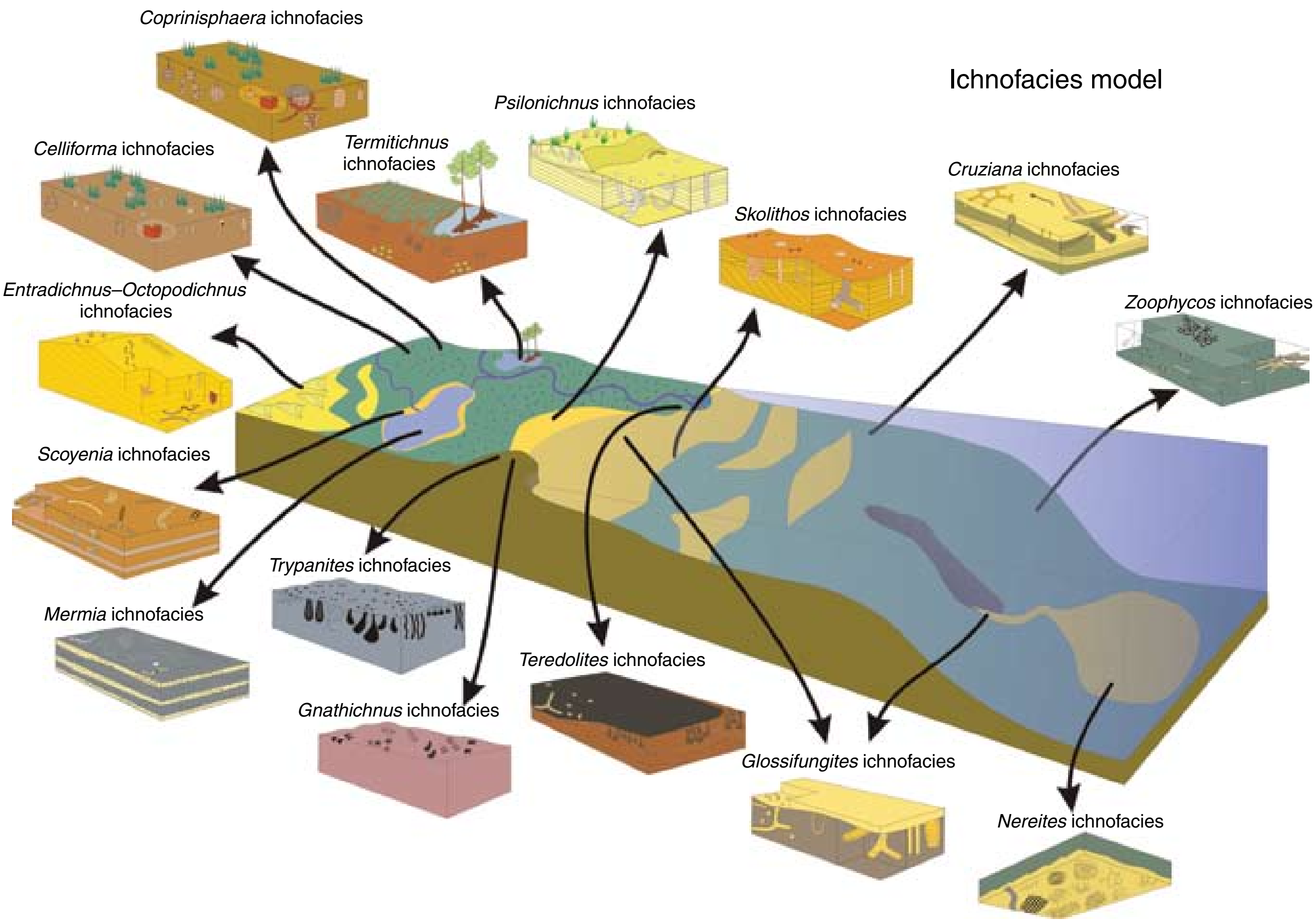

Figure 4.22 Schematic illustration of the ichnofacies model for invertebrate trace fossils. Individual ichnofacies indicate a precise set of environmental conditions rather than a depositional environment.

2001; MacEachern *et al.*, 2007a), it is impossible to avoid the feeling that this model is still poorly understood. Because the ichnofacies model has been historically seen by some authors (e.g. Goldring, 1993, 1995) as competing against the ichnofabric approach, it will be discussed and evaluated in more detail at the end of the next chapter, which deals with ichnofabrics. However, some comments seem pertinent here.

A common misconception is to assume a direct correlation between ichnofacies and depositional environments. Ichnofacies are not indicators of sedimentary environments, but reflect the complex interplay of a set of environmental factors (Fig. 4.22). As expressed by Frey *et al.* (1990), ichnofacies are not intended to be paleobathymeters either. A well-known and repeated example is the occurrence of the *Skolithos* ichnofacies, typical of nearshore settings, in offshore tempestites and deep-marine turbidites (e.g. Crimes, 1977; Pemberton and Frey, 1984a; Pemberton and MacEachern, 1997). The *Cruziana* ichnofacies, though typical of lower-shoreface to offshore deposits, may be present in shallower settings, commonly intertidal flats of tide-influenced shorelines (e.g. Mángano *et al.*, 2002a; Mángano and Buatois, 2004a, b). Regardless of the depositional environment, it is the animal response to a set of particular environmental conditions that defines an ichnofacies.

This is also true for continental ichnofacies and, therefore, the search for exact equivalences between continental ichnofacies and depositional environments is futile. Individual invertebrate ichnofacies occur in a wide variety of environmental settings. In these cases, water availability is a fundamental control in trace-fossil distribution (Gierlowski-Kordesch, 1991) and sediment water content strongly influences substrate consistency. The role of substrate consolidation as controlling trace-fossil preservation is remarkable (e.g. Buatois *et al.*, 1997a; Buatois and Mángano, 2002, 2004a, 2007) and the *Scoyenia* and *Mermia* ichnofacies can be seen, at least in some sense, as taphofacies *sensu* Bromley and Asgaard (1991). As is the case of substrate-controlled ichnofacies in marine carbonates (e.g. Bromley, 1975), a single continental bed may represent the activity of more than one substrate-controlled suite, revealing the presence of composite ichnofacies (Buatois and Mángano, 2002, 2004a; Scott *et al.*, 2009).

Further confusion derives from the idea that ichnofacies characterization is equivalent to the mere listing of presence or absence of morphological patterns, as in the approach undertaken by Keighley and Pickerill (2003) to analyze continental ichnofacies. There are two main flaws in this approach (see also Melchor *et al.*, 2006 for a critical re-evaluation). First, an ichnofacies is more than a collection of morphologies. Just to name a few additional aspects, ichnodiversity, relative abundance of their different components, preservational styles, and trophic types represented are equally important. Second, mere documentation of the presence of certain morphologies, albeit "objective", may not be informative because without a proper analysis in terms of functional morphology and behavior involved, the actual significance of the trace fossil cannot be evaluated (see Section 2.1). For example, group I of Keighley and Pickerill (2003) is labeled "Systematic-coverage branching burrow networks", and is exemplified by *Paleodictyon* and *Vagorichnus*. However, both ichnotaxa have little in common with respect to behavior, feeding strategies, and preservational style and, therefore, the presence of group I in a particular trace-fossil assemblage does not provide any precise information. Obviously, ichnofacies characterization and recognition imply to a certain degree interpretation, but this is intrinsic to any scientific enterprise: there is no algorithm that allows us to recognize an ichnofacies or to interpret a depositional environment.

Another misunderstanding is the idea that ichnofacies can be replaced by ichnocoenosis (e.g. Hasiotis, 2004). Both are very different notions and are applicable to different scales of analysis, so replacing ichnofacies by ichnocoenosis is not advisable, in fact, it is not possible without damaging the hierarchical conceptual framework of ichnology (Bromley *et al.*, 2007) (see Box 1.1). Ichnofacies are not real entities of the biological world, but constructs. One ichnofacies embraces a number of recorded ichnocoenoses in the fossil record and an unknown number of potential ichnocoenoses awaiting to be identified; here is rooted the predictive strength of the ichnofacies model. The ichnofacies extracts the biological signal to a complex interplay of physical parameters. In short, attempts to replace ichnofacies by ichnocoenosis represent a step backward in our search for common themes that allow us to use trace fossils as a predictive tool in facies modeling.

Finally, a common pitfall is the assertion that if a particular trace-fossil assemblage or ichnocoenosis cannot readily be ascribed to one ichnofacies, then the ichnofacies model is not valid (e.g. Hasiotis, 2004). On the contrary, the ichnofacies model serves as a norm and departures may serve to recognize anomalous situations. For example, the absence of the *Cruziana* ichnofacies in offshore deposits may be linked to the presence of some stress factor (e.g. limited oxygen). In the absence of a norm that helps in establishing predictions, it would be impossible to detect an anomaly, and any attempt to link a certain set of biogenic structures with environmental factors would be doomed.

5 The ichnofabric approach

> I confess frankly, it was the warning voice of David Hume that first, years ago, roused me from dogmatic slumbers, and gave a new direction to my investigations in the field of speculative philosophy.
>
> Immanuel Kant
> *Critique of Pure Reason* (1781)

> We now come to the more immediate subject of this volume, namely the amount of earth which is brought up by worms from beneath the surface.
>
> Charles Darwin
> *The Formation of Vegetable Mould Through the Action of Worms with Observations on their Habits* (1881)

The ichnofabric approach represents a relatively new trend in ichnology that started in the second half of the eighties, becoming much more popular since the nineties. As is the case of the ichnofacies model, the ichnofabric approach has been frequently misunderstood. Earlier studies involving ichnofabrics put too much emphasis on assessing bioturbation and other more significant aspects, such as tiering or evaluation of successive bioturbation events, were commonly overlooked. Even worse, the idea that measuring the intensity of bioturbation could replace trace-fossil identification as ground data for paleoenvironmental interpretations persisted for some years. At present, the idea that ichnofabric analysis is simply measuring the degree of bioturbation has been mercifully abandoned by all serious workers. If the ichnofabric approach is understood as a comprehensive way of analyzing bioturbated deposits, then the wealth of information that may be obtained is huge and not only restricted to paleoenvironmental reconstructions but also of significant potential in understanding reservoir properties, benthic paleoecology, and evolutionary paleoecology. German philosopher Immanuel Kant expressed that his reading of his British peer David Hume roused him from his dogmatic slumber and led him to become a "critical philosopher". In the same vein, the focus of this chapter, the ichnofabric approach, with its emphasis on taphonomic aspects, helps us to avoid taking the trace-fossil record at face value, permeating the whole interpretative process with some healthy criticism. We will start by providing the basics of the tiering concept before moving into a review of the ichnofabric concept, including aspects of quantifying the degree of bioturbation, visual strategies to present ichnofabric data, the paramount role of taphonomy, and the different types of ichnofabrics. Then, we will present the concept of ichnoguild, which, in our view, is central to the ichnofabric approach. Later, we will briefly review recent developments in the field of paleosol ichnofabrics. We will then address the general role of bioturbation, bioerosion, and biodeposition, before moving to the issue of bioturbation-enhanced permeability and reservoir characterization, a recently developed topic, which is having a strong impact in the petroleum industry. Finally, we will compare the ichnofacies and ichnofabric approaches.

5.1 TIERING

Tiering consists of the vertical partitioning of the habitat (Ausich and Bottjer, 1982; Bromley and Ekdale, 1986). It is in fact a synonym of ecological stratification (Seilacher, 1978), but this may be confused with the current use that geologists give to the term "stratification", and has not met with acceptance. Subaqueous substrates occupied by endobenthic communities are vertically zoned as a response to physical, chemical, and biological parameters (Bromley, 1990, 1996). Also, the water column displays vertical partitioning, and epifaunal and infaunal suspension-feeding animals obtain their food at several levels above the sediment surface (Ausich and Bottjer, 1982).

The tiering concept applied to the study of endobenthic communities has been incorporated in ichnology. The most important environmental factors that control tiering of endobenthic communities are consolidation of the substrate, organic matter, and oxygen (Bromley, 1990, 1996). Sediment compaction due to vertical accretion of the sea floor and progressive burial leads to dewatering and an increase in substrate consistency. As a result, shallow-tier organisms burrow in poorly compacted soft sediment, while deeper structures are emplaced in dehydrated and firm sediment (Bromley and Ekdale, 1986). The vertical distribution of organic matter displays a peak in abundance in the proximity of the sediment–water interface, resulting in the profusion of detritus and shallow-tier deposit feeders. Deeper within the sediment, organic matter decreases in abundance, resulting in a reduction of the biomass (Bromley, 1990, 1996). Oxygen content follows a similar trend, decreasing within the sediment; the redox discontinuity separates oxic from anoxic sediment.

Studies on modern ocean sediments allow reconstruction of the tiered structure of the infaunal community (Berger *et al.*, 1979; Ekdale *et al.*, 1984). The uppermost centimeters of the sediment are referred to as the mixed zone. In this zone, sediment is saturated in water and totally homogenized by bioturbation, but no discrete traces are recognized. Below this zone lies the transition zone, which is extremely heterogeneous due to the activity of deep burrowers, and displays tiered endobenthic communities (Savrda, 1992). The deepest sediment zone is the historical zone, which is located beyond the reach of even the deepest burrowers and, therefore, does not display active bioturbation. Because of continuous vertical accretion of sea-floor sediment, the mixed and transition zones of a given time are buried and become the historical zone. The typical record consists of an indistinctive burrow mottling formed in the mixed zone overprinted by well-defined discrete traces emplaced in the transition zone.

Unraveling the tiering structure of fossil examples can be a difficult task particularly in intensely bioturbated deposits in which trace fossils display complex cross-cutting relationships. The tiering structure and timing of emplacement in a given ichnofabric can be established by looking at cross-cutting relationships, burrow walls, and burrow fill, and by comparisons with modern examples (Bromley and Ekdale, 1986; Bromley, 1990, 1996; Taylor *et al.*, 2003). Under vertical accretion of the sea floor due to suspension fallout, deeper structures cross-cut shallow traces. If the rate of sedimentation is too low, the shallow-tier structures are totally obliterated by the activity of deep bioturbators. In addition, deep-tier trace fossils display well-defined morphologies and sharp boundaries as a result of their emplacement in stiffer substrates. Burrow-fills of these deep-tier structures tend to contrast with the host rock, reflecting active particle sorting by the organisms or material that is piped down from the surface (Bromley, 1990, 1996; Taylor and Goldring, 1993). Furthermore, deep-tier trace fossils are filled with chemically dynamic material (e.g. fecal sediment, surface material, metabolic products) within the reducing organic-poor host sediment, therefore promoting the formation of a digenetic microenvironment that helps to initiate mineralization, enhancing the visibility of the biogenic structures (Bromley, 1990, 1996). As a result, the preservation potential and visibility of deep-tier trace fossils is higher than those of shallower structures (Wetzel and Werner, 1981; Werner and Wetzel, 1982).

5.2 ICHNOFABRICS: CONCEPTS AND METHODS

An ichnofabric refers to any aspect of the texture and internal structure of a substrate resulting from bioturbation and bioerosion at any scale (Bromley and Ekdale, 1986). The related term bioturbate texture (Frey, 1973) shares many aspects in common with ichnofabric, but it does not include textures and structures resulting from bioerosion, and has not been extensively used. Application of the ichnofabric concept to paleoenvironmental reconstructions resulted in the so-called "ichnofabric approach". This approach represents a relatively new trend in ichnology that has been actively promoted since the organization of the first of a series of ichnofabric workshops in 1991. In more traditional ichnological studies, there is commonly a tendency to analyze only those structures that one can classify following current ichnotaxonomic procedures (i.e. discrete trace fossils). However, both discrete traces and poorly defined burrow mottling are taken into consideration in the ichnofabric approach (Bottjer and Droser, 1991). In addition, ichnofabric analyses are usually based on observations in cross-sections, where cross-cutting relationships and tiering structure can be evaluated. As with the ichnofacies model, the ichnofabric approach emphasizes the synecology of the endobenthic community, although an ichnofabric may represent the work of more than one community. However, tiering analysis is a key component of the ichnofabric approach, but has not been traditionally included within the ichnofacies paradigm.

5.2.1 QUANTIFYING BIOTURBATION AND ILLUSTRATING ICHNOFABRICS

Initially, a lot of effort was devoted to scaling degree of bioturbation. An early scheme was proposed by Moore and Scrutton (1957), but the proposal by Reineck (1963, 1967) is the one that has gained subsequent acceptance (e.g. Howard and Frey, 1975; Frey and Wheatcroft, 1989; Taylor and Goldring, 1993; Taylor *et al.*, 2003). In Reineck's scheme seven grades of bioturbation are distinguished, ranging from 0 for unbioturbated sediments to 6 for those that have undegone complete bioturbation. Subsequently, Droser and Bottjer (1986, 1989) put forward a semiquantitative field classification of ichnofabrics based on five ichnofabric indexes displayed by a series of flashcards designed for different environmental situations (e.g. high-energy clastics with *Ophiomorpha* or *Skolithos*, pelagic fine-grained sediments with mottlings). Although quite attractive in terms of providing a visual aid to evaluate bioturbation intensity, it needs to be used with caution because it does not address the composite nature of most ichnofabrics. More recently, Taylor and Goldring (1993) defined bioturbation indexes based on the categories established by Reineck. However, they noted that the original grades proposed by Reineck were based on a measurement of the percentage area bioturbated, although bioturbation should be measured as a unit volume per unit time, as stated by Frey and Wheatcroft (1989). Because such a procedure is extremely time consuming and difficult to follow, Taylor and Goldring (1993) favored a descriptive approach instead of a semiquantitative one. Accordingly, they maintained the original categories by Reineck, but based their definition in terms of burrow density, amount of burrow overlap, and the sharpness of the original fabric (Fig. 5.1). This scheme has been adopted in many ichnological studies because it is more precise and particularly appropriate for describing composite ichnofabrics (Ekdale and Bromley, 1991). In addition, as noted by Frey and Pemberton (1991), to characterize an unbioturbated layer with a bioturbation index of 0 (Taylor and Goldring, 1993) seems to be more logical than using an ichnofabric index of 1 (Droser and Bottjer, 1986, 1989). Another scheme by Miller and Smail (1997) is used to establish the density of biogenic structures along bedding planes, while that of Montague *et al.* (2010) has been proposed for microbioerosion.

Scaling of bioturbation is important because the establishment of well-defined grades conveys more information than simply stating that sediment is sparsely bioturbated or intensely bioturbated. However, other aspects, such as tiering or evaluation of successive bioturbation events, should not be overlooked.

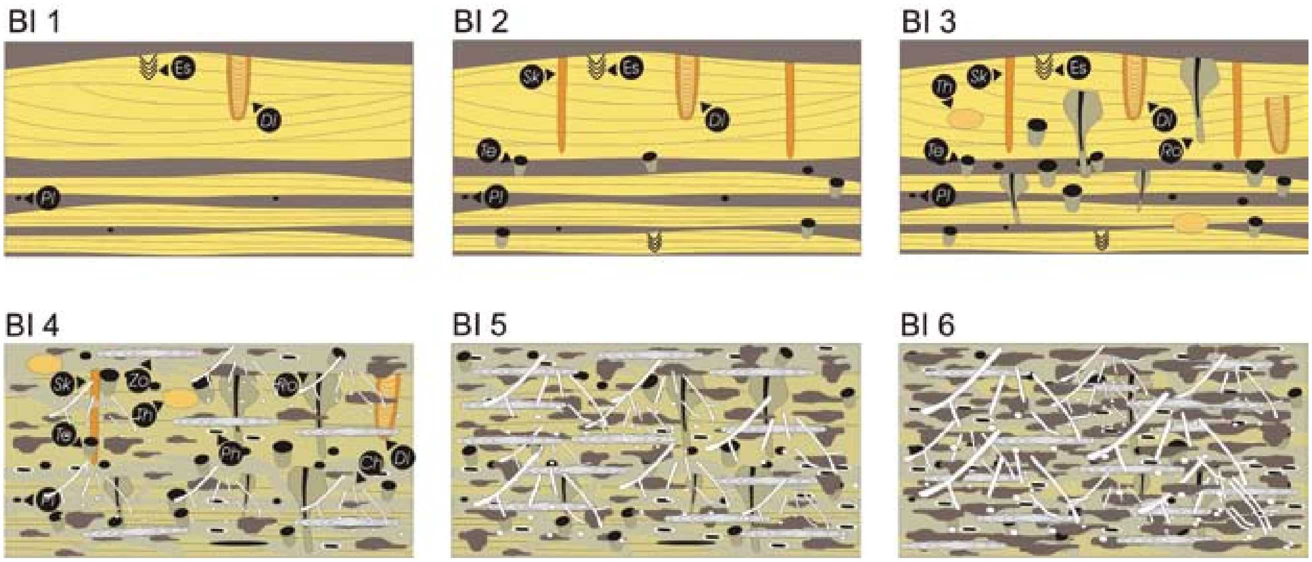

Figure 5.1 Graphic illustration of the different categories of bioturbation index of Taylor and Goldring (1993). BI = 0 is characterized by no bioturbation (0%). BI = 1 (1–4%) is for sparse bioturbation with few discrete traces. In the example illustrated, a few biogenic structures, such as *Planolites* (*Pl*), *Diplocraterion* (*Di*) and escape trace fossils (Es), exist in the storm and fair-weather deposits. BI = 2 (5–30%) is represented by low bioturbation in sediment that still has preserved sedimentary structures. This is illustrated by the presence of a number of burrows, including *Planolites* (*Pl*), *Diplocraterion* (*Di*), *Teichichnus*(*Te*), *Skolithos* (*Sk*), and escape trace fossils (Es), in both storm and fair-weather deposits. BI = 3 (31–60%) describes an ichnofabric with discrete trace fossils, moderate bioturbation and still distinguishable bedding boundaries. In addition to the ichnotaxa previously mentioned, *Thalassinoides* (*Th*) and *Rosselia* (*Ro*) are added in the example. BI = 4 (61–90%) is represented by intense bioturbation, high trace-fossil density, common overlap of trace fossils, and primary sedimentary structures are mostly erased. Some deep-tier trace fossils, such as *Zoophycos* (*Zo*) and *Chondrites* (*Ch*), are added in the example, together with undifferentiated burrow mottlings. BI = 5 (91–99%) is characterized by sediment with completely disturbed bedding and intense bioturbation. BI = 6 (100%) is for completely bioturbated and reworked sediment, related to repeated overprinting of trace fossils.

Visual graphics are useful to illustrate the main characteristics and origin of ichnofabrics. In particular, Taylor and Goldring (1993) proposed ichnofabric constituent diagrams as a way to illustrate the type and size of trace fossils, the percentage of bioturbated area, the depth and order of emplacement of each ichnotaxon, and the associated physical sedimentary structures in an ichnofabric. Although these diagrams summarized a large amount of data, they may be hard to visualize in some cases and their elaboration is rather time consuming. A more straightforward way of illustrating ichnofabrics was suggested by Bromley (1996), who combined ichnofabric icons, tiering diagrams, and estimation of degree of bioturbation for each tier (Fig. 5.2).

5.2.2 TAPHONOMY OF ICHNOFABRICS

One of the most important lessons learnt from the ichnofabric approach is the importance of taphonomy (Bromley, 1990, 1996). As in the case of body fossils, the fossilization barrier is a powerful taphonomic filter that separates the vast amount of biogenic structures produced in the sediment from the small proportion that become fossilized, passing to the trace-fossil record (Seilacher, 1967a). Trace fossils are subjected to their own taphonomic rules that result in a series of preservational biases. A careful evaluation of the taphonomic aspects involved helps to avoid the pitfalls associated with a naive reading of the trace-fossil record. The different biogenic structures produced in the sediment have variable preservation potential (Fig. 5.3a–c). Accordingly, the preserved ichnofabrics do not represent the exact copy of the original endobenthic community. As noted previously, although most of animal activity is concentrated in the uppermost centimeters of the substrate, the preservation potential of these shallow-tier structures is very low. In contrast, some deep-tier structures produced by mobile tracemakers represent the activity of key bioturbators that may obliterate any evidence of shallower tiers (Fig. 5.4a). Therefore, these deep-tier trace fossils are commonly the dominant component in an ichnofabric and have been referred to as elite trace fossils (Bromley, 1990, 1996). Also, elite trace fossils may be produced by preferential diagenesis. For example, *Thalassinoides* may be diagenetically enhanced due to the formation of minerals and associated concretionary growth (Bromley and Ekdale, 1984a) (Fig. 5.5). Unfortunately, shallow-tier traces are most sensitive to environmental fluctuations because they are formed close to the sediment–water interface, while deep-tier traces do not reflect sea-bottom conditions with such precision (Bromley and Ekdale, 1986). This problem lies at the core of the current controversies surrounding the paleoenvironmental implications of the *Zoophycos* ichnofacies (see Section 4.3.4). In fact, overlooking the taphonomic bias of some intensely bioturbated ichnofabrics may result in erroneous interpretations. Monospecific ichnofaunas are commonly linked to stress factors (e.g. dysaerobic or brackish-water conditions) typical of unstable environments. However, if monospecific ichnofaunas occur in intensely bioturbated ichnofabrics resulting from the activity of deep bioturbators, the low ichnodiversity may be a taphonomic artifact that reflects slow rates of sedimentation in a very stable environment.

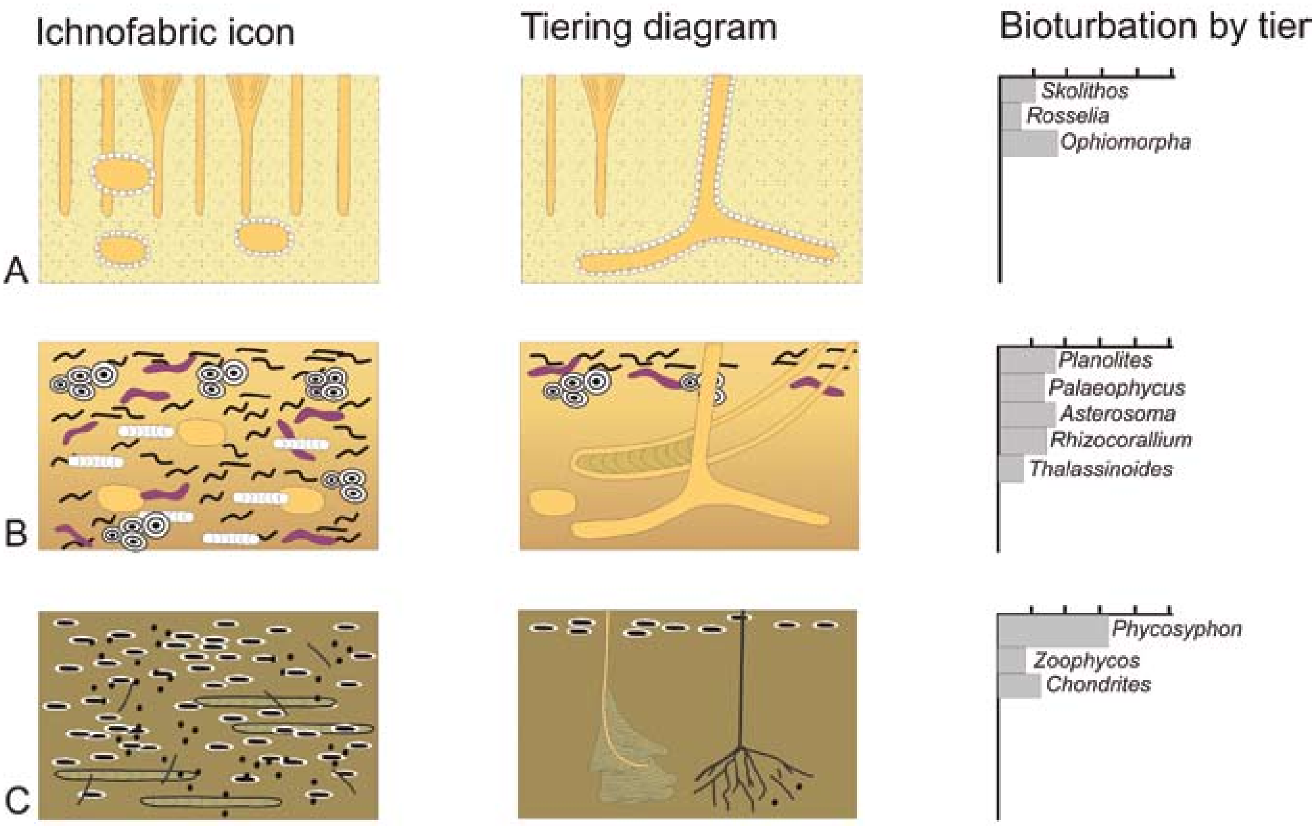

Figure 5.2 Visualization of ichnofabrics using ichnofabric icons, tiering diagrams and percentage of bioturbation per tier according to Bromley (1996). (a) Ichnofabric dominated by mid- to deep-tier vertical burrows in a high-energy middle-shoreface sandstone. (b) Ichnofabric characteristic of a low-energy offshore, displaying a complex tiering structure. (c) Ichnofabric of low-energy shelf deposits displaying low diversity of trace fossils and a combination of shallow and deep tiers.

In short, although degree of bioturbation and ichnodiversity are two different aspects (see Section 6.3), they should be considered in conjunction while performing an ichnological study.

Exceptionally shallow-tier structures may be preferentially preserved in the fossil record, commonly forming frozen-tiering profiles (Savrda and Bottjer, 1986). A typical example is related to episodic sedimentation that leads to cessation of bioturbation due to rapid burial (Orr, 1994) (Fig. 5.4b). Preservation of upper tiers is complete under no erosion and partial if some erosion is involved (Fig. 5.4c). The classic example is the preservation of shallow-tier graphoglyptids at the base of thin-bedded turbidites (e.g. Seilacher, 1962; Kern, 1980; Uchman, 1995). Similar situations may occur in distal tempestites of shallow-marine environments and ash fall deposits of volcanic terranes. When erosion occurs and the tiering structure of the endobenthic community is known, estimation of the minimum amount of erosion of the sea floor can be established based on the study of the washed-out tiers preserved as casts on the base of the event bed, thereby providing a measure of stratigraphic completeness (Wetzel and Aigner, 1986). A different way of generating frozen tiering profiles is due to a rapid deoxygenation event that leads to an immediate suppression of bioturbation and the preservation of all tiers, including those formed in the mixed zone (Savrda and Ozalas, 1993) (Fig. 5.4d). This situation is common in oxygen-depleted pelagic settings, typically shelf to deep-marine environments (see Section 6.1.3). Shallow-tier trace fossils can also be preserved in environments characterized by short breaks in sedimentation and, therefore, short duration of the colonization window (see Section 6.1.3). This is typical of slack-water deposition in intertidal settings, followed by minimal erosion during deposition of the subsequent flood or ebb event, as illustrated by tidal rhythmites in inner-estuarine settings (e.g. Buatois *et al.*, 1997b). Another excellent example of preservation of very shallow-tier structures occurs in Burgess Shale-type deposits. In this case, pristine preservation of subsuperficial structures results from the absence of deep-tier bioturbation (the *Zoophycos–Chondrites* ichnoguild) in dysoxic settings below storm wave base (Mángano, 2011) (see Sections 6.1.3 and 6.2).

5.3 TYPES OF ICHNOFABRICS

Two main types of ichnofabrics, simple and composite (Box 5.1), have been recognized by Bromley and Ekdale (1986). Simple ichnofabrics result from the activity of a single endobenthic community at a given moment and are, therefore, the product of a single bioturbation or bioerosion event (Fig. 5.6a). They are commonly characterized by single-tier colonization as a result of the activity of opportunistic forms (Taylor *et al.*, 2003). In this case, the associated colonization surface occurs at the top of the event bed. However, in other cases no colonization is involved and organisms may enter the event bed from

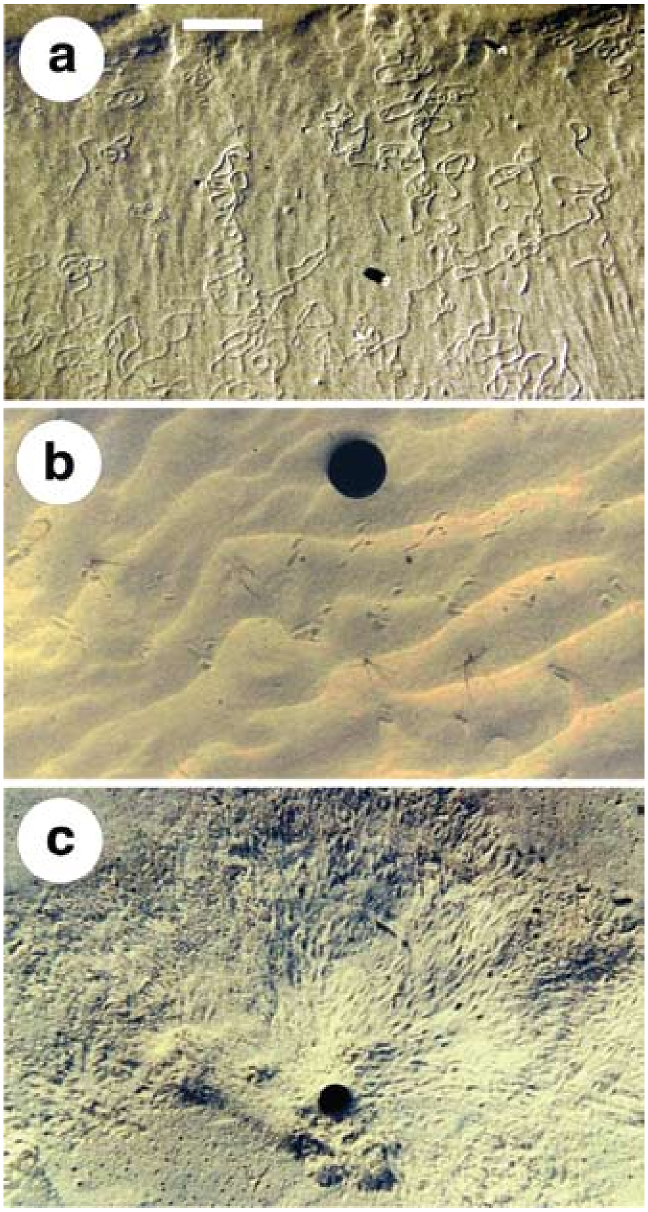

Figure 5.3 Variable preservation potential of intertidal biogenic structures. (a) Grazing trails produced on a tidal flat. Beach near Estancia Maria Luisa, Tierra del Fuego, Argentina. Scale bar is 2 cm. (b) Trackways produced by the crab *Uca* on a backshore. Aracaju, northeast Brazil. Lens cap is 5.5 cm. (c) Burrow entrance and scratch marks of the crab *Uca* in backshore sediments. Aracaju, northeast Brazil. Lens cap is 5.5 cm. The preservation potential of the trails, trackways, and scratch marks is essentially zero. The only structure with relatively high preservation potential is the *Uca* burrow (incipient *Psilonichnus*).

below by moving upwards, forming adjustment or escape trace fossils (Taylor *et al.*, 2003).

Composite ichnofabrics are much more common than simple ichnofabrics in the stratigraphic record, and are produced by the replacement of successive communities or by the upward migration of a tiered community. In the first case, community replacement results from a change in environmental conditions, such as a progressive increase in the degree of consolidation of a substrate, which is conducive to the cross-cutting of previously emplaced burrows by subsequent burrows and borings (e.g. Bromley, 1975; Mángano and Buatois, 1991; Lewis and Ekdale, 1992) (Fig. 5.6b). In the second case, vertical migration and trace-fossil cross-cutting reflect gradual accretion of the sea floor due to slow, steady sedimentation (Bromley and Ekdale, 1986; Orr, 1994) (Fig. 5.6c). An increase in substrate consistency results from compaction during vertical accretion of the substrate, leading to the emplacement of deeper burrows in a firmer substrate. However, no lithification is involved in the latter case and different tiers (deep-tiers cross-cutting shallower ones) are involved. Bedding planes displaying superposition of ichnocoenoses from successive communities are known as palimpsest surfaces.

A not always obvious case of composite ichnofabric is illustrated by a dense surface covered by *Lockeia siliquaria* in Carboniferous intertidal sandstones (Mángano *et al.*, 1998, 2002a). Detailed analysis of the surface reveals at least two colonization events, resulting in a palimpsest surface. The first bivalve population was eroded away, leaving only the basal resting structures. This was followed by sedimentation and a new colonization event. Cross-cutting relationships and burrow infill provide evidence for a composite ichnofabric in a monospecific trace-fossil assemblage. A similar situation may explain many occurrences of *Skolithos* and *Syringomorpha* ichnofabrics (e.g. Mángano and Buatois, 2004b; Desjardins *et al.*, 2010a) (Box 5.1). In the absence of clear colonization surfaces, the lack of lithological contrast in burrow infill from different populations makes it almost impossible to distinguish successive colonization events.

Although not always possible, establishing the colonization surface associated with each bioturbation or bioerosion event is of paramount importance in the analysis of composite ichnofabrics, because it allows the unraveling of the depositional history of the sedimentary unit and its associated environmental significance. In some cases, the environmental conditions operating at the time of deposition have little connection with those of the bioturbation or bioerosion event. The deeper a trace fossil is emplaced, the more cautious our approach should be in linking the colonization event with environmental conditions at the time of deposition. For example, coastal-eolian dune deposits may contain specimens of *Ophiomorpha*, penetrating from an overlying marine transgressive deposit. A careless examination of this situation may lead to the misinterpretation of *Ophiomorpha* as formed under terrestrial conditions. The problematic Lower Silurian fossil plant *Pinnatiramosus qianensis* has challenged our present knowledge on the origin and early evolution of vascular plants, which seem to have occurred by the Early Devonian. However, recent research suggests that the plant fossil is in fact a root system penetrating from overlying Permian deposits (Edwards *et al.*, 2007). Supposed Mesoproterozoic burrows have ended up as being identified as recent termite burrows emplaced within the Precambrian rocks (Cloud *et al.*, 1980).

5.4 THE ICHNOGUILD CONCEPT

Analysis of infaunal tiering structure suggests that organisms tend to group together within the same tier to exploit

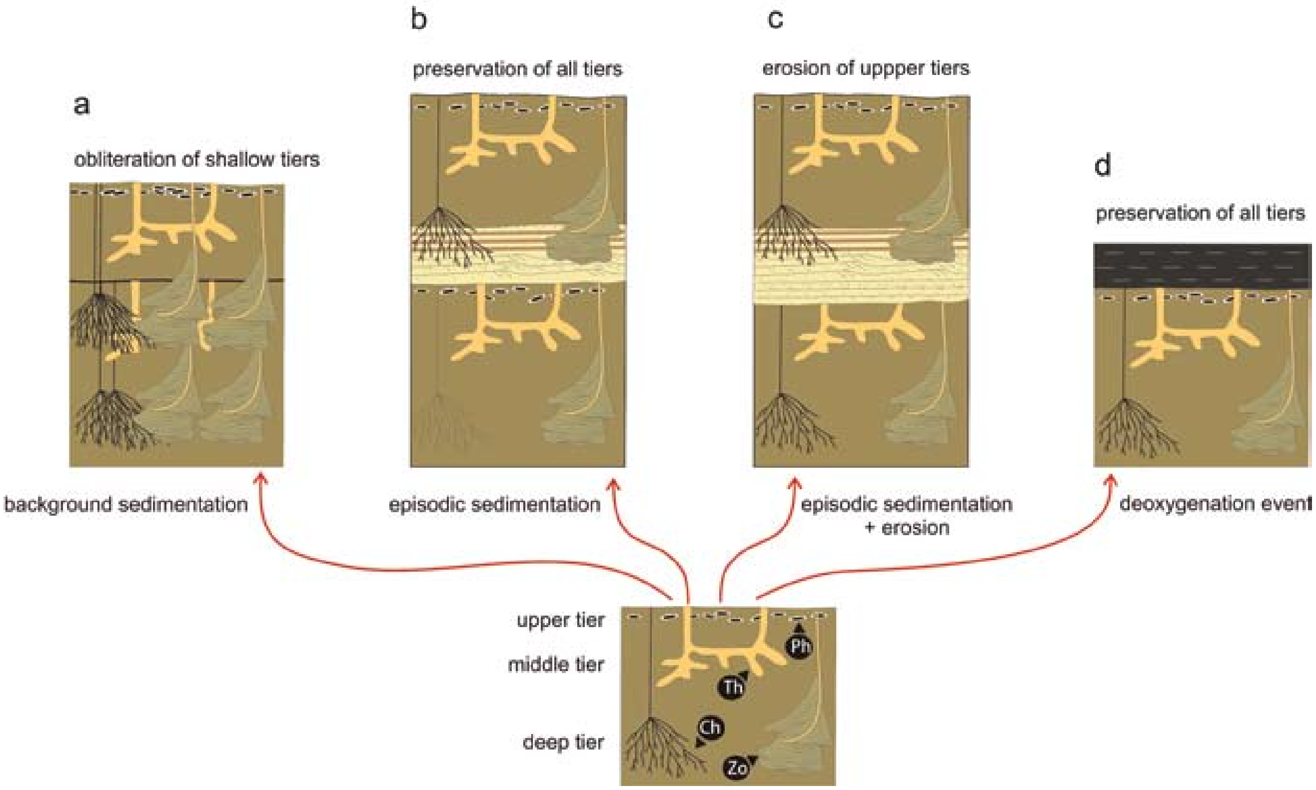

Figure 5.4 Formation of tiering profiles. (a) Tiering profiles formed during background sedimentation characterized by vertical accretion of the sea floor. Deep-tier structures migrate upwards to keep pace with sedimentation and obliterate shallow-tier structures. (b) Formation of frozen-tiering profiles associated with episodic sedimentation. In the absence of erosion, even the shallowest tiers are preserved. (c) With erosion, the upper tiers are removed. (d) Formation of frozen-tiering profiles associated with deoxygenation events that allow preservation of shallow tiers. *Phycosiphon* (*Ph*) represents the shallow tier, while *Thalassinoides* (*Th*) is a middle-tier form. *Chondrites* (*Ch*) and *Zoophycos* (*Zo*) make up the deep tier.

Figure 5.5 Nodular limestone containing *Thalassinoides* representing elite trace fossils. Upper Jurassic, Coralline Oolite Formation, Carr Naze, North Yorkshire Coast, England. Lens cap is 5.5 cm. see Fürsich (1972).

the same resources in similar ways. This fact led Bromley (1990, 1996) to propose the ichnoguild concept, following the utilization of the term guild in ornithology (Root, 1967) and invertebrate paleontology (Bambach, 1983). An ichnoguild reflects three parameters: (1) bauplan; (2) food source; and (3) use of space (Bromley, 1990, 1996) (Fig. 5.8). In terms of bauplan, biogenic structures are categorized as permanent to semi-permanent burrows produced by stationary organisms, or transitory structures made by vagile animals. Food source is reflected by trophic analysis of trace

Box 5.1 Simple and composite *Syringomorpha* ichnofabrics in Cambrian tidal flats and shorefaces

Lower to Middle Cambrian shallow-marine deposits of the Campanario Formation in northwest Argentina contain abundant *Syringomorpha* ichnofabrics. A high density of specimens occurs in intertidal areas, where they form a composite ichnofabric that records multiple colonization events (Fig. 5.7a). The composite nature of this ichnofabric is revealed by complex cross-cutting relationships of specimens. Pervasive bioturbation results from the activity of successive suites of deep-infaunal organisms. A high degree of bioturbation and preferential preservation of closely spaced, vertical components make this ichnofabric analogous to *Skolithos* pipe rock. Like *Skolithos* pipe rock, the *Syringomorpha* ichnofabric occurs in moderate- to high-energy settings, being particularly abundant in sand flats. Tide-dominated deposits are locally interbedded with storm-dominated facies. Bioturbation is sparse in these storm deposits. *Syringomorpha nilssoni* occurs in moderate to low densities in hummocky cross-stratified sandstone (Fig. 5.7b). This ichnofauna records opportunistic colonization after storms. Causative burrows extend from a colonization surface at the top of storm deposits, developing a wide spreite structure at the lower part of the tempestite. In contrast to tidal-flat examples, this ichnofabric is simple and represents a single bioturbation event following episodic sedimentation. The high density of vertical burrows in tidal-flat facies reveals that the "Agronomic Revolution" was not restricted to open-marine, shelfal environments (see Section 14.1.3). The depth and extent of bioturbation record colonization of a relatively deep-infaunal ecospace mostly by organisms feeding on epigranular microbes on sand grains and meiofauna.

Reference: Mángano and Buatois (2004b).

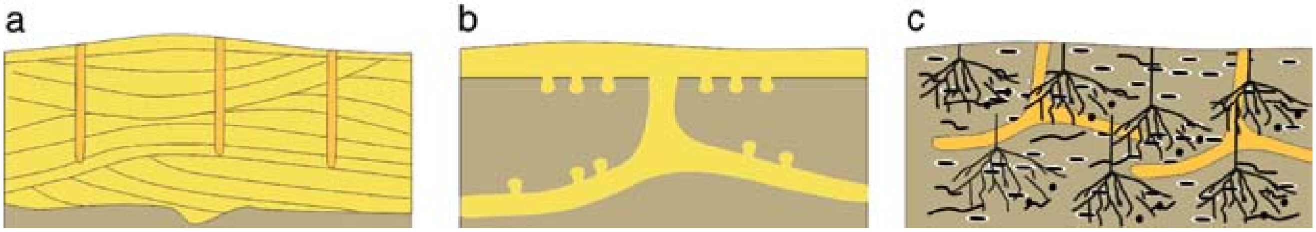

Figure 5.6 Types of ichnofabrics (a) Simple ichnofabric reflecting a single event of colonization after storm deposition. (b) Composite ichnofabric recording the replacement of a firmground trace-fossil suite by a hardground trace-fossil suite after substrate lithification. (c) Composite ichnofabric produced by the upward migration of a tiered community in response to vertical accretion of the sea floor.

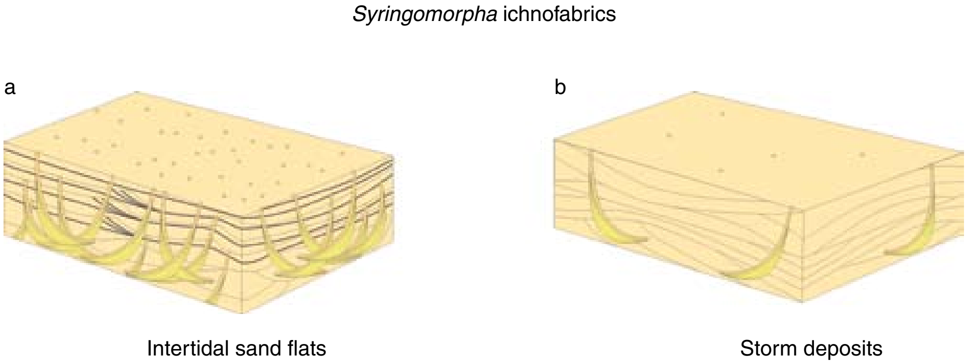

Figure 5.7 *Syringomorpha* ichnofabrics in Lower to Middle Cambrian shallow-marine deposits. (a) Composite ichnofabric recording multiple colonization events in tidal-flat deposits. (b) Simple ichnofabric recording single colonization events in lower-shoreface deposits.

fossils, including categories such as detritus feeding, deposit feeding, suspension feeding, gardening, and chemosymbiosis. Use of space is essentially equivalent to the vertical position within substrate recorded by the tiering structure. Ichnoguilds are named after their dominant ichnotaxa (Bromley, 1990, 1996). Bambachian guilds provide valuable information for understanding patterns of ecospace utilization through geological time (Bambach, 1983). Ichnoguild analysis may supply additional information to that recorded by body fossils. In the same way as guilds, ichnoguilds are useful tools to understand the adaptive strategies displayed by benthic organisms. As noted by Bromley (1990, 1996), ichnoguilds are well suited for characterizing the ecological complexity of ichnofaunas. Recognition and comparison of ichnoguilds from specific ecosystems through geological time become particularly useful in evolutionary paleoecology (e.g. Buatois *et al.*, 1998c).

The ichnoguild concept was originally applied to the study of chalk (Ekdale and Bromley, 1991; Bromley, 1996). Chalks are

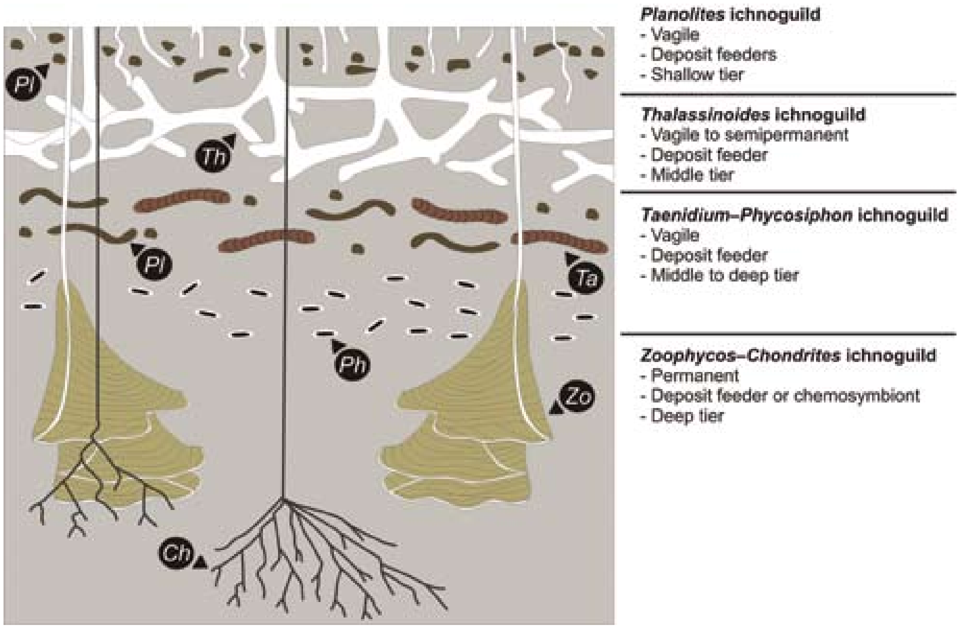

Figure 5.8 Ichnoguilds and tiering structure in Upper Cretaceous chalk of Denmark (modified from Ekdale and Bromley, 1991). Shallow tier is represented by *Planolites* (*Pl*), while *Thalassinoides* (*Th*) is a middle-tier form. The middle-to-deep tier is occupied by *Taenidium* (*Ta*) and *Phycosiphon* (*Ph*). The deep tier is represented by *Zoophycos* (*Zo*) and *Chondrites* (*Ch*).

Box 5.2 Composite ichnofabrics and ichnoguilds in Cretaceous chalk

Chalk ichnofabrics rank among the most complex of all. In particular, Cretaceous chalk ichnofabrics from Denmark have been thoroughly analyzed, and, in fact, represent the birthplace of the ichnofabric approach (Fig. 5.8). The rate of sedimentation in these pelagic environments was remarkably exceeded by the rate of bioturbation. The intensity of bioturbation in these shelf pelagic deposits is so high that virtually every grain of sediment has been processed by several animals. The resulting composite ichnofabrics represent the activity of multitiered endobenthic communities that moved upwards during continuous vertical accretion of the sea floor. The uppermost tier corresponds to indistinct burrow mottlings produced in the mixed layer by organisms that inhabited a soupground. The resulting structures are preserved as deformed and diffuse mottles that cannot be assigned to any particular ichnotaxa. Four ichnoguilds have been recognized. The *Planolites* ichnoguild typifies vagile, shallow-tier deposit-feeder structures. The *Thalassinoides* ichnoguild consists of semi-vagile and vagile, mid-tier deposit-feeder structures. The *Taenidium–Phycosiphon* ichnoguild is characterized by vagile, middle-to-deep-tier deposit-feeder structures. The *Zoophycos–Chondrites* ichnoguild is represented by non-vagile, deep-tier deposit-feeder or chemosymbiont structures. While the first three ichnoguilds were emplaced in softground, the deepest one records bioturbation in stiff, more compacted sediment. The zone of active bioturbation extended many centimeters below the sea floor.

Reference: Ekdale and Bromley (1991).

particularly appropriate for ichnoguild analysis because they are commonly intensely bioturbated and their tiering structure can be unraveled by careful analysis of cross-cutting relationships (Ekdale and Bromley, 1991) (Fig. 5.8; Box 5.2). Subsequently, ichnoguild analyses were expanded to include bioerosion structures (Bromley, 1994; Tapanila, 2008), tidal-flat ichnofaunas (Mángano *et al.*, 2002a; Mángano and Buatois, 2004b; Baldwin *et al.*, 2004), continental ichnofaunas (Buatois *et al.*, 1998c), and earliest Cambrian ichnofaunas (Buatois and Mángano, 2003a, 2004b). In some settings, tiering and ichnoguild analysis is complicated due to different factors, such as temporal instability of community structure, time averaging of fossil faunas, and limited cross-cutting relationships (Mángano *et al.*, 2002a). The ichnoguild concept is still an underutilized tool that has plenty of potential to illuminate paleoecological and evolutionary aspects of ichnofaunas (see Chapter 14).

5.5 PALEOSOL ICHNOFABRICS

Although the ichnofabric approach has become quite popular during the last two decades, still little is known about the characteristics and origin of continental ichnofabrics and review papers are almost exclusively based on marine examples (e.g. Taylor *et al.*, 2003). More recently, a conceptual and methodological framework for the analysis of paleosol ichnofabrics has been advanced by Genise *et al.* (2004b). In subaqueously produced ichnofabrics, the sharpness of the primary sedimentary fabric is commonly a function of the degree of bioturbation. However, in terrestrial ichnofabrics, soil features may disrupt the primary fabric without the intervention of bioturbation, generating what is referred to as pedofabric (Genise *et al.*, 2004b). Accordingly, these authors suggested that ichnofabric analysis in paleosols requires modifications to the standard methodology developed from marine examples. Genise *et al.* (2004b) proposed the construction of tiering diagrams, independent evaluation of the pedofabric and the ichnofabric, and construction of ternary diagrams showing percentages of bioturbation, pedofabric, and original bedding (Fig. 5.9). These authors illustrated their methodology with examples from Mesozoic and Cenozoic paleosols from Argentina, Uruguay, and Egypt.

5.6 THE ROLE OF BIOTURBATION, BIOEROSION, AND BIODEPOSITION

Organisms interact with and, therefore, affect the substrate in many different ways. Bioturbation involves all kinds of particle displacement and physicochemical sediment modifications resulting from the activity of organisms (Häntzschel and Frey, 1978). Bioturbation commonly leads to destruction of original sediment stratification and primary structures. However, the activity of organisms living in pore spaces may result in a localized displacement of sedimentary particles without actually destroying sedimentary structures, which results in so-called cryptobioturbation (Pemberton *et al.*, 2008) (Fig. 5.10). In turn, bioturbation does not necessarily imply sediment homogenization. Rather, in many cases organisms may provide the substrate with a new structure, such as the concentration of fine-grained sediment within the concentric infill of burrows hosted in clean quartzose sandstone (e.g. *Rosselia* ichnofabric in sandstone bars). Another long-recognized example is the generation of biogenic graded bedding by upward advection by earthworms (Darwin, 1881). In marine settings, maldanid worms are also well known for their conveyor-belt activities, transporting subsurface particles to the surface (Mangum, 1964; Fauchald and Jumars, 1979) and from the surface to a feeding cavity at depth (Levin *et al.*, 1997).

The bioturbation process has significant effects on sediment composition, stability, and texture (Ekdale *et al.*, 1984). Chemical processes result in changes in composition, such as concentration of trace elements, fluctuations in redox potential, flow of chemicals, changes in organic content of sediments, concentration of metals on boring walls, and alteration of clay minerals as a result of ingestion (Pryor, 1975) (Box 5.3). For example, the structures of infaunal burrowers feeding on suspended particles result in an increase in oxygen circulation within the sediment with the redox-potential discontinuity being extended at depth. Sediment stability may increase or decrease as a result of bioturbation (see Section 6.7). Most mobile epifauna and infauna, involving both deposit- and detritus-feeders and some sedentary organisms, whose feeding and defecation activities provide a considerable number of suspended particles, cause substrate instability (Rhoads, 1974). In contrast, sedentary organisms building mucus-reinforced tubes cause reduction in resuspension and erosion, and behave as sediment-stabilizing elements. In turn, pellet development significantly alters sediment consistency, which may result in decreased substrate stability (Ekdale *et al.*, 1984). Sediment texture may change in several ways as a result of bioturbation, particularly through the combination of sedimentary layers of varying grain size and mechanical sorting of sediment particles.

In addition, biodeposition, the production or concentration of sediment by the activities of an organism (Frey and Wheatcroft, 1989), also contributes to a change in sediment texture due to particle ingestion and excretion during the feeding process. For example, in carbonate sediments, pellet development and aggregation usually involves conversion of argillaceous and silty material into sand size. From the hydraulic viewpoint, these pellets behave like sand grains. Pryor (1975) noted that along the coast of Georgia and the Gulf of Mexico, *Callianassa major* annually generates pelletoidal material that is equivalent to a layer approximately 0.5 cm thick. Curran and Harris (1996) analyzed bioturbation by *Glypturus acanthochirus* in tidal-flat deposits of San Salvador Island, Bahamas, and estimated that this shrimp can move 118.6 kg sediment/m^2 to the surface every year (see also Section 6.2).

Bioerosion, every form of biological penetration and corrosion of hard substrates (Neumann, 1966; Bromley, 1992), also plays a major role in degrading lithified materials. For example, recent experiments in high-latitude settings demonstrated that foraminiferans are significant contributors during an early phase of bioerosion (Wisshak and Rüggeberg, 2006). During an advanced phase, sponges become dominant as agents of hard substrate degradation. Hardbottoms in the North Carolina continental margin are degraded by the activity of mechanical and chemical bioeroders (Riggs *et al.*, 1998). The main bioeroders in this case are bivalves, shrimps, and macroalgal pluckers. As a result of bioerosion, the substrate is degraded, relief is developed on hardbottom surfaces, and significant volumes of new sediment are supplied to the continental shelf.

5.7 BIOTURBATION-ENHANCED PERMEABILITY AND RESERVOIR CHARACTERIZATION

The destruction of sediment porosity and permeability by bioturbation has been a dogma in reservoir characterization for many years. However, a number of recent studies demonstrated that this is not always the case. Buatois *et al.* (1999) documented porosity/permeability relations, and bioturbation types in Carboniferous clastic reservoirs of Kansas. These studies showed that reductions in permeabilities and porosities are common where sediment is affected by intense bioturbation by deposit feeders. In contrast, passively filled structures of suspension feeders may even result in a significant increase in porosity and permeability as the degree of interconnectivity between layers is increased. In some cases, hydrocarbons may even be held in such burrows (Fig. 5.11). Gingras *et al.* (1999a) documented dramatic differences between burrow-fill permeabilities and matrix

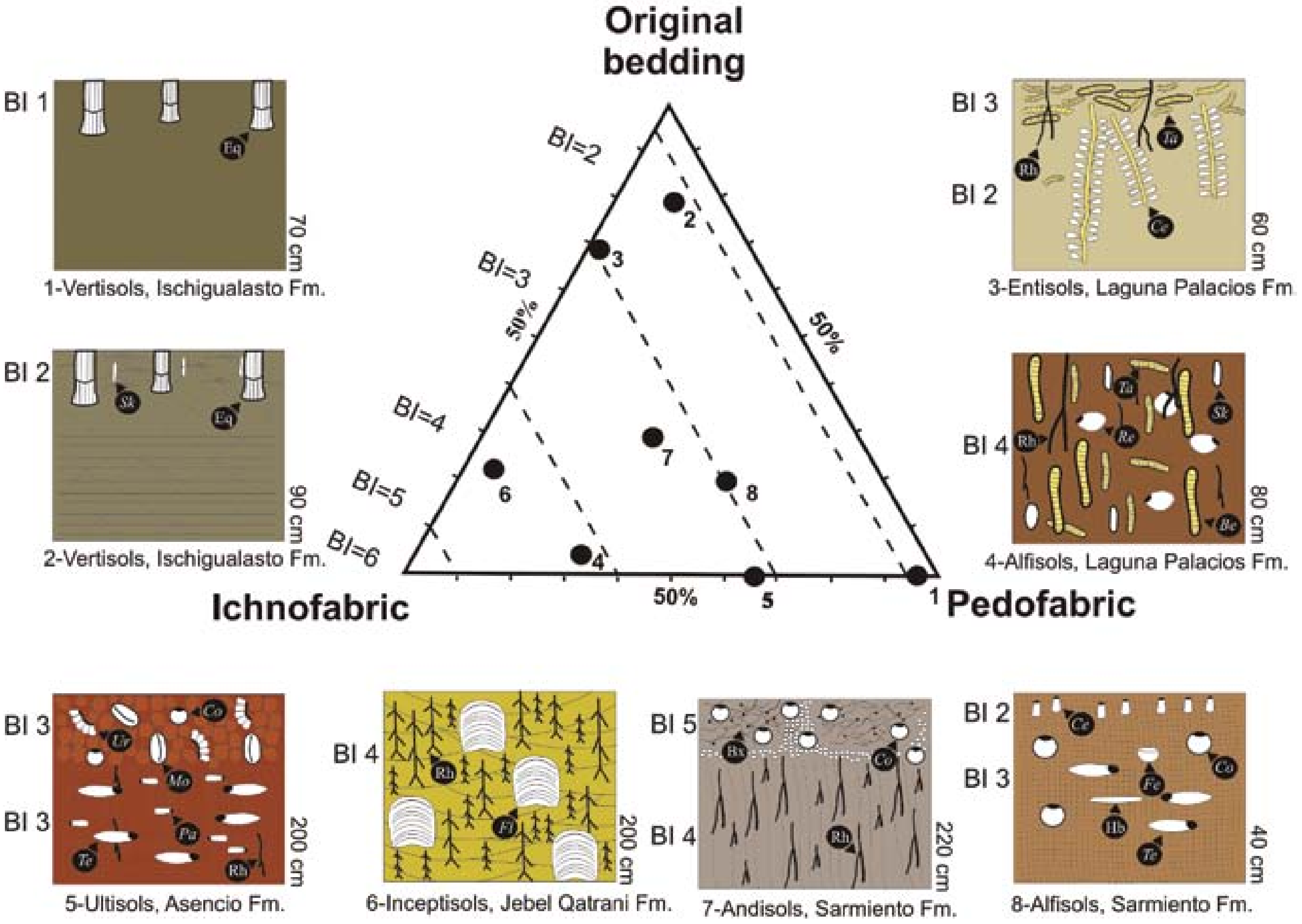

Figure 5.9 Ternary diagram for assessing paleosol ichnofabrics, pedofabric, original bedding, and grades of bioturbation (modified from Genise *et al.*, 2004b). Vertisols from the Triassic Ischigualasto Formation of western Argentina show different degrees of maturity. Example 1 is a well-developed vertisol with a uniform pedofabric characterized by small, angular blocky peds and closely spaced slickensides. No original bedding is preserved and stems of equisetales (Eq) in life position represent the only biotic evidence. Example 2 is a less-developed vertisol with primary fabric still preserved. Equisetales (Eq) stems and *Skolithos* (*Sk*) are present. Examples 3 and 4 from the Cretaceous Laguna Palacios Formation of Patagonia, Argentina, include an entisol and an alfisol. Example 3 is an entisol developed in tuff. The upper tier consists of *Taenidium barretti* (*Ta*), and the lower tier consists of the bee nest *Cellicalichnus chubutensis* (*Ce*). Rhizoliths (Rh) are present. Pedofabric is absent and the original bedding is relatively well preserved. Example 4 is a well-developed alfisol in tuffaceous sandstone. It is intensely bioturbated and the original bedding is only scarcely preserved in the upper horizon. The paleosol shows a well-developed upper elluvial horizon with platy peds, and a lower illuvial horizon with angular to subangular blocky peds. The ichnofauna consists of the probable coleopteran nest *Rebuffoichnus casamiquelai* (*Re*), *Taenidium barretti* (*Ta*), *Skolithos linearis* (*Sk*), and *Beaconites coronus* (*Be*). Thin rhizoliths (Rh) are present. Example 5 is an ultisol from the Paleogene Asencio Formation of Uruguay. Two interfingered horizons are present in this paleosol, one nodular and poorly consolidated, and the other one well indurated displaying columnar structures and total disturbance of the primary sedimentary fabric. Bioturbation is moderate in both horizons. The nodular horizon is dominated by the beetle nests *Coprinisphaera* (*Co*) and *Monesichnus* (*Mo*), and the bee cell *Uruguay* (*Ur*). The indurated horizon contains the bee ichnotaxon *Palmiraichnus* (*Pa*) and the probable coleopteran pupation chamber *Teisseirei* (*Te*). Rhizoliths (Rh) occur in this horizon. Example 6 is a poorly developed inceptisol from the Eocene–Oligocene Jebel Qatrani Formation of Egypt. This paleosol developed in a meandering channel point-bar sandstone, and relict trough cross-bedding is preserved. No horizons or soil structures are recognized. The ichnofauna is dominated by the termite nest *Fleaglellius pagodus* (*Fl*) and small rhizoliths (Rh). Examples 7 and 8 from the Eocene–Miocene Sarmiento Formation of Patagonia, Argentina, include an andisol and an alfisol. Example 7 is a weakly to moderately developed andisol present in a tuff. Two horizons have been recognized. The upper horizon is indurated and intensely bioturbated, and contains scattered specimens of the beetle nest *Coprinisphaera* (*Co*). The intense bioturbation is due to a boxwork of sinuous interconnected burrows (Bx) that resemble termite nests. The lower horizon shows columnar structures and sparse bioturbation. Very thin long root trace fossils (Rh) are present. Example 8 is a moderately developed alfisol associated with an erosive unconformity. Relict preservation of the primary fabric is noted. The pedofabric consists of subangular blocky peds with ferruginous crusts at the top. The ichnofabric consists of two tiers. The upper tier is represented by the bee nest *Celliforma* (*Ce*), while the lower tier includes *Coprinisphaera* (*Co*), *Teisseirei barattinia* (*Te*), *Feoichnus* (*Fe*) and large horizontal burrows (Hb). Bioturbation is low in the upper tier and moderate in the lower one.

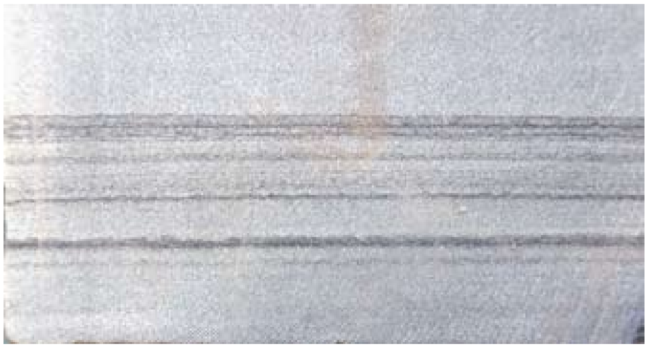

Figure 5.10 Cryptobioturbation in delta-front hummocky cross-stratified sandstone. Note the fuzzy lamination. Lower Miocene, Tácata Field, Eastern Venezuelan Basin. Core width is 9 cm. See Buatois *et al.* (2008).

permeabilities in a discontinuity surface at Willapa Bay. Substrates were colonized by crustaceans producing gallery systems representing the *Glossifungites* ichnofacies. Buatois and Mángano (2000) suggested that burrows passing through several layers, or multi-layer colonizers, generally cause an increase in permeability in the vertical direction to the bedding plane (Fig. 5.12). For example, crustacean galleries passing through sand turbidites provided pathways for fluid migration through mudstone intercalations, which would have normally acted as impermeable barriers (Schuppers, 1993). Similar situations occur in intertidal heterolithic facies where vertical *Skolithos* burrows pass through mud partings and connect sand layers (Buatois *et al.*, 1999). Gerard and Bromley (2008) illustrated spectacular examples of the contribution of three-dimensional *Thalassinoides* burrows to reservoir heterogeneity and of *Ophiomorpha* systems to fluid circulation. Tomkin *et al.* (2010) documented an increase of porosity and permeability associated with *Thalassinoides* burrows, but a decrease linked to *Ophiomorpha* systems.

Certainly, the role of bioturbation in enhancing permeability extends beyond the field of petroleum geology. Muñoz (1994) demonstrated that extensive *Thalassinoides* systems caused leaking in a dam, and Martin *et al.* (1994) established correlations between bioturbation and porosity fluctuations in aquifers. More recently, Cunningham *et al.* (2009) evaluated the impact of post-depositional *Ophiomorpha* burrows in increasing macroporosity in karst aquifers. These authors noted that burrow systems provide an alternative pathway for concentrated groundwater flow that differs from the standard model for karst aquifers, which is based on the role of fractures and cavernous dissolution features.

This emerging view on the relationships between permeability and bioturbation has received a more systematic treatment (Pemberton and Gingras, 2005). In a seminal paper, these authors recognized five different situations: (1) surface-constrained textural heterogeneities; (2) non-constrained textural heterogeneities; (3) weakly defined textural heterogeneities; (4) diagenetic textural heterogeneities, and (5) cryptic bioturbation (Fig. 5.13).

Surface-constrained textural heterogeneities occur in connection with discontinuity surfaces delineated by the *Glossifungites* ichnofacies. These heterogeneities are represented by high-permeability burrows that penetrate a low-permeability firm substrate. Therefore, elements of the *Glossifungites* ichnofacies introduce discretely packaged coarse-grained sediment into the underlying matrix, enhancing vertical permeability and creating a dual porosity-permeability system. Although permeability enhancement is

Figure 5.11 *Ophiomorpha* saturated in oil. No hydrocarbons occur in the impermeable pelletoidal wall. Lower Miocene, Oficina Formation, Oritupano Field, Eastern Venezuela Basin. Core width is 7 cm.

Box 5.3 Burrowing, accelerated weathering, and mineral authigenesis

Experiments with the annelid *Arenicola marina* have illustrated the importance of bioturbation and biodeposition in changing the chemical properties of the substrate. Two experimental tanks containing mature sand and mud consisting of quartz, chlorite, and muscovite were prepared. *Arenicola marina* was introduced into one and the other one was kept separate as a control. The annelids introduced into the experimental tank constructed J-shaped burrows penetrating up to 20 cm below the sediment–water interface, and significantly mixing the sediment. After 20 weeks, the mud in the control tank remained unchanged. In contrast, sediment in the tank populated with *A. marina* underwent significant mineralogical changes. Chlorite was preferentially destroyed during digestion and neoformed minerals were detected in the cast samples. It has been suggested that the lowered pH microenvironment in the organisms' guts accelerated mineral dissolution and precipitation processes during digestion. This experiment demonstrated that burrowing significantly changes substrate properties. By causing the growth of authigenic clays, digestive processes of *A. marina* influence the porosity and permeability of potential reservoir facies. Attempts to predict rates of mineral weathering and authigenesis without taking biogenic processes into account are unlikely to be accurate.

Reference: McIlroy *et al.* (2003).

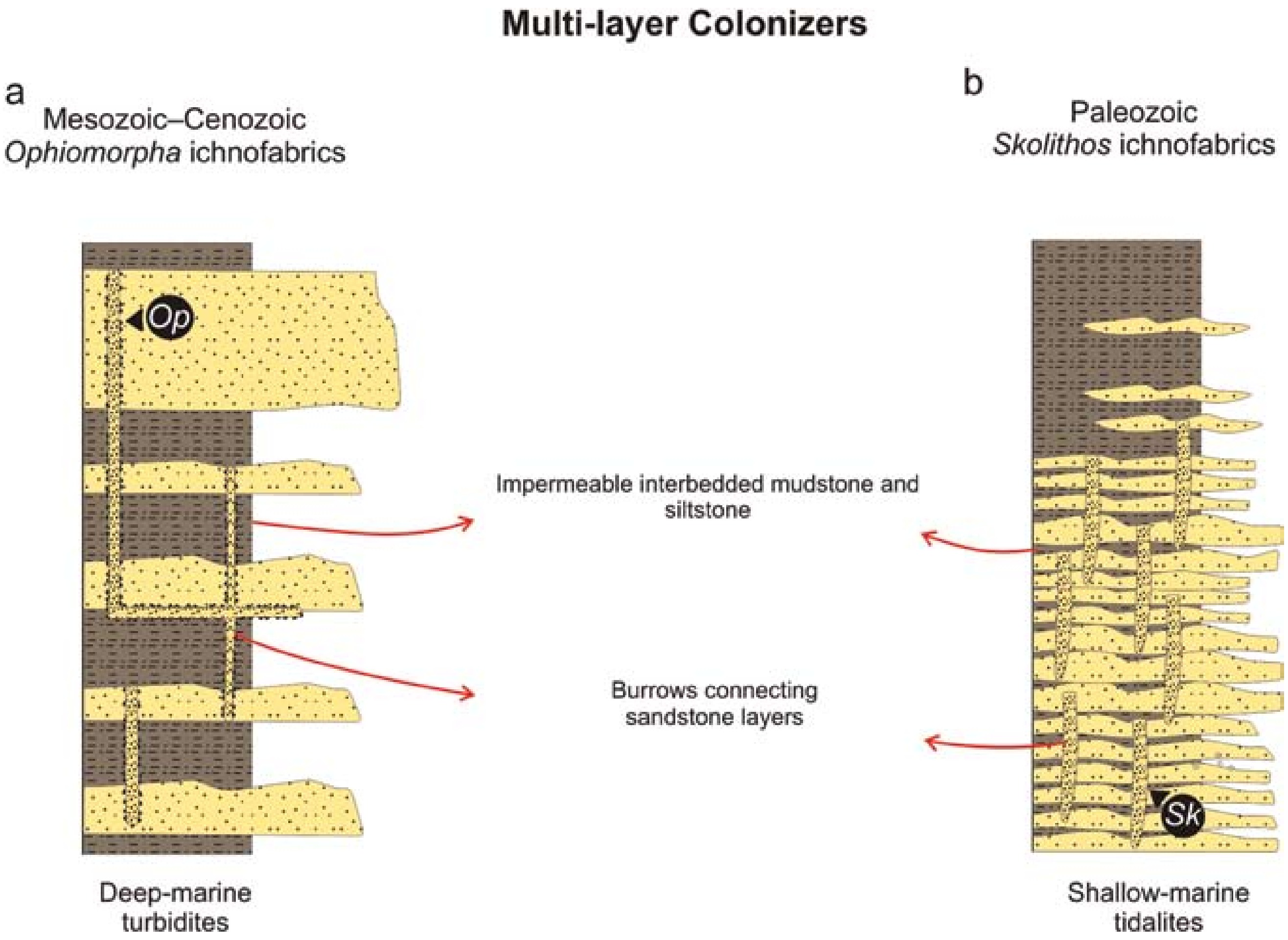

Figure 5.12 Multilayer colonizers and their role on vertical transmissivity of fluids. (a) *Ophiomorpha* (*Op*) ichnofabric in Mesozoic and Cenozoic thin-bedded turbidites. (b) *Skolithos* (*Sk*) ichnofabrics in lower Paleozoic intertidal heterolithic facies. Burrows passing through several layers may cause an increase in vertical permeability. Modified from Buatois and Mángano (2000).

limited in thickness, some of these surfaces (e.g. wave ravinement surfaces) have remarkable lateral extension. In some cases (e.g. Ghawar field of Saudi Arabia), firmground *Thalassinoides* burrows represent a biogenic plumbing system, conducive to stratiform super-permeability (Super-K).

Non-constrained textural heterogeneities are represented by discrete, sediment-filled burrows, encased by low-permeability sediment, which are not associated with a discontinuity surface. The host sediment commonly records low-energy background deposition, while the coarser-grained burrow-fill is delivered

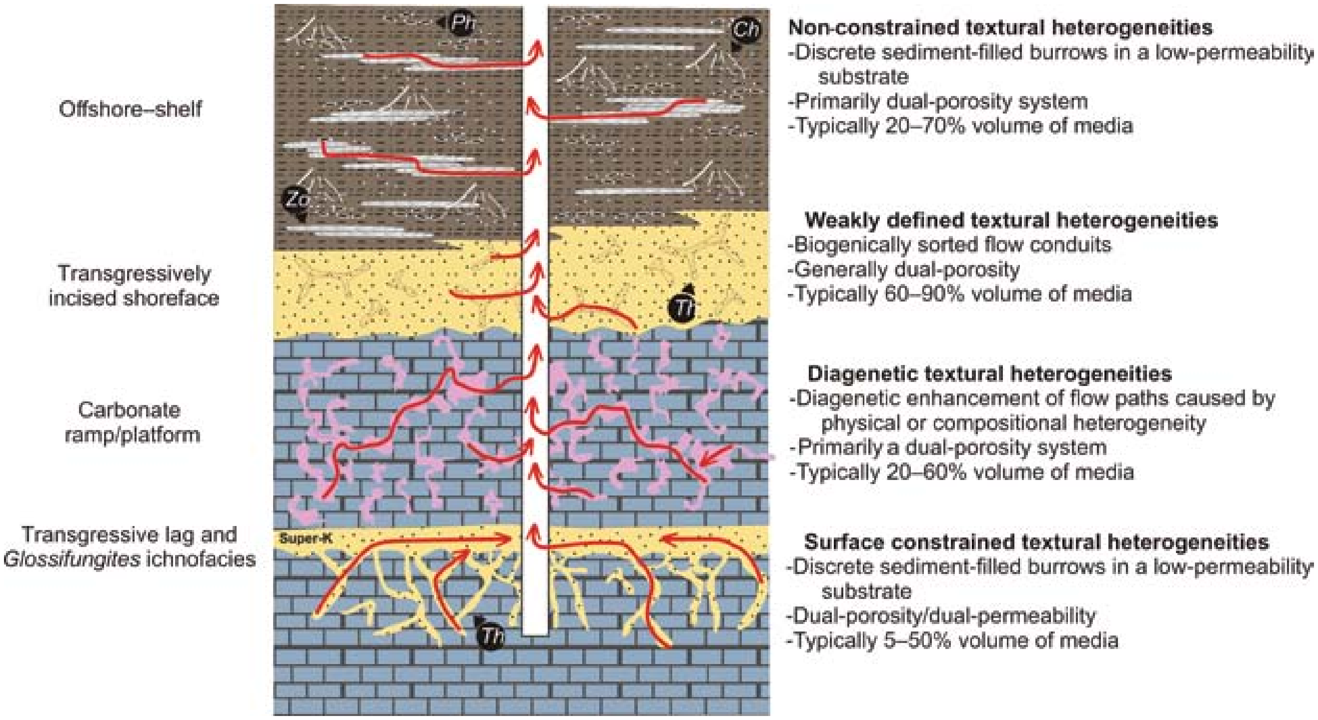

Figure 5.13 Relationships between permeability and bioturbation In the case of non-constrained textural heterogeneities, selective feeding in *Zoophycos* (*Zo*), *Chondrites* (*Ch*), and *Phycosiphon* (*Ph*) results in coarser-grained burrow fill in comparison with the host low-permeability silt-dominated sediment. Weakly-defined textural heterogeneities are illustrated by coarser sand-filled *Thalassinoides* (*Th*) penetrating into a finer-grained sandy matrix. Permeability contrast is subtler than in the previous case. Diagenetic textural heterogeneities are typically associated with diagenetic processes induced by bioturbation, resulting in the formation of tortuous pathways for fluid transmission in mottled carbonates. Surface-constrained textural heterogeneities are associated with discontinuity surfaces delineated by the *Glossifungites* ichnofacies, in which *Thalassinoides* (*Th*) burrow systems introduce discretely packaged coarse-grained sediment into the underlying low-permeability matrix, enhancing vertical permeability (Super-K). Modified from Pemberton and Gingras (2005).

during high-energy sedimentation events or results from selective feeding. Vertical burrows that penetrate into the substrate may interconnect permeable layers separated by low-permeability interbeds that may otherwise serve as barriers to fluid migration. A typical example is represented by vertical burrows of the *Skolithos* ichnofacies connecting thinly bedded sandstone and mudstone successions. In some cases (e.g. Terang–Sirasun field of Indonesia), a similar effect is attained by *Zoophycos* filled with empty globigerinid tests that penetrates into pelagic carbonates, increasing vertical permeability and breaching possible barriers. Another example is illustrated by *Macaronichnus*. In this case, the host sediment records high-energy conditions and the tracemaker causes significant mineralogical heterogeneity, leading to significant changes in permeability (Gingras *et al.*, 2002). Selective feeding in *Nereites missouriensis* and *Phycosiphon incertum* may play a key role in promoting gas transmissivity in low permeability gas-prone reservoirs (Fig. 5.14).

Weakly defined textural heterogeneities consist of discrete burrows infilled with sediment that slightly differs from the encompassing sediment. This situation is commonly illustrated by coarser sand-filled *Thalassinoides* penetrating into a finer-grained sandy matrix. Flow paths are tortuous as a result of the chaotic distribution of burrow conduits. Although the contrast between the burrows and the matrix is subtler than in previous scenarios, permeability contrasts may still influence production from these burrowed units.

Diagenetic textural heterogeneities typically result from dolomitization in bioturbated limestone. Burrowing in carbonates creates significant physical and compositional heterogeneities. The former includes changes and redistribution of grain size, sorting, and compaction. Compositional heterogeneities are caused by the concentration of organic material in the form of mucous or fecal material. Burrowing creates a microenvironment that is conducive to bacterial colonization. Diagenetic processes induced by bioturbation result in changes in porosity and permeability. Typical examples are represented by burrow systems, such as *Thalassinoides*, which create tortuous pathways for fluid transmission in mottled carbonates.

Cryptic bioturbation is a very subtle type of permeability enhancement characterized by non-discrete biogenic structures that completely alter the sediment, mostly resulting from the activity of meiofauna or small infauna. The high intensity of cryptic bioturbation may create zones of high permeability in sediment that in other aspects (e.g. grain size) shows little heterogeneity. Cryptobioturbation is common in shallow- to marginal-marine clastic deposits where it may affect considerable volumes of sediment.

The study by Pemberton and Gingras (2005) demonstrated that bioturbation has been commonly overlooked as a process that enhanced permeability in clastic and carbonate reservoirs. Of most importance, petrophysical studies are not usually focused at the trace-fossil scale. While the applications of ichnology in facies analysis and sequence stratigraphy are currently

Figure 5.14 High-density of *Nereites missouriensis* in offshore-transition deposits illustrating an example of non-constrained textural heterogeneities. Presence of this ichnofabric promotes gas and light oil transmissivity in low permeability reservoirs in many fields in North America. Upper Devonian–Lower Mississippian, Bakken Formation, Saskatchewan, Canada. Core width is 9.5 cm. See Angulo and Buatois (2009).

taken into consideration in the petroleum industry, the role of bioturbation as a modifying agent of porosity and permeability has been essentially neglected.

5.8 CRITICAL EVALUATION: ICHNOFABRICS VERSUS ICHNOFACIES OR ICHNOFABRICS AND ICHNOFACIES?

We believe that ideas derived from the ichnofabric approach should be used within the broader framework of the ichnofacies model. Both research strategies may be employed in conjunction, resulting in a more comprehensive and consistent view of the trace-fossil record. A well-balanced eclecticism may be a healthy approach to the ichnological record. As noted by McIlroy (2008), the confrontation between the ichnofabric approach and the ichnofacies model is misleading. The notion that ichnofabric analysis should replace ichnofacies put forward by Goldring (1993, 1995) is not supported by present developments in the field.

The ichnofabric approach is ideally suited to the study of cores (e.g. Bockelie, 1991; Martin and Pollard, 1996; McIlroy, 2004b; Gerard and Bromley, 2008). However, ichnofacies have proved to be extremely successful in paleoenvironmental and sequence-stratigraphic studies in cores (e.g. Pemberton *et al.*, 2001). In addition, both approaches have been routinely employed in outcrops. The ichnofabric approach is particularly useful in fully bioturbated deposits, as illustrated by chalk facies (e.g. Ekdale and Bromley, 1991), and some fine-grained shallow-marine units, such as the Jurassic Fulmar Formation of the North Sea (Martin and Pollard, 1996; Gowland, 1996; Gerard and Bromley, 2008) or the Miocene Chenque Formation of Patagonia (Buatois *et al.*, 2003; Carmona *et al.*, 2008). In contrast, many depositional settings are characterized by limited development of ichnofabrics. For example, delayed evolutionary innovations of the terrestrial and freshwater biotas constrained the development of continental ichnofabrics (Buatois and Mángano, 1998, 2007). Paleozoic fluvio-lacustrine and fluvio-estuarine ichnofaunas are dominated by bedding-plane, very shallow trace fossils, mostly grazing trails and arthropod trackways that produce little or no bedding disruption. Consequently, trail- and trackway-bearing deposits are commonly seen in cross-section as unbioturbated, fine-grained, thinly laminated rocks, precluding traditional ichnofabric analysis (Buatois *et al.*, 1998d). Ediacaran to earliest Cambrian deposits also contain bedding-plane trace fossils with almost no disturbance of primary fabric (see Sections 14.1.2 and 14.1.3). To a lesser degree, the same is shown by thinly bedded turbidites, which contain highly diverse graphoglyptid ichnocoenoses (e.g. Książkiewicz, 1977; Leszczyński and Seilacher, 1991; Uchman, 1995, 1998).

It has been emphasized that the ichnofabric approach provides a finer paleoenvironmental resolution because there are more ichnofabrics than ichnofacies. Although this is theoretically true, in practice the strategy to be undertaken is largely dependent on the scale of analysis. In addition, it is unclear if a large number of ichnofabrics recognized in a studied interval results in a more precise paleoenvironmental characterization. For example, Goldring *et al.* (1991) recognized seven different *Phycosiphon* ichnofabrics, but they mostly occur between the offshore transition and the upper offshore. This fact may point to the existence of several ichnocoenosis and the commonly overlooked issue of spatial heterogeneity (e.g. Mángano *et al.*, 2002a; McIlroy, 2007a). Moreover, ichnofacies practitioners do not restrict themselves to mere ichnofacies recognition; in fact, ichnofacies are subdivided in case-by-case studies allowing detailed subdivision of different environments (e.g. MacEachern *et al.*, 1999a).

The strength of the ichnofacies model relies on its archetypal nature (see Sections 4.1 and 4.6). The strength of the ichnofabric approach resides in the evaluation of the taphonomic controls that filter the biogenic signal through the fossilization barrier. Accordingly, taphonomy may illuminate the nature of some ichnofacies (taphofacies of Bromley and Asgaard, 1991). Analysis of tiering structure and ichnoguild characterization are strong conceptual and methodological tools derived from the ichnofabric approach. These tools are particularly useful to evaluate composite ichnofabrics that result from successive bioturbation events. Also, ichnoguilds provide a conceptual approach to the study of ecospace utilization through geological time, yielding valuable insights into evolutionary paleoecology (see Chapter 14).

Part II Spatial trends

6 Trace fossils and paleoecology

> Decían que había como mil pichis escondidos en la tierra, ¡enterrados! Que tenían de todo: comida, todo. Muchos decían tener ganas de hacerse pichis cada vez que se venían los Harrier soltando cohetes.
>
> Rodolfo Foghill
> *Los Pichiciegos* (1994)

Organisms burrow in response to many biotic and environmental factors. Ichnological studies provide detailed information on environmental parameters involved during sediment deposition and, therefore, serve as a basis for sedimentary environment and facies analysis. To that end, ichnological analysis should focus on the paleoecological aspects of trace-fossil associations (e.g. ethology, feeding strategies, ichnodiversity) and should avoid the simple use of a checklist approach because this may lead to paleoenvironmental misinterpretations. The paleoecological approach needs to be integrated with facies analysis, and should never aim to replace it. Many factors define the niche and survival range of animal species. However, the key to the analysis is the identification of major control factors, which are called limiting factors (Brenchley and Harper, 1998). In this chapter, we revise the response of benthic organisms to different environmental parameters, evaluate the role of taphonomy, and address a set of concepts that should be employed in paleoecological analysis of trace fossils, such as ichnodiversity and ichnodisparity, population strategies, and the notion of resident and colonization ichnofaunas. Then, based on the concept of ecosystem engineering, we discuss how organisms affect the environment. Finally, we address what biogenic structures can tell us about organism–organism interactions and spatial heterogeneity.

6.1 RESPONSE TO ENVIRONMENTAL PARAMETERS

As organism behavior is highly sensitive to certain parameter fluctuations (e.g. salinity, oxygen), biogenic structures may provide information that cannot be derived from conventional facies analysis strictly based on physical evidence (e.g. Gerard and Bromley, 2008). Ideally, sedimentological and ichnological data should be integrated with paleoecological information derived from the associated body fossils (e.g. Scasso *et al*., 1991; Mángano and Buatois, 1996). In any case, integrated paleoenvironmental studies have shown that the level of resolution obtained using trace fossils commonly supersedes those based on palynofossils and foraminifers (MacEachern *et al*., 1999b; Aquino *et al*., 2001). Also, it has been suggested that sedimentary and ichnological features should be carefully analyzed in order to provide constraints to guide geochemical sampling and interpretation (Schieber, 2003).

Although in this chapter environmental factors are considered separately, it is important to understand that the limits of tolerance of benthic organisms are defined in terms of multi-variable responses, rather than in terms of isolated factors (Newell, 1979). For example, in tidal-flat environments, salinity, temperature, and exposure to subaerial conditions are intimately linked, and are strongly dependent on latitudinal position and climate (Mángano *et al*., 2002a). On the other hand, hydrodynamic energy and substrate conditions are also interconnected and dependent on coastal topography and physiography. The resultant ichnofauna is therefore shaped by the interplay of key environmental parameters overprinted by taphonomic factors (see Section 6.2).

6.1.1 HYDRODYNAMIC ENERGY

Hydrodynamic energy is one of the most common limiting factors in trace-fossil distribution, influencing both the behaviors of the tracemakers, as well as the preservation potential of their respective biogenic structures. Trace-fossil associations from low- and high-energy settings are remarkably different (Fig. 6.1). Ichnofaunas developed under low-energy conditions are dominated by horizontal traces of deposit and detritus feeders, as well as active predators. In deep-marine environments, other more sophisticated feeding strategies, such as farming and capture of microorganisms, are commonly involved (Seilacher, 1977a). Overall, marine low-energy trace-fossil associations display high ichnodiversity and are typically included in the *Cruziana* and *Nereites* ichnofacies. In the freshwater realm, associations are less varied, and represented by the *Scoyenia* and *Mermia* ichnofacies.

High-energy ichnofaunas are typically characterized by the dominance of vertical dwelling structures of infaunal suspension feeders and/or passive predators, forming low-diversity suites that are commonly included in the *Skolithos* ichnofacies. Burrow systems, such as *Thalassinoides* and *Ophiomorpha*, tend to show a higher proportion of vertical components under conditions of increasing energy (Howard and Frey, 1984; Anderson and Droser, 1998). The high energy of tides, waves, and currents strongly

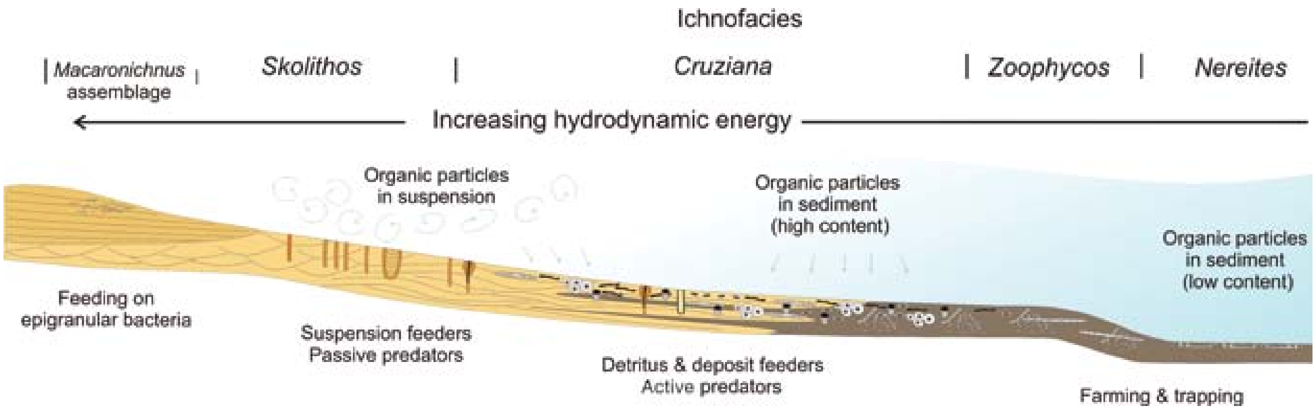

Figure 6.1 Relationship between trace-fossil associations, hydrodynamic energy, and food supply. Episodic sedimentation (i.e. storms and turbidity currents) generates environmental disturbances and may introduce organic particles in suspension favoring seaward displacement of suspension-feeding infauna. A wave-dominated regime is assumed.

Box 6.1 Response of the polychaete *Euzonus* to beach morphodynamics

Some sandy beaches of central Japan are characterized by wave dominance and high energy. The opheliid polychaete *Euzonus* is abundant at mid intertidal levels of the foreshore, producing incipient *Macaronichnus*. A detailed study was conducted during almost every spring tide from June to December in 2006. Distribution of *Euzonus* and orientation of its traces were plotted along a transect line. During fair-weather conditions, beach sediments accumulate landward, with the beach face developing as a steep slope. During storm conditions, the beach face is eroded by large waves, generating a gentle slope. *Euzonus* moves horizontally seaward and landward within the substrate in response to the shifting beach face as a result of changes in wave conditions. Under fair-weather conditions this polychaete burrows horizontally without any preferential direction. In contrast, under heavy erosion due to storm waves, *Euzonus* moves landward. The infaunal mode of life prevents *Euzonus* from excessive burial and washing out due to beach morphodynamics.

References: Seike (2008, 2009).

controls patterns of trace-fossil distribution along tidal shorelines. High-energy zones of tidal flats are typically dominated by vertical burrows, such as *Diplocraterion* or *Skolithos* (e.g. Cornish, 1986; Simpson, 1991). Deposits formed in these settings commonly contain deep gutter casts, flute marks, truncated vertical shafts, palimpsest surfaces, and transported burrows, which result from events of high energy that sculpt the tidal-flat surface and move a considerable amount of sediment (Mángano *et al*., 2002a).

Overall features of high-energy ichnofaunas are strongly influenced by taphonomic controls. Modern coastal high-energy environments may contain a moderate number of horizontal trails and burrows. However, their preservation potential in these settings is very low. For example, any enthusiastic diver knows that modern high-energy subtidal environments of tropical-carbonate systems, such as those in the Bahamas, are plagued with horizontal biogenic structures of starfish, large heavy gastropods, and crawling crabs, but their Pleistocene counterparts are commonly dominated by vertical *Ophiomorpha* burrows (Curran, 1994).

Interestingly, under very high-energy conditions, some ichnofaunas display characteristics that are in sharp contrast to those of the *Skolithos* ichnofacies. These ichnofaunas are dominated by horizontal trace fossils produced by mobile deposit feeder polychaetes assigned to the ichnogenus *Macaronichnus* (Pemberton *et al*., 2001; Seike, 2008, 2009; Quiroz *et al*., 2010) (Box 6.1). These organisms feed on epigranular bacteria around sand grains and inhabit well below the sediment–water interface as a result of strong infiltration that produces well-oxygenated and nutrient-rich environments within the sediment. In contrast to shallow- to mid-tier horizontal traces, the deep emplacement of *Macaronichnus* provides high preservation potential under high-energy conditions (MacEachern and Pemberton, 1992; Pemberton *et al*., 2001).

In shallow-marine environments, local fluctuations in hydrodynamic energy are recorded by the alternation of the *Cruziana* and *Skolithos* ichnofacies. In storm-dominated settings, the former represents fair-weather conditions, while the latter is storm related (Pemberton and Frey, 1984a; Pemberton *et al*., 1992c; Pemberton and MacEachern, 1997). In tide-influenced environments, the *Cruziana* ichnofacies may be associated with slack-water periods, while the *Skolithos* ichnofacies is more typical of higher-energetic traction sedimentation (Mángano and Buatois, 2004a, b). An analogous situation occurs in deep-marine environments where the *Nereites* and *Skolithos* ichnofacies alternate due to repeated times of pelagic and turbidite sedimentation, respectively (Crimes, 1977).

6.1.2 SUBSTRATE

Whereas the anatomy of body fossils is controlled by inherited genetic factors, the morphology of trace fossils is strongly influenced by extrinsic factors in addition to the constraints imposed by animal anatomy (Goldring *et al*., 1997). Substrate type and consistency are important external factors in determining both burrowing technique and infaunal community composition (Bromley, 1990, 1996). Substrate consistency embraces the intricate interplay of multiple factors (e.g. grain size, sorting, water content, organic matter content, mucus binding) that define the mechanical properties of the sediment (Bromley, 1990, 1996). In turn, sediment composition directly influences substrate consistency. The degree of substrate consolidation may change laterally, vertically, or temporally. Lateral changes occur along a sediment surface at different scales as a response to environmental heterogeneity (e.g. intertidal areas having both emergent zones and submerged pools). Vertical changes result from a decrease in sediment water content and increase in compaction within the sediment, thereby influencing infaunal tiering. Temporal changes result from a progressive increase of substrate consolidation either as a result of desiccation (e.g. overbank sediment) or early diagenesis (e.g. carbonate substrates).

Carbonate substrates may be subjected to progressive dewatering, and a series of stages based on degree of consolidation have been defined. These include soupground, softground, firmground, and hardground, which are associated with increasing compaction and cementation (Ekdale *et al*., 1984; Ekdale, 1985; Lewis and Ekdale, 1992). These categories also apply for siliciclastic substrates, although hardgrounds are exceedingly rare in siliciclastic rocks. To this list we should add xylic substrates or woodgrounds (Bromley *et al*., 1984). Substrate-controlled ichnofacies are defined based on these substrate categories (see Section 4.3). In the case of modern sediments, a series of field methods have been developed to determine substrate firmness (e.g. Gingras and Pemberton, 2000; Rodríguez-Tovar and Delgado, 2006).

Soupgrounds are saturated in water and incompetent. Organisms may move in these substrates; in many cases they swim through them using undulatory movements (Bromley, 1990, 1996). However, the preservation potential of these structures is nearly zero (Ekdale, 1985). Softgrounds represent unconsolidated sediment, and are inhabited by a large number of burrowers, becoming the most appropriate substrate for production and preservation of biogenic structures. Most of the established ichnotaxa typically belong to softgrounds. Goldring (1995) introduced the term “looseground” for soft sand and gravel as distinct from soft mud and silt (softground). Loosegrounds commonly contain robust burrows with reinforced walls (e.g. *Ophiomorpha*). Wetzel and Uchman (1998b) introduced the concept of stiffground, which has been further expanded by Lettley *et al*. (2007a) to include stiff, but not fully compacted mud, commonly developed along inclined surfaces in heterolithic sediment. Stiffgrounds contain medium- to small-sized unlined burrows that may suffer significant compaction after emplacement. Firmgrounds are compacted and dewatered sediment that have not yet undergone cementation. They typically contain abundant burrows and pseudoborings, although ichnodiversity is rather low. Burrows are typically unlined, display bioglyphs, and do not suffer significant compaction (Bromley, 1975). Hardgrounds are cemented substrates, which may contain bioerosion structures (see Section 1.1). In contrast to the rigidity of hardgrounds, woodgrounds are flexible, formed by organic matter, and experience rapid biodegradation (Bromley *et al*., 1984). Bivalves and insects are typical tracemakers in xylic substrates. In recent years, increased attention has been paid to sediment surfaces stabilized my microbial action, referred to as matgrounds (Seilacher, 1999; Baucon, 2008; Buatois and Mángano, 2003a, 2010). Some grazing trails and feeding traces (e.g. *Oldhamia*) may reflect strategies to exploit microbial mats (see Section 14.1.2).

Most studies concerning substrate-controlled trace fossils have focused on the evolution of carbonate substrates and how this affects community composition (e.g. Bromley, 1975; Goldring and Kaźmierczak, 1974; Mángano and Buatois, 1991; Bromley and Allouc, 1992; Lewis and Ekdale, 1992; Taylor and Wilson, 2003), or on the erosional exhumation of firm siliciclastic sediments and its implications in sequence stratigraphy (e.g. MacEachern *et al*., 1992; Pemberton *et al*., 2004). However, recent work emphasizes that the process of dewatering, and the concomitant changes in substrate properties, is a continuum rather than a series of compartmentalized stages, allowing the establishment of a scale of morphological variation of ichnofossils depicting substrate evolution (e.g. Buatois *et al*., 1997a; Lobza and Schieber, 1999; Mángano *et al*., 2002a; Schieber, 2003; Uchman and Pervesler, 2006; Davis *et al*., 2007; Carmona *et al*., 2010). Therefore, trace fossils serve as useful tools for evaluating substrate properties. In defining a range of substrate conditions, the presence of impregnated walls, sharpness of delicate morphological details, and degree of deformation are important observations (Goldring, 1991). In addition, changes in burrowing mechanisms, from swimming through sediment (soupground) and sediment feeding with active backfilling (softground) to sediment feeding with passive filling (firmground) occur as a response to increasing substrate consistency (Schieber, 2003) (Fig. 6.2). Although in theory it should be possible to identify ichnotaxa irrespective of substrate effects, occasionally deformation is so severe that accurate identification cannot be achieved. In soupgrounds, only biodeformational structures can be identified.

Morphological changes in trace fossils due to different degrees of substrate consolidation are common in water bodies and floodplain environments subject to desiccation or stabilized by microbial mats. Buatois *et al*. (1997a) documented changes in morphology in Permian floodplain trace fossils due to increased consolidation of the substrate. Morphological details are very poorly preserved in specimens of *Cochlichnus anguineus*, which were emplaced in a water-saturated substrate (Fig. 6.3a). These poorly preserved traces may be cross-cut by better-defined softground trace fossils, reflecting increasing compaction. This second suite includes *Helminthoidichnites tenuis*, *Helminthopsis abeli*, and another generation of *Cochlichnus*

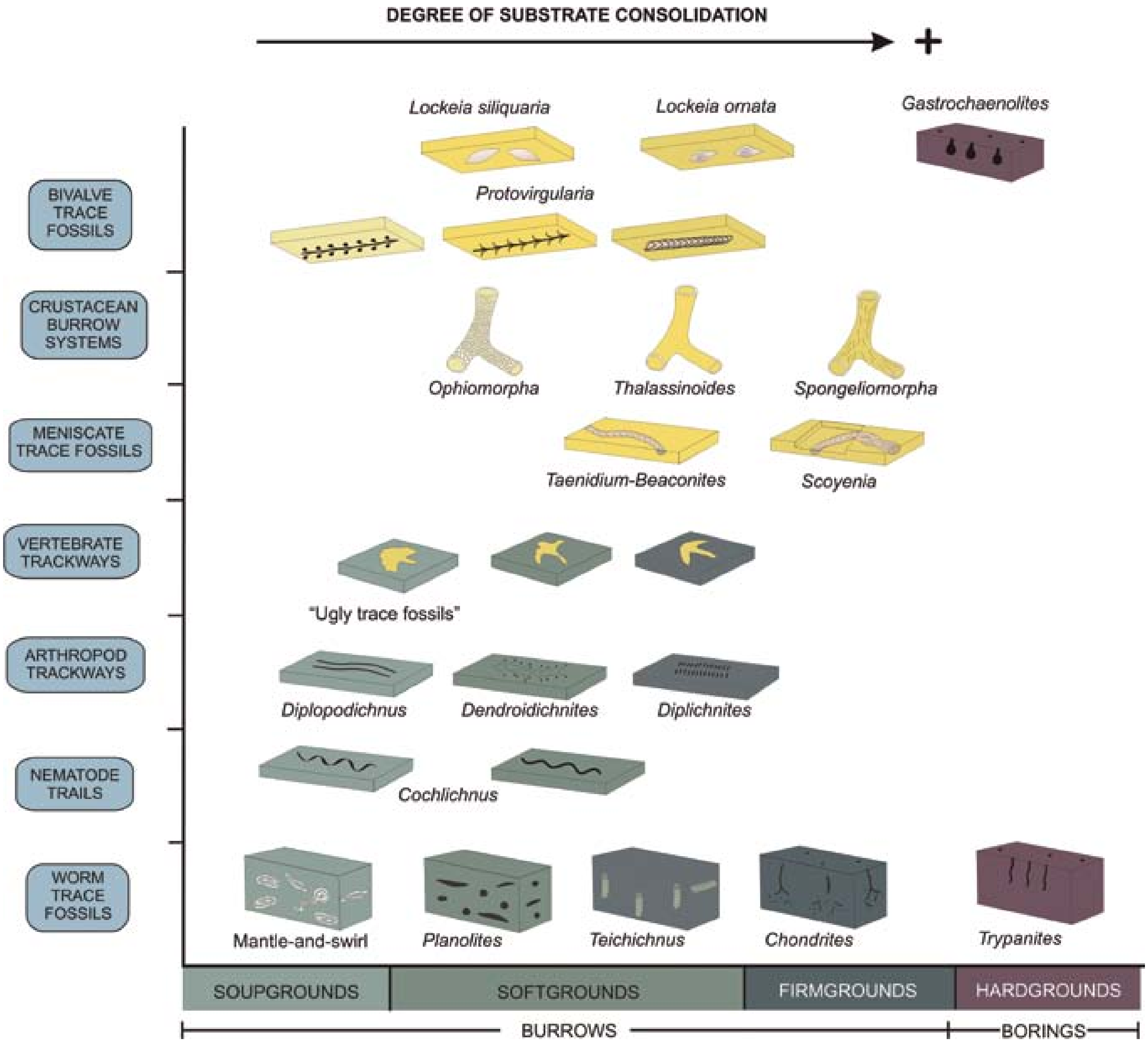

Figure 6.2 Relationship between morphology of different groups of trace fossils and degree of substrate consolidation. In general, quality of morphological definition increases parallel to increased cohesiveness.

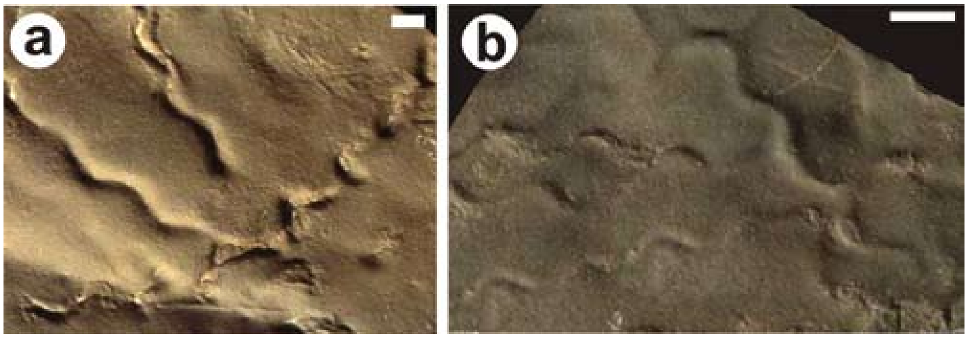

Figure 6.3 Trace-fossil morphology and degree of substrate consolidation in Permian overbank deposits, La Golondrina Formation, Patagonia, Argentina. See Buatois *et al.* (1997a). (a) Extremely deformed *Cochlichnus anguineus*. Note bedding-plane expression of *Ctenopholeus kutscheri* shafts cross-cutting *C. anguineus*. (b) Well-preserved specimens of *C. anguineus*. Scale bars are 1 cm.

anguineus (Fig. 6.3b). The dwelling traces *Ctenopholeus kutscheri* and *Palaeophycus striatus* were emplaced in slightly stiffer substrates. The overall features of this ichnofauna reflect subaqueous emplacement in a water body. Other ancient floodplain deposits exhibit suites formed in even more compacted sediment. The softground suite is characterized by meniscate, backfilled structures without ornamentation (e.g. *Taenidium*, *Beaconites*), and the firmground suite is typified by striated trace fossils (e.g. *Scoyenia*, *Spongeliomorpha*), cross-cutting the former. The resulting palimpsest surfaces reflect progressive desiccation of sediment accumulated along the margins of freshwater bodies (Buatois and Mángano, 2002, 2004a).

Tidal-flat trace fossils also display striking morphological variations depending on the degree of consolidation of the substrate (Mángano *et al.*, 1998, 2002a; Uchman and Pervesler, 2006). Studies on marine benthic ecology demonstrate that vertical and horizontal differences in substrate conditions influence the diversity, abundance, and distribution of intertidal organisms (Newell, 1979; Reise, 1985). Because tidal flats are regularly exposed and submerged by the tides, the concomitant pore-fluid content within the sediment will vary during a tidal cycle. On the other hand, the low-tide landscape is commonly characterized by the presence of tide pools within a generally emerged area, resulting in a range of substrate conditions along an isochronous surface.

Trueman *et al.* (1966) analyzed the effects of substrate, particularly grain size, on the rate of burrowing by soft-bodied animals, concluding that the easier the penetration, the worse the anchorage, and vice versa. A dilatant medium becomes firm and more resistant to shear as increased force is applied, whereas a thixotropic system shows reduced resistance to increased rates of shear. As a consequence, anchorage requires a substance with dilatant qualities, whereas motion is facilitated by a thixotropic system (Trueman and Ansell, 1969). Factors involved in the penetration and protraction phase tend to compensate one another so that the difference in the rate of burrowing may not be determined solely by grain size. However, Trueman *et al.* (1966) noticed that compacted sediment is stiffer, which results in a decreased burrowing rate. Accordingly, the frequency of the digging cycle and depth of penetration in each sequential movement decrease as burrowing into deeper levels proceeds (Ansell, 1962). Within any given grain-size range, a more compacted sediment will be less fluid and stiffer, offering increased resistance to penetration.

Several studies have investigated controls by substrate fluidity on the morphological variability of protobranch bivalve trace fossils (Mángano *et al.*, 1998, 2002a; Carmona *et al.*, 2010). These structures exhibit a complex array of relationships controlled by bivalve behavior, substrate character, and toponomy. In bivalve chevron locomotion traces (i.e. *Protovirgularia*), the distance between two chevrons represents each sequential set of movements, the chevron indicating the site the foot flaps were anchored within the sediment. Sharp, closely spaced chevrons account for short steps, with the animal struggling to advance in stiff, resistant sediment (Fig. 6.4a). Mángano *et al.* (1998) documented striking changes in the morphology of *Protovirgularia* in a Carboniferous tidal flat. The sharp chevrons of *Protovirgularia bidirectionalis* provide evidence of penetration in relatively firm, dewatered substrates. Structures with sharp, closely spaced chevrons represent what can be characterized as the firmer end of the softground range. Longer distances between chevrons, such as those observed in some delicate *Protovirgularia dichotoma* may reflect relatively coherent, but less resistant substrates, resulting in lower shell friction, and allowing smoother and easier movement during the protraction phase. Fluid sediment is conducive to the formation of irregular and highly deformed biogenic structures, reflecting complications in obtaining a secure anchorage (Fig. 6.4b). Similar substrate controls on the morphology of *Protovirgularia* have been documented in Miocene tide-dominated deltaic deposits (Carmona *et al.*, 2010).

Uchman and Pervesler (2006) analyzed how substrate properties influence amphipod and isopod structures in a modern tidal flat. As in the previous cases, they noted that a variety of biogenic structures reflects the stiffness of the substrate and the organism's ability to cope with it. Semi-fluid substrates prevent preservation of biogenic structures, while increasing stiffness leads to preservation of morphological details. Interestingly, on stiff and very stiff substrates these crustaceans move by jumping rather than penetrating into the substrate.

Substrate consistency also plays a major role in the morphological fidelity of arthropod and vertebrate trackways. Davis *et al.* (2007) conducted detailed neoichnological experiments that addressed trackway formation in substrates of various grain sizes and degrees of consolidation simulating subaerial and transitional subaerial–subaqueous environments. These authors noted that with increased firmness of the substrate there is a tendency to increased definition of individual tracks, decreased track width, and loss of tracks within series. Locomotion by heavier arthropods resulted in trackways formed across a broader spectrum of grain size and moisture.

Recently, Scott *et al.* (2010) investigated controls exerted on vertebrate track morphology by wetting and drying cycles in substrates containing different clay minerals in an attempt to evaluate the taphonomy of biogenic structures around saline lakes. These studies suggested that track morphology in smectitic substrates is altered rapidly by wetting and drying, particularly

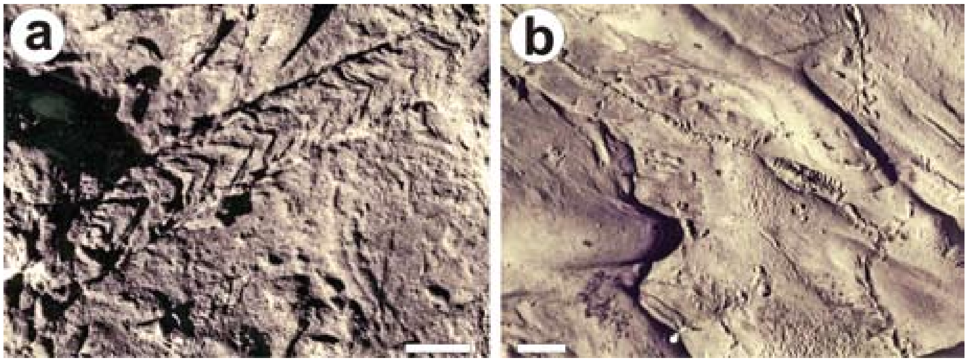

Figure 6.4 Relationship between morphology of bivalve locomotion trace fossils (*Protovirgularia rugosa*) and degree of substrate consolidation, Stull Shale, Waverly trace-fossil site, Kansas, United States. See Mángano *et al.* (1998, 2002a). (a) Sharp, closely spaced chevrons recording relatively stiff sediment. (b) Delicate, poorly defined chevrons. Note flute casts that suggest relatively fluid, poorly cohesive sediment. Scale bars are 1 cm.

in the case of substrates containing saline pore waters. In contrast, track morphology is less affected in non-swelling clays (e.g. kaolinite). These authors also noted that the degree of morphological alteration and/or resistance to wetting and drying is controlled by the rate of substrate drying and the type of resulting salt efflorescence (e.g. interstitial versus surficial crust).

Bromley (2001) noted that if the substrate is too rigid and the animal is not too heavy, no vertebrate footprints are preserved, while, in relatively firm substrates, tracks preserve very delicate structures of the track-making limb (e.g. hairs, scales, claws). With increasing fluidity and softness, however, morphological features become blurred, and the impression of the limb causes significant sediment flow and disruption. Bromley (2001) coined the name "ugly trace fossils" for this type of footprint. Assigning these tracks to specific producers may be difficult due to the lack of diagnostic features. In some cases, track misinterpretations are far from trivial. This is the case of elongate indistinct Cretaceous trackways in Texas that were attributed to humans in pseudoscientific and creationist circles, including some popular movies during the seventies. More serious analysis indicated that these are deformed theropod dinosaur tracks (Kuban, 1989)! In any case, Bromley (2001) noted that these footprints convey significant environmental information, particularly with respect to sediment shear strength and pore-water content, and ultimately the environmental setting of formation (e.g. Marsicano *et al.*, 2010). This situation is reminiscent of taphonomy's motto of the late eighties "Ecology's loss is sedimentology's gain" (Thomas, 1986). In the case of trackways, it is "Anatomy's loss is sedimentology's gain."

6.1.3 OXYGENATION

The importance of oxygen content as a limiting factor has been outlined in different ichnological studies (Bromley and Ekdale, 1984b; Ekdale and Mason, 1988; Savrda and Bottjer, 1986, 1989, 1991; Wignall, 1991; Leszczyński, 1991a; Savrda, 1992, 2007a; Martin, 2004). Rhoads and Morse (1971) proposed a subdivision of marine waters and associated biofacies in three categories based on their oxygen content. These studies indicated that aerobic or fully oxygenated water contains oxygen in excess of 1.0 ml O_2/l H_2O, dysaerobic or poorly oxygenated water contains between 1.0 and 0.1 ml O_2/l H_2O, and anaerobic or anoxic water is characterized by less than 0.1 ml O_2/l H_2O. Subsequent studies slightly modified this scheme and suggested separate terms for the oxygenation regime and the biofacies (Tyson and Pearson, 1991). This revised scheme of oxygenation levels includes oxic (8.0–2.0 ml O_2/l H_2O), dysoxic (2.0–0.2 ml O_2/l H_2O), suboxic (0.2–0.0 ml O_2/l H_2O), and anoxic (0.0 ml O_2/l H_2O). The corresponding biofacies for these four categories are aerobic, dysaerobic, quasi-anaerobic, and anaerobic.

Studies in modern environments demonstrate that diverse shelly faunas tend to flourish under aerobic conditions, while dysaerobic associations are commonly dominated by poorly diverse, small soft-bodied organisms (Rhoads and Morse, 1971; Byers, 1977; Savrda *et al.*, 1991; Tyson and Pearson, 1991). It has been a tenet that quasi-anaerobic biofacies lacks macrofauna, but has *in situ* benthic meio- and microfauna (Neira *et al.*, 2001). The 0.2 ml O_2/l H_2O boundary seems to mark the disappearance of infaunal bioturbation (Tyson and Pearson, 1991). Traditionally, in ichnological models the quasi-anaerobic zone has been considered together with the anoxic zone. Anoxic settings are essentially devoid of metazoan life. The so-called "exaerobic zone" was further introduced based on the presence of calcified invertebrates (Savrda and Bottjer, 1987), and is now regarded as corresponding, at least in part, to the quasi-anaerobic biofacies. In addition, it has been noted that these divisions do not account for rapid seasonal changes (Oschmann, 1993). Recent studies documented intense bioturbation in near-anoxic sediment (0.02–0.03 ml O_2/l H_2O), suggesting that the oxygen limit of macrofaunal bioturbation may be significantly lower than previously estimated (Levin *et al.*, 2003). Bacterial communities have also been reported as blooming under anoxic conditions (e.g. Caumette, 1986; Jorgensen, 1996).

Several attempts have been made to link trace-fossil suites to specific conditions of oxygen content in both the bottom waters and the interstitial waters of a given sediment. Some of these models are very general (e.g. Ekdale and Mason, 1988), while others are exclusive for pelagic (e.g. Savrda and Bottjer, 1986, 1989, 1991) or turbiditic sedimentation (e.g. Leszczyński, 1991a). All these models generally agree that the density of bioturbation, trace-fossil diversity, maximum penetration, and burrow size tend to decrease with decreasing oxygen (Fig. 6.5). However, some of these conclusions have been challenged by studies in modern environments revealing no correlation between decreasing oxygen and depth of bioturbation and burrow size in the Arabian Sea (Smith *et al.*, 2000), and documenting intense bioturbation by symbiont-bearing oligochaetes in a nearly anoxic basin on the Peru margin (Levin *et al.*, 2003). However, two important issues are critical to extrapolate information from modern studies to assess the validity of trace-fossil models: the elusive macroevolutionary component and the time-averaged constraint. It is clear that oxygen-controlled communities have changed through time (Martin, 2004; Mángano, 2011). The issue of whether modern marine oligochaetes record a recent invasion of an underexploited niche deserves further exploration. Although posing a cautionary note on established ichnological models, its implications for the geological record may be limited. Also, oxygen fluctuations at the ecological timescale may not be reflected in the fossil record. Time-averaging is inherent to trace fossils and may represent a complication because short-term redox cycles or events may not be revealed (Savrda, 2007a).

In addition, it has been suggested that in some cases, it is difficult to discriminate between oxygen and substrate controls, particularly in the case of a very low diversity of trace fossils, which may reflect either dysaerobic conditions or soupy substrates (Wignall, 1993; Savrda, 2007a). Careful analysis of trace-fossil morphological details is the key in this case (see Section 6.1.2).

Ekdale and Mason (1988) proposed a general model that attempts to link certain ethological categories with oxygen content. Although some objections were raised (e.g. Wheatcroft,

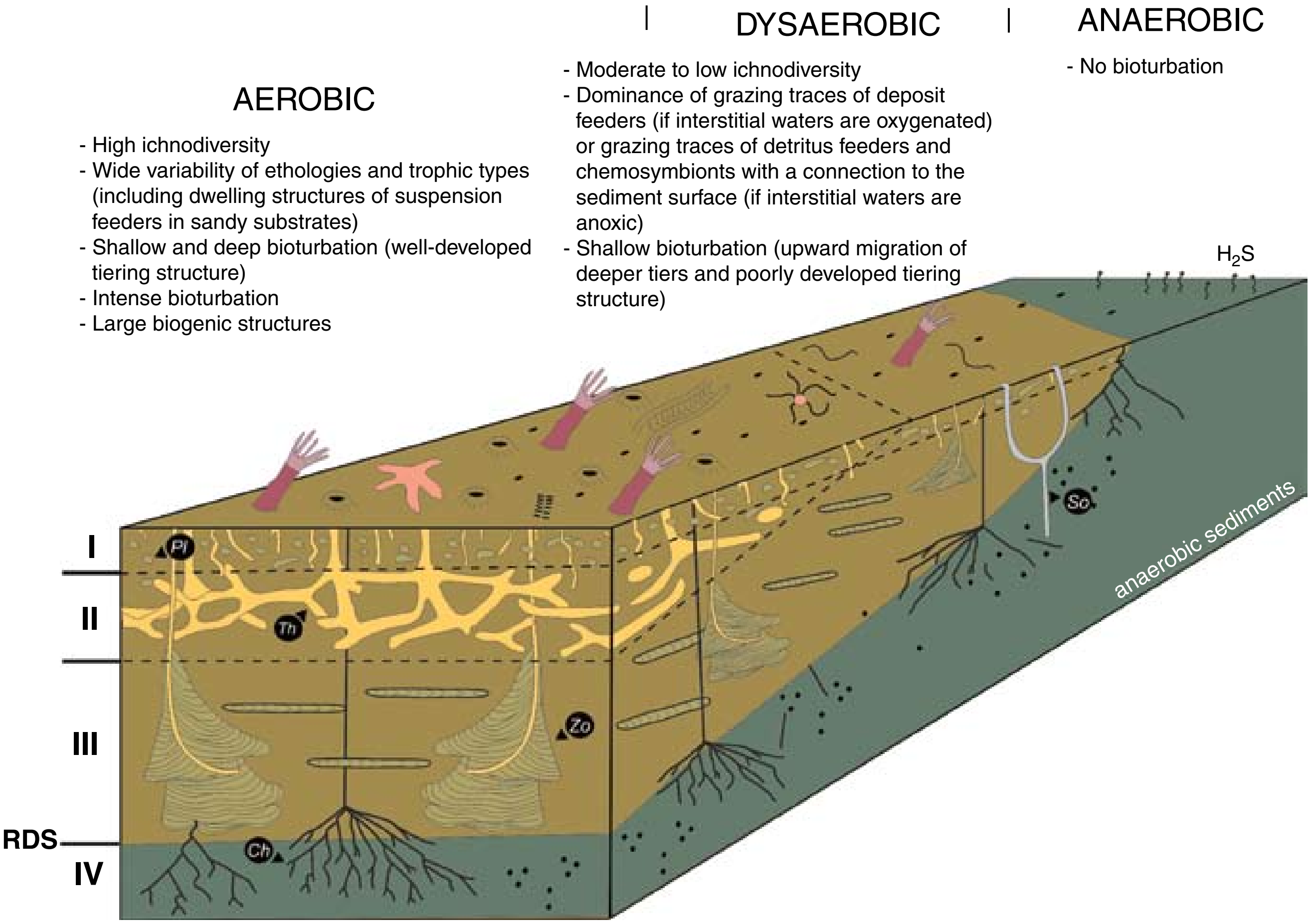

Figure 6.5 Relationship between trace fossils and oxygen content. Aerobic, dysaerobic, and anaerobic refer to oxygenation of bottom waters. Under aerobic conditions in both the interstitial and bottom waters, endobenthic communities tend to display complex tiering structures. Four tiers, shallow (I – *Planolites* or *Pl*), mid (II – *Thalassinoides* or *Th*), deep (III – *Zoophycos* or *Zo*), and very deep (IV – *Chondrites* or *Ch*, *Solemyatuba* or *So*), are illustrated in the example. Burrows maintaining a connection with the oxygenated sediment surface are able to penetrate in anaerobic sediment below the redox discontinuity surface (RDS). No bioturbation develops under anaerobic bottom waters.

1989; Martin, 2004), the model is useful for the study of ancient marine successions and modern sediments, particularly if other controlling factors are taken into consideration (Buatois and Mángano, 1992; Levin *et al.*, 2003). According to this model, if both the bottom and interstitial waters are anoxic, no bioturbation occurs and the sediment is typically dark and well laminated. If anoxic conditions exist in interstitial waters, but bottom waters are at least dysoxic, fodinichnia is the dominant ethology, essentially represented by permanent burrow systems that maintain a connection with the sediment–water interface allowing the circulation of the more oxygenated waters into the anoxic sediment. Ichnodiversity is typically low, and monospecific associations are common. *Zoophycos* and *Chondrites* (Fig. 6.6a) (and, in some cases, *Teichichnus* and *Trichichnus*) are the classical components. If the interstitial waters are dysoxic and the bottom waters are either dysoxic or oxic, pascichnia becomes dominant. The assumption here is that grazing trails are temporary structures formed by infaunal deposit feeders. Because these organisms backfill their structures, no connection is maintained with the sea bottom, and the sediment cannot be totally anoxic. Although grazing trails are also produced at the sediment–water interface, and thereby they do not require oxygen within the sediment, their preservation in marine environments is very low. Finally, under fully oxic conditions in both the bottom and interstitial waters, domichnia is the dominant ethological group. Permanent domiciles of suspension feeders, such as *Skolithos*, represent the typical structures.

Savrda and Bottjer (1986, 1987, 1991) proposed a model that attempts to explain trace-fossil distribution in pelagic or hemipelagic sediments unaffected by sediment gravity flows. They characterized oxygen-related ichnocoenoses (ORI), which occur in stratal units that accumulate under similar conditions of oxygenation of bottom waters. Their method allows the construction of oxygenation curves for sedimentary successions. The general trend under decreasing oxygen content is a decrease in ichnodiversity, burrow diameter, and burrowing depth. Accordingly, structures that occupy deep tiers in oxygenated sediments tend to move upwards as a result of the upward migration of the redox discontinuity under oxygen-depleted conditions. Under extreme dysoxic conditions monospecific

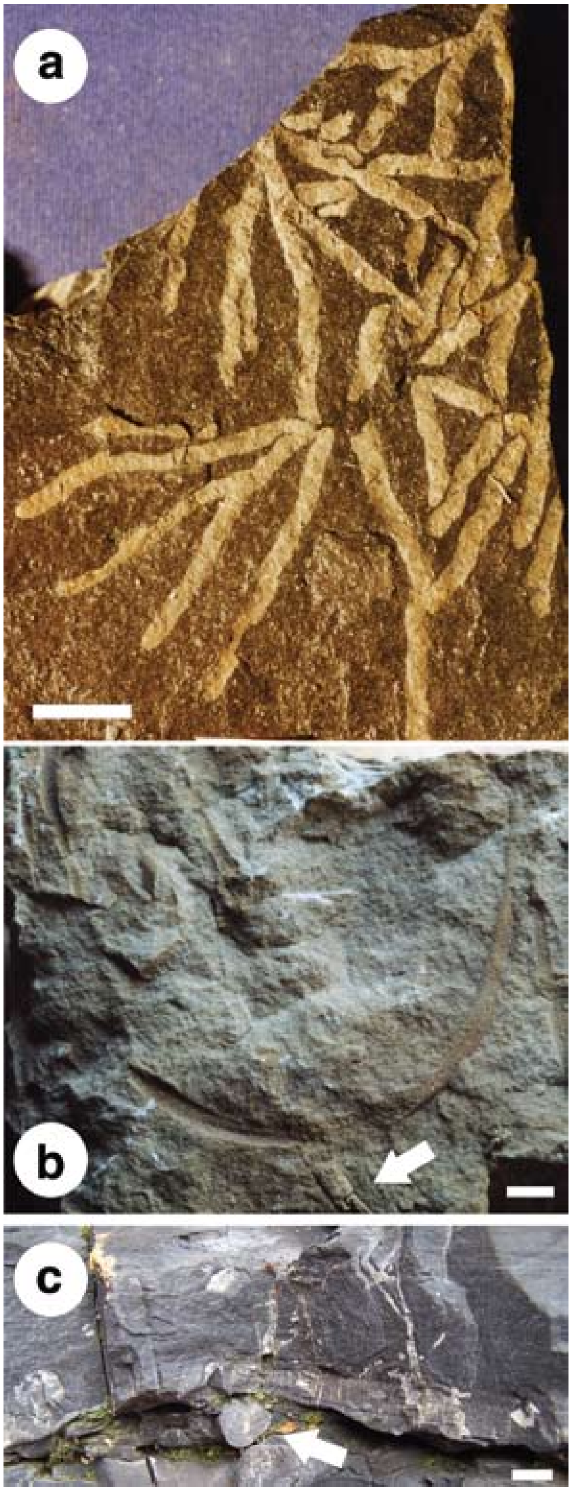

Figure 6.6 Typical ichnotaxa of oxygen-depleted conditions. (a) *Chondrites* isp. Upper Carboniferous, near Eudora town, Eudora Shale, eastern Kansas, United States. (b) *Solemyatuba ypsilon* showing lower extension tube (arrow). Upper Triassic, Rhaetian Sandstone, Olgahain, southern Germany. See Seilacher (1990a). (c) Cross-section view of *Protovirgularia obliterata* (arrow) at the base of a turbidite. Veřovice Beds, Lower Cretaceous, Zagórnik, Outer Carpathians, Poland. See Uchman (2004b). All scale bars are 1 cm.

suites of deep-tier traces in shallow-tier positions occur, with *Chondrites* being the typical ichnotaxon (see also Bromley and Ekdale, 1984b). Under totally anoxic conditions, no bioturbation occurs. These ideas have been applied to the study of a large number of pelagic successions (e.g. Savrda and Bottjer, 1989, 1994; Savrda *et al*., 1991; Savrda and Ozalas, 1993; Ozalas *et al*., 1994; Locklair and Savrda, 1998a, b; Savrda, 1998; Olóriz and Rodríguez-Tovar, 2002; Martin, 2004).

Leszczyński (1991a) proposed a model to examine the links between oxygen conditions and trace-fossil distribution in turbidite successions. He distinguished five ichnocoenoses reflecting progressive oxygenation of the deep sea that are revealed by trace fossils preserved at the base of thin-bedded turbidites. Some of the trends under increasing oxygen content are an increase in ichnodiversity and size of the trace fossils. Graphoglyptids (agrichnia) reach their climax in relatively well-oxygenated settings, while turbidites formed under poorly oxygenated conditions display undifferentiated biogenic structures. Subsequent studies, however, suggest that food supply and sedimentation rate may have also played a role in trace-fossil distribution in this case (Wetzel and Uchman, 1998a).

The model developed by Wignall (1991), based on a single case study (the Jurassic Kimmeridge Clay of England), does not agree with some tenets of the more general models. For example, *Chondrites* does not correspond to his dysoxic end member, being replaced by the supposed Pascichnion *Astacimorphichnus etchesi*. However, this ichnotaxon is only known from this unit and its overall morphology does not agree with a grazing trace ethology.

In addition to *Chondrites* (Fig. 6.6a), other ichnotaxa have been suggested to reflect particular adaptations to oxygen-depleted settings. Some of these are produced by chemosymbiotic bivalves (Seilacher, 1990a). The U-shaped burrow *Solemyatuba* (Fig. 6.6b) has been regarded as the dwelling structure of relatives of the modern bivalve *Solemya*, which endosymbiotically farms bacteria in its gills (Seilacher, 1990a). Deep-tier occurrences of *Protovirgularia* (Fig. 6.6c) have been also attributed to the work of chemosymbiotic bivalves in anoxic sediment (Uchman, 2004b).

While previous models attempt to explain behavioral adaptations to oxygen deficiency, there are cases of animals living in nearshore well-oxygenated settings that are transported basinward into anoxic settings via sediment gravity flows or hyperpycnal flows. These are the so-called “doomed pioneers” of Föllmi and Grimm (1990), and Grimm and Föllmi (1994). Doomed pioneers construct burrows in completely anoxic sediments, but do not persist in such settings, dying from suffocation (Fig. 6.7a–d). Decapod crustaceans, having skeletonized resistant body parts, are typical doomed pioneers. Commonly, sandy substrates with *Thalassinoides* or *Gyrolithes* intercalate with totally anoxic mudstone reflecting short-term burrowing events. The ability of crustaceans to survive for short periods under anoxic conditions has been inferred from the presence of “dying” trackways (mortichnia) associated with their body fossils in the Jurassic Solenhöfen Limestone of Germany (e.g. Janicke, 1969; Viohl, 1990; Barthel *et al*., 1990). The same situation has been proposed for Cretaceous lacustrine limestones of

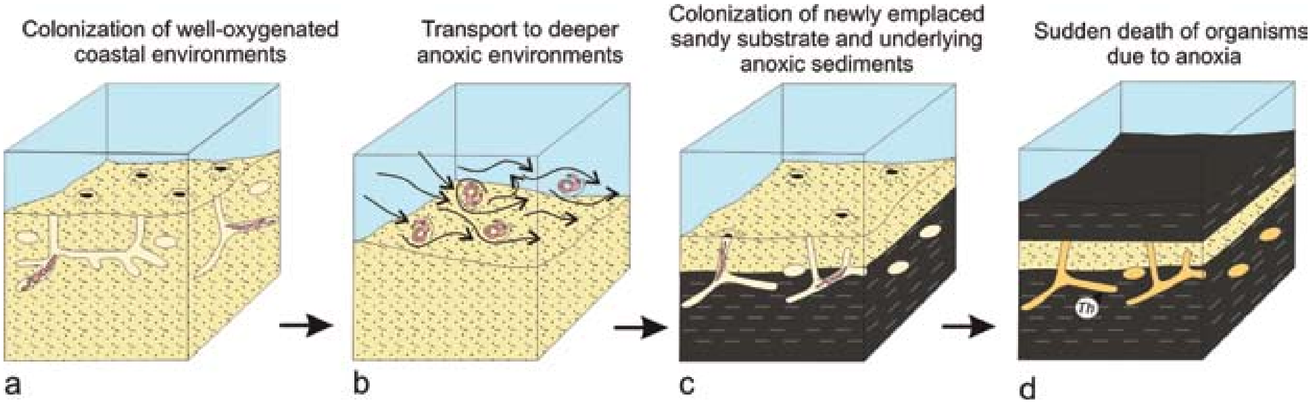

Figure 6.7 Doomed pioneers model (based on Föllmi and Grimm, 1990, and Grimm and Föllmi, 1994). (a) A benthic community in established in well-oxygenated nearshore environments. (b) Sediment gravity flows or hyperpycnal flows transport these nearshore components to deeper-water anoxic environment. (c) These anoxic sediments are colonized by the doomed pioneers and *Thalassinoides* (*Th*) burrows are emplaced. (d) The organisms die rapidly due to anoxia.

Spain that contain deep-water anoxic sediments with the crustacean trackway *Hamipes* (Gibert *et al.*, 2000).

6.1.4 SALINITY

The importance of salinity as a limiting factor in coastal areas has been emphasized in different studies (e.g. Howard and Frey, 1975; Howard *et al.*, 1975; Wightman *et al.*, 1987; Pemberton and Wightman, 1992; Rindsberg, 1992; MacEachern and Pemberton, 1994; Buatois *et al.*, 1997b, 2010a; Mángano and Buatois, 2004a; MacEachern and Gingras, 2007). In particular, it has been noted that while the distribution of physical sedimentary structures is mainly salinity-independent, the distribution of benthos is not and, accordingly, ichnology represents a powerful tool to reconstruct paleosalinity (Buatois *et al.*, 1997b). Salinity levels are classified into limnetic (less than 0.5‰), oligohaline (0.5–5‰), mesohaline (5–18‰), polyhaline (18–30‰), and euryhaline (30–40‰) (Remane and Schlieper, 1971; Knox, 1986). Limnetic is equivalent to freshwater, while oligohaline, mesohaline, and polyhaline correspond to brackish water. Fully marine conditions fall within the euryhaline category with mean seawater salinity at approximately 35‰ (McLusky, 1989). Bromley and Asgaard (1991) emphasized that behavioral convergence leads some ichnotaxa to occur on both sides of the salinity barrier, although this does not imply the identity of the producers. The classic example is that of *Cruziana* and *Rusophycus*, which are commonly produced by trilobites in marine environments (Seilacher, 1970, 1985) and by branchiopods or notostracans in freshwater (Bromley and Asgaard, 1972b; Pollard, 1985). In any case and regardless of behavioral convergence, salinity is of paramount importance in trace-fossil distribution (Fig. 6.8).

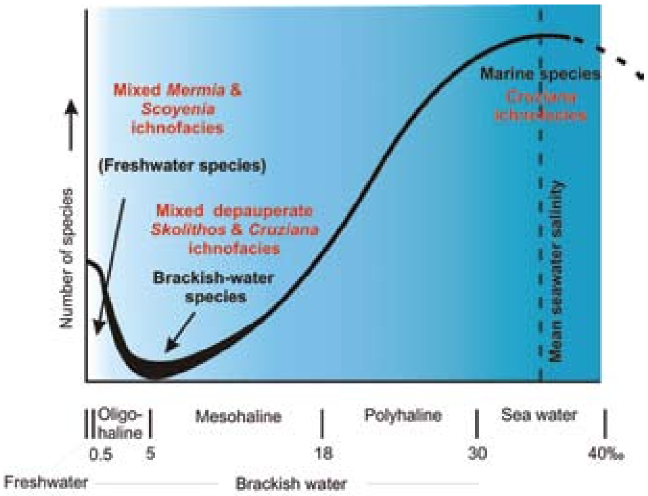

Figure 6.8 Relationship between trace-fossil associations, ichnodiversity, and salinity Modified from Buatois *et al.* (1997b), and Mángano and Buatois (2004a).

Ichnofaunas developed under normal-marine salinity conditions in nearshore to offshore zones are characterized by: (1) high ichnodiversity; (2) marine ichnotaxa produced by both euryhaline and stenohaline organisms; (3) onshore–offshore trends displayed by the *Skolithos* and *Cruziana* ichnofacies; (4) presence of both infaunal and epifaunal traces; (5) presence of simple and complex structures produced by presumed trophic generalists and specialists, respectively; (6) presence of multispecific associations, which become more common towards distal settings; (7) high density; and (8) wide size ranges (Mángano and Buatois, 2004a). These ichnofaunas reflect the activity of benthic organisms that inhabited shallow-marine areas dominated by euryhaline conditions. These benthic faunas experience less salinity stress than those developed in brackish-water ecosystems, characterized by steep salinity gradients. Fully marine deposits are typically extensively bioturbated, and contain a wide range of ethological categories and ichnotaxa. Ichnodiversity commonly reaches a maximum peak under euryhaline conditions (Buatois *et al.*, 1997b). Although it is difficult to pinpoint ichnotaxa exclusive of fully marine conditions in shallow-marine areas, *Chondrites*, *Phycosiphon*, *Scolicia*, and *Zoophycos* are common indicators.

A large number of studies have focused on the diagnostic features of brackish-water benthic faunas. Valuable information has been obtained from studies of marine benthic ecology in modern estuaries and bays (e.g. Remane and Schlieper, 1971; Croghan, 1983; McLusky, 1989; Hudson, 1990), and ichnological studies of marginal-marine ecosystems as well (e.g. Howard and Frey, 1975; Howard *et al*., 1975; Rindsberg, 1992; Gingras *et al*., 1999b). This ecological and neoichnological information has been subsequently integrated with data from the fossil record, initially from the Mesozoic of the Canadian region of the Western Interior Seaway (e.g. Wightman *et al*., 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994, 1997; MacEachern and Gingras, 2007), resulting in the so-called "brackish-water model".

Very few animals have the physiological adaptations necessary to survive in brackish water (Croghan, 1983). This reflects the harsh conditions of brackish-water ecosystems that result from fluctuating environmental parameters, mostly salinity but also temperature, oxygen, and water turbidity. In modern estuaries, salinity fluctuations from 30‰ to 10‰ in one hour have been documented (Ferguson *et al*., 1981). Therefore, brackish-water faunas are less diverse than their marine and freshwater equivalents (e.g. Croghan, 1983; McLusky, 1989; Hudson, 1990; Pickerill and Brenchley, 1991). As a result, the abundance and particularly the diversity of biogenic structures in brackish-water settings are very low, reaching a minimum under mesohaline to oligohaline conditions (Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Buatois *et al*., 1997b; Mángano and Buatois, 2004a).

Some marine organisms referred to as euryhaline are usually capable of colonizing brackish-water environments, as they are highly tolerant to changes in salinity. In contrast, continental organisms living in freshwater are not physiologically fit to survive in a brackish ecosystem. Diversity of freshwater animals tends to decline rapidly, even with slight increases in salinity, whereas marine organisms experience a more gradual decrease in number under dilution of normal-marine salinity (Pemberton and Wightman, 1992; Buatois *et al*., 1997b; Mángano and Buatois, 2004a). As a result, the ichnofauna from estuarine environments is represented by an association of biogenic structures produced by an impoverished marine fauna rather than from a combination of fully marine and freshwater forms. This is reflected by ichnofacies distribution, with brackish-water ecosystems characterized by a mixed of depauperate *Skolithos* and *Cruziana* ichnofacies (Wightman *et al*., 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994).

Burrowing is a key strategy intended to minimize salinity variations as salinity fluctuations are considerably lower a few centimeters into the substrate than at the water–sediment interface because the presence of impermeable fine sediment slows down the exchange of pore water (Sanders *et al*., 1965; Johnson, 1967; Rhoads, 1975). Thus, brackish-water associations tend to be dominated by structures of infaunal organisms rather than surface epifaunal trails.

Organisms able to foray into brackish-water settings are commonly opportunistic (see Section 6.4). Accordingly, ichnofaunas from brackish-water settings contain very simple forms produced by nonspecialized r-selected animals, which are typically adapted to environments of high physiological stress (Miller and Johnson, 1981; Ekdale, 1985; Pemberton and Wightman, 1992; Beynon and Pemberton, 1992). In terms of trophic types, euryhaline animals are either omnivorous or trophic generalists (Wolff, 1973).

It has been noted that reduced size is one of the most notable features of brackish-water associations (Hakes 1976, 1985). Although Taylor *et al*. (2003) have expressed doubts on the connection between size reduction and brackish water, this link is in agreement with studies of marine benthic ecology and observations from the ichnological record, which have documented reduced size in brackish-water faunas, particularly ophiuroids, bivalves, and some worms (Remane and Schlieper, 1971; Spaargaren, 1979, 1995; Mángano *et al*., 1999; Gingras *et al*., 1999b; Mángano and Buatois, 2004a). However, Gingras *et al*. (1999b) noted that crustaceans do not display size reduction in brackish-water environments. It has further been postulated that size reduction in response to salinity occurs either as a morphological adaptation or as a result of population dynamics (Gingras *et al*., 1999b). In the first case, decreasing size allows the organism to increase its surface area to mass ratio to control osmotic transfer. In the second case, large populations of small forms that attain full growth result in the same biomass.

In short, brackish-water trace-fossil associations are characterized by: (1) low ichnodiversity; (2) forms typically found in marine environments; (3) mixture of vertical and horizontal trace fossils from the *Skolithos* and *Cruziana* ichnofacies; (4) dominance of infaunal traces rather than epifaunal trails; (5) simple structures produced by trophic generalists; (6) variable abundance; (7) presence of monospecific associations; and (8) small size (Wightman *et al*., 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Mángano and Buatois, 2004a). Typical components of brackish-water environments are *Teichichnus* (Fig. 6.9) (Buatois *et al*., 2005) and the spiral burrow *Gyrolithes* (Wetzel *et al*., 2010), together with *Skolithos*, *Diplocraterion*, *Palaeophycus*, *Protovirgularia*, *Lockeia*, and *Planolites*.

In contrast, freshwater ichnofaunas, such as those present at the fluvio-estuarine transition, are characterized by: (1) moderate to relatively high diversity; (2) forms typically present in continental environments; (3) a mixture of trace fossils belonging to the *Scoyenia* and *Mermia* ichnofacies; (4) the dominance of surface trails and meniscate trace fossils; (5) temporary structures produced by mobile detritus and deposit-feeding fauna; (6) moderate density of individual ichnotaxa; (7) presence of multispecific associations; and (8) small size (Buatois *et al*., 1997b; Mángano and Buatois, 2004a). The relatively high ichnodiversity records a secondary peak in diversity typically associated with the activity of freshwater, and terrestrial organisms along a salinity gradient (Buatois *et al*., 1997b). The freshwater benthos inhabiting this zone does not have the special adaptations necessary to survive in the brackish environment. While fully marine ichnofaunas gradually decrease in diversity into brackish-water settings, freshwater ichnofaunas from fluvio-estuarine transitions do not intergrade with those from brackish water. Arthropods are the

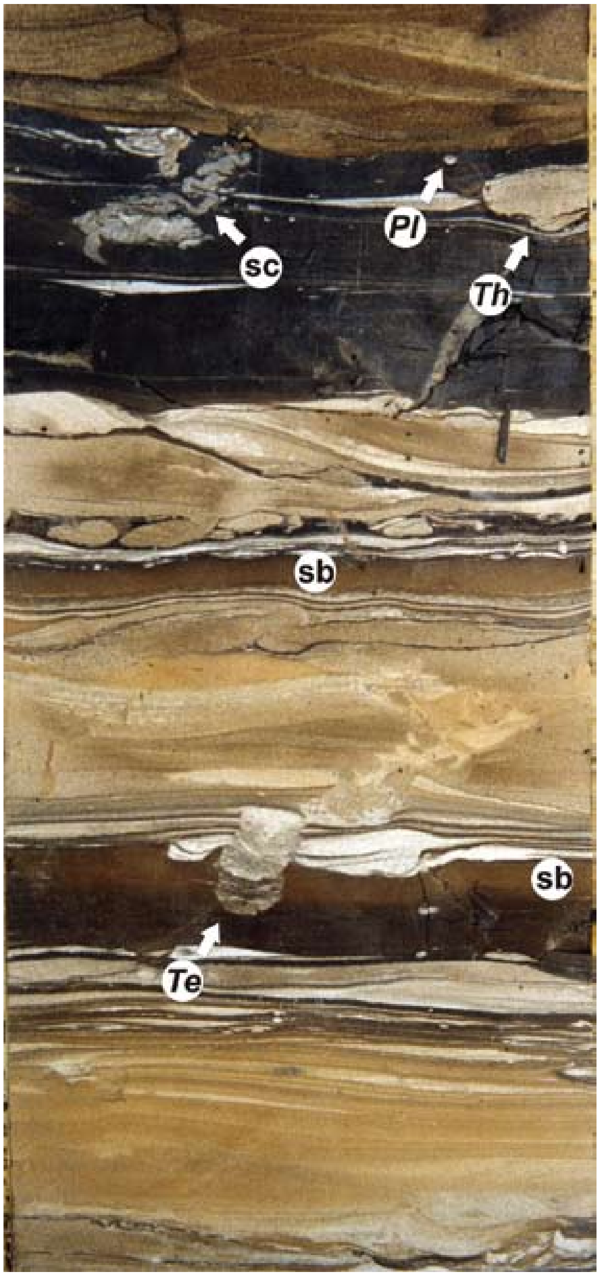

Figure 6.9 Typical aspect of a brackish-water deposit as expressed in core. Bioturbation intensity and ichnodiversity is low. The trace-fossil association consists of *Teichichnus* (*Te*), small *Planolites* (*Pl*), and *Thalassinoides* (*Th*). Synaeresis cracks (sc) and siderite bands (sb) are common. Lower Miocene, Oficina Formation, Oritupano Field, Eastern Venezuelan Basin. Core width is 7 cm.

dominant tracemakers. Typical elements are trackways (e.g. *Dendroidichnites*, *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Stiallia*, *Stiaria*) and resting traces (e.g. *Tonganoxichnus*), as well as grazing (e.g. *Gordia*, *Helminthoidichnites*, *Helminthopsis*) and feeding traces (e.g. *Circulichnis*, *Treptichnus*). Vertebrate trace fossils are represented by fish trails (*Undichna*) and tetrapod trackways (e.g. *Serpentichnus*), and illustrate the *Serpentichnus* ichnocoenosis of Hunt and Lucas (2006a, 2007).

Suppressed erosion during rising tides allowed excellent preservation of delicate surface structures (Archer *et al*., 1994). Additionally, the absence of pervasive burrowers in such settings (particularly in Paleozoic examples) improves the preservation potential of surface traces because the activity by infaunal organisms would have lead to the destruction of the uppermost tiers (Bromley, 1990, 1996; Buatois *et al*., 1997b).

Finally, stressful conditions linked to salinity are extreme under hypersaline conditions, such as those typical of sabkhas and saline lakes (e.g. Price and McCann, 1990). Ekdale *et al*. (1984) noted that hypersaline lakes and thermal pools generally have no benthic fauna and, therefore, no biogenic structures. However, Scott *et al*. (2007a) noted that hot springs provide favorable sites for insects, mammals, birds, and reptiles. In saline lakes, freshwater inflow is higher around ephemeral streams, hot springs, and ground-water seepage, allowing a concentration of animals that produce trackways, trails, and burrows. Ichnofaunas from restricted, hypersaline seas described from the fossil record are dominated by small, poorly specialized trace fossils (Gibert and Ekdale, 1999). Typically marine hypersaline deposits are scarcely bioturbated and contain low-diversity trace-fossil associations (Jaglarz and Uchman, 2010).

6.1.5 SEDIMENTATION RATE

Ichnological evidence commonly reflects the complex interplay between sedimentation rate, erosion, and biogenic activity, therefore revealing information on depositional rhythms. Continuous and slow sedimentation usually allow for intense bioturbation and destruction of physical sedimentary structures, particularly in the absence of any other stress factor (Howard, 1978; Howard and Reineck, 1981; Monaco, 1995). Application of this simple principle allows re-examination of Cretaceous-Tertiary deposits attributed to tsunami events that were in fact intensely bioturbated, suggesting slow rates of sedimentation rather than episodic deposition (Savrda, 1993; Ekdale and Stinnesbeck, 1998). Episodic deposits commonly contain burrows only in the top of layers, revealing post-event colonization (Howard, 1978; Frey and Goldring, 1992). Where storm deposits alternate with intensely bioturbated background sedimentation units, these deposits are characterized by the so-called “Lam-Scram” pattern (see Section 7.1.5).

Pollard *et al*. (1993) introduced the notion of the colonization window or time available for occupation of the substrate to understand burrowing in high-energy settings. Colonization of shifting sands, such as those forming subtidal bars, is impossible under high-energy conditions, but may occur during short periods of quiescence, revealing brief colonization windows. In contrast, under slow accretion (e.g. lower offshore) the colonization window is more or less continuously open. In fluvial successions, it is not unusual that the only trace fossils occur in fine-grained overbank and pond deposits interbedded within unbioturbated, stacked channel deposits, recording brief colonization windows (Buatois *et al*., 1997a) (see Section 10.2.2). In any case, in some settings brief periods of sedimentation breaks may be enough for benthic

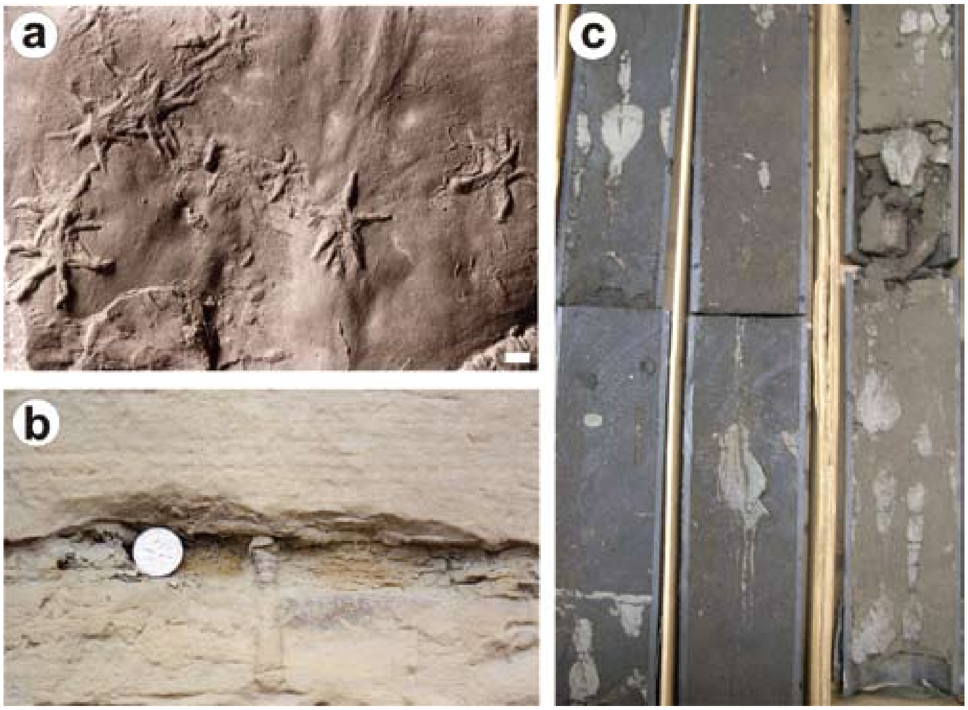

Figure 6.10 Trace fossils and sedimentation rate. (a) *Asteriacites lumbricalis* in tidal-flat deposits forming imbricated structures that document vertical movement though the sediment (from lower left to upper right). Pennsylvanian, Rock Lake Shale, Stanton Formation, Western Missouri, United States. See Mángano *et al.* (1999). Scale bar is 1 cm. (b) Truncated *Ophiomorpha* in hummocky cross-stratified sandstone recording storms in offshore-transition deposits. Intense storm scouring truncated the top of the burrow. Upper Cretaceous, Desert Member, Blackhawk Formation, Book Cliffs, Utah, United States. Coin is 1.4 cm wide. (c) Stacked *Rosselia socialis* in lower-shoreface deposits, reflecting re-equilibration of burrows after storm deposition. Lower Cretaceous, Grand Rapids Formation, Alberta, Canada. Core is read from base at lower left to top at upper right. See Pemberton *et al.* (2001). Core width is 9 cm.

organisms to graze on the substrate. Sedimentation rates of 3.8 m/yr were estimated for Carboniferous tidal-flat deposits formed in a fluvio-estuarine transition (Lanier *et al.*, 1993). However, clay drapes along bedding planes are covered by trackways and trails, reflecting arthropod ability to use available resources during short-term slack-water periods (Buatois *et al.*, 1997b).

Some ichnotaxa, particularly those regarded as equilibrium structures, are useful to detect changes in the balance between deposition and erosion. Goldring (1964) illustrated the upward and downward movements of *Diplocraterion yoyo* in response to aggradation and degradation of the substrate, respectively. Burrowing sea anemones slowly move upwards during gradual vertical accretion of the substrate, but move faster if sedimentation is episodic (Schäfer, 1962). Horizontal and vertical repetition is recorded by multiple impressions of the ophiuroid resting trace *Asteriacites lumbricalis*. These structures record slight horizontal relocation and the punctuated upward motion of the animal through the sediment, and most likely document an escape strategy (Seilacher, 1953b; Mángano *et al.*, 1999) (Fig. 6.10a). In high-energy nearshore settings, truncated specimens of *Ophiomorpha* indicate erosive events (Howard, 1978) (Fig. 6.10b).

The ichnogenus *Rosselia* commonly reflects adjustments of the burrow as a response to sedimentation events (Nara, 1997, 2002; Pemberton *et al.*, 2001; Campbell *et al.*, 2006). Nara (1995, 1997) described Pleistocene funnel- and spindle-shaped specimens of *Rosselia*, attributed to terebellid polychaetes that are vertically stacked reflecting upward migration to avoid burial due to episodic sedimentation in a storm-dominated shallow-marine setting. Pemberton *et al.* (2001) illustrated up to seven Cretaceous stacked *Rosselia* reflecting burrow readjustments after storms in a lower shoreface (Fig. 6.10c). Identically, Howell *et al.* (2007) documented seven stages of upward migration and readjustment in *Rosselia* throughout an approximately 1-m thick amalgamated sandstone unit, resulting from repeated storms in a delta-front environment. These findings provide a new source of data to estimate sedimentation rate and frequency of storms in wave-dominated shallow-marine environments. Campbell *et al.* (2006) analyzed Pleistocene specimens of *Rosselia* displaying a simple morphology that were regarded as extreme-event end members. These specimens occur in mudstone and siltstone interpreted as oceanic-flood deposits from an adjacent river system, and record adaptation of terebellid polychaetes to allow them to thrive under conditions of very high sedimentation rates that caused the exclusion of any other benthic fauna.

6.1.6 FOOD SUPPLY

The type and amount of food supply ranks among the most important controlling factors in determining feeding strategy (Fig. 6.1) (see Section 3.1). Suspension feeders tend to be dominant in high-energy settings where organic particles are kept in suspension by waves or currents. In contrast, organic particles accumulate in the sediment in tranquil waters and animals tend to develop deposit- and detritus-feeding strategies. Food supply tends to vary in a predictable way along onshore–offshore trends, resulting in what has been termed the food resource paradigm by Pemberton *et al.* (2001). Another gradient occurs within the sediment in relation to the vertical distribution of organic matter (see Section 5.1). Organic matter is more abundant close to the sediment–water interface, which results in a peak of available food for detritus and deposit feeders occupying superficial to shallow tiers (Fig. 6.11).

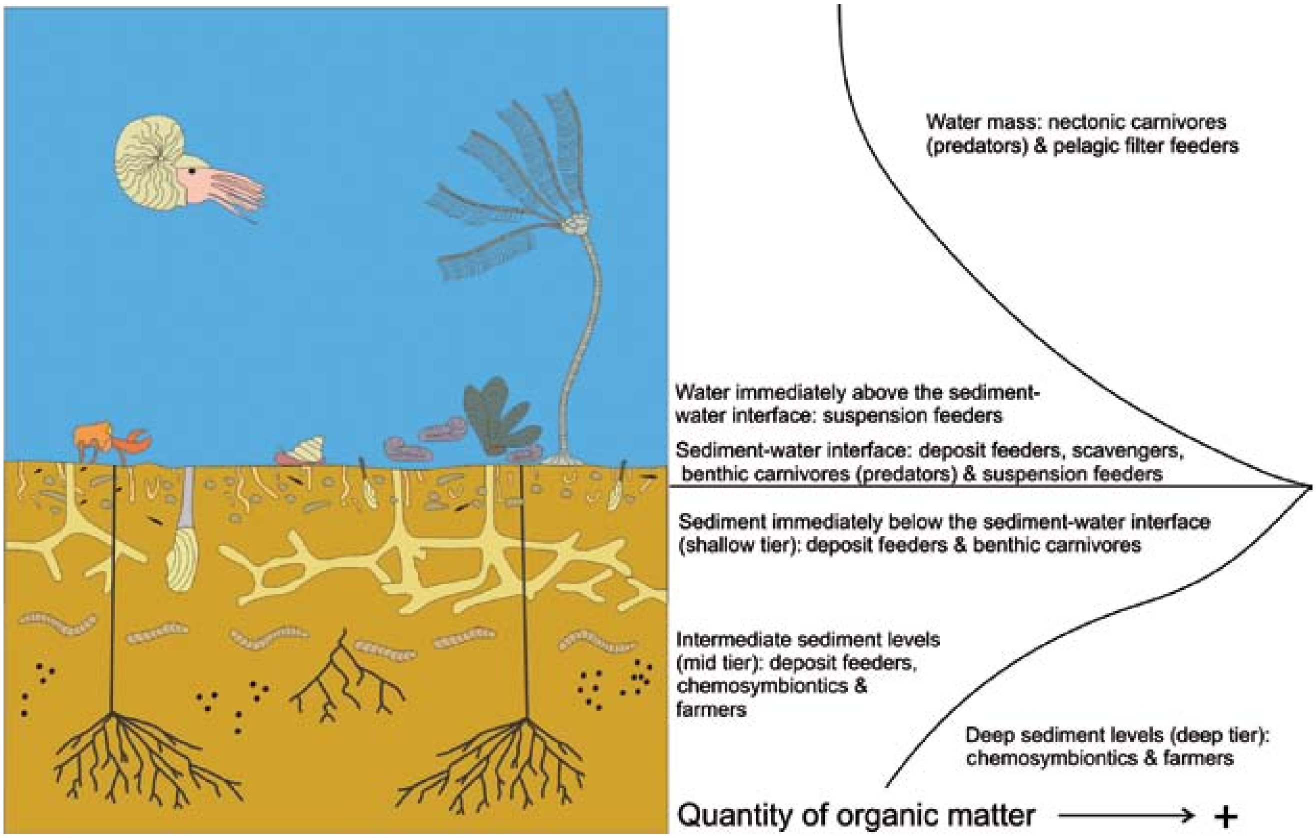

Figure 6.11 Relationship between tier position, feeding strategies, and quantity of organic matter. Note that the highest amount of organic matter is near the sediment–water interface. In deep-marine environments burrows produced by chemosymbionts and farmers (i.e. graphoglyptids) occupy a very shallow tier. Modified from Mángano and Buatois (1999a).

Under conditions of scarce food supply, animals developed sophisticated feeding strategies, including gardening and chemosymbiosis. This is the case of deep-marine environments, which are dominated by graphoglyptids and complex grazing trace fossils, typical of the *Nereites* ichnofacies (Seilacher, 1977a; W. Miller, 1991a). Conversely, it has been argued that high frequency of sediment gravity flows supplying organic detritus to deep-marine ecosystems precludes the development of ichnofaunas dominated by agrichnia and ornate pascichnia (Buatois and López Angriman, 1992b).

The importance of food supply in deep-marine ichnofaunas has been emphasized by Wetzel and Uchman (1998a). These authors suggested that high amounts of food supply are indicated by: (1) dark-colored sediments, (2) complete bioturbation, (3) high density of shallow-tier trace fossils, (4) rarity or absence of graphoglyptids, and (5) deep tiers totally bioturbated by feeding traces that have a connection to the surface. Also, in settings with seasonal strongly fluctuating input of organic matter (e.g. under monsoonal regimes), a double nutritional strategy is adopted by some organisms, detritus feeding during bloom times and deposit feeding during non-bloom times (Wetzel, 2008, 2010). During times of benthic food richness, oxygenation of interstitial water decreases and, as a result, organisms move upward. In areas of marked seasonality of organic matter input, biogenic structures tend to show pronounced upward and downward movements (Wetzel, 2010). On the other hand, predominance of horizontal burrows without evidence of vertical displacement indicates a more constant input of organic matter. Up-and-down movements of endobenthic organisms affect near-surface burrowers. Consequently, graphoglyptids tend to be absent in deep-sea regions affected by pronounced seasonality of primary production (Wetzel, 2010).

In lacustrine environments, grazing patterns are nonspecialized, as exemplified by the ichnogenus *Mermia*, which displays looping and a high level of self-overcrossing, recording the repeated passage of the tracemaker across the same portion of sediment. Such nonspecialized trophic strategies most likely reflect the abundance and accessibility of food in lacustrine systems (Buatois and Mángano, 1998). A similar situation has been recorded in modern tidal flats with grazing trails of the isopod *Chirodotea coeca* (Hauck *et al*., 2008). These authors documented an increase in trail tortuosity and self-overcrossing parallel to an increase in food content.

6.1.7 BATHYMETRY

Originally, bathymetry was emphasized in earlier ichnological studies that attempted to establish links between trace-fossil associations and depositional environments (e.g. Seilacher, 1967b). However, it soon became clear that ichnofacies and trace-fossil distribution reflect sets of environmental factors rather than sedimentary environments and specific bathymetric zones (see Section 4.6). Exceptions to the standard bathymetric model are countless (e.g. Henbest, 1960; Crimes, 1977; Crimes *et al.*, 1981; Pemberton and Frey, 1984b). As noted by Frey *et al.* (1990), bathymetry per se is only very rarely a governing factor. As a consequence, bathymetric implications should be established with caution. In any case, the relative success of the ichnofacies model in bathymetric assessments is based on the fact that in some cases most direct controls (e.g. substrate type, food supply, energy) vary parallel to water depth (Fig. 6.1). A very general bathymetric trend is the dominance of dwelling structures in shallow water, the abundance of feeding, locomotion, and resting traces at intermediate depths and the dominance of farming and grazing traces in food-starved deep-water sediments (Ekdale, 1985).

A different picture emerges from the study of microborings produced by microendolithic algae, bacteria, and fungi. Because many microborers are photosynthetic, they reflect adaptations to different light intensities and wave frequencies and, therefore, display a direct relationship with water depth (Glaub, 1994, 2004; Vogel *et al.*, 1995, 1999, 2000; Glaub *et al.*, 2001, 2002, 2007; Perry and MacDonald, 2002; Vogel and Marincovich, 2004; Glaub and Vogel, 2004). Microborings can be used to differentiate euphotic, dysphotic, and aphotic zones, and index ichnocoenoses have been defined (Glaub, 1994; Glaub *et al.*, 2001, 2002) (Fig. 6.12). Although this scheme was originally based on bathymetric studies in modern environments and Mesozoic–Cenozoic successions, further studies demonstrated that it is applicable in the Paleozoic (Glaub and Vogel, 2004). The lower limit of the euphotic zone is located where the surface light is reduced to approximately 1%. This zone includes the supratidal, intertidal, and the well-illuminated subtidal (Liebau, 1984). The euphotic zone is essentially dominated by photoautotrophic endoliths, such as cyanobacteria, green algae, and red algae.

Analysis of microbioerosion allows us in turn to subdivide the euphotic zone into four subzones, three for the shallow euphotic region and one for the deep euphotic region (Glaub *et al.*, 2001, 2002; Glaub, 2004). Shallow euphotic subzone I is more or less equivalent to the supratidal zone, and is dominated by microborings of cyanobacteria that protect themselves from sunburn damage by sheath pigmentation. No index ichnocoenose has been defined from this zone because no ancient counterparts are known. Shallow euphotic subzone II is coincident with the intertidal zone, and is dominated by cyanobacterial microborings oriented perpendicular to the substrate. The index ichnocoenose of this subzone is the *Fasciculus acinosus*/*Fasciculus dactylus* ichnocoenose. The changing level in hydrodynamic energy is also a significant controlling factor in the intertidal zone. Shallow euphotic subzone III includes the well-illuminated portion of the subtidal area, and is dominated by microborings of cyanobacteria, red algae, and green algae that commonly display perpendicular orientations but may include parallel components, particularly with increasing water depth. The index ichnocoenose of this subzone is the *Fasciculus dactylus*/*Palaeoconchocelis starmachii* ichnocoenose. The deep euphotic subzone represents the less illuminated region of the euphotic zone, and is dominated by red and green algal microborings that are oriented parallel to the substrate. The index ichnocoenose of this subzone is the *Palaeoconchocelis starmachii*/*Reticulina elegans* ichnocoenose.

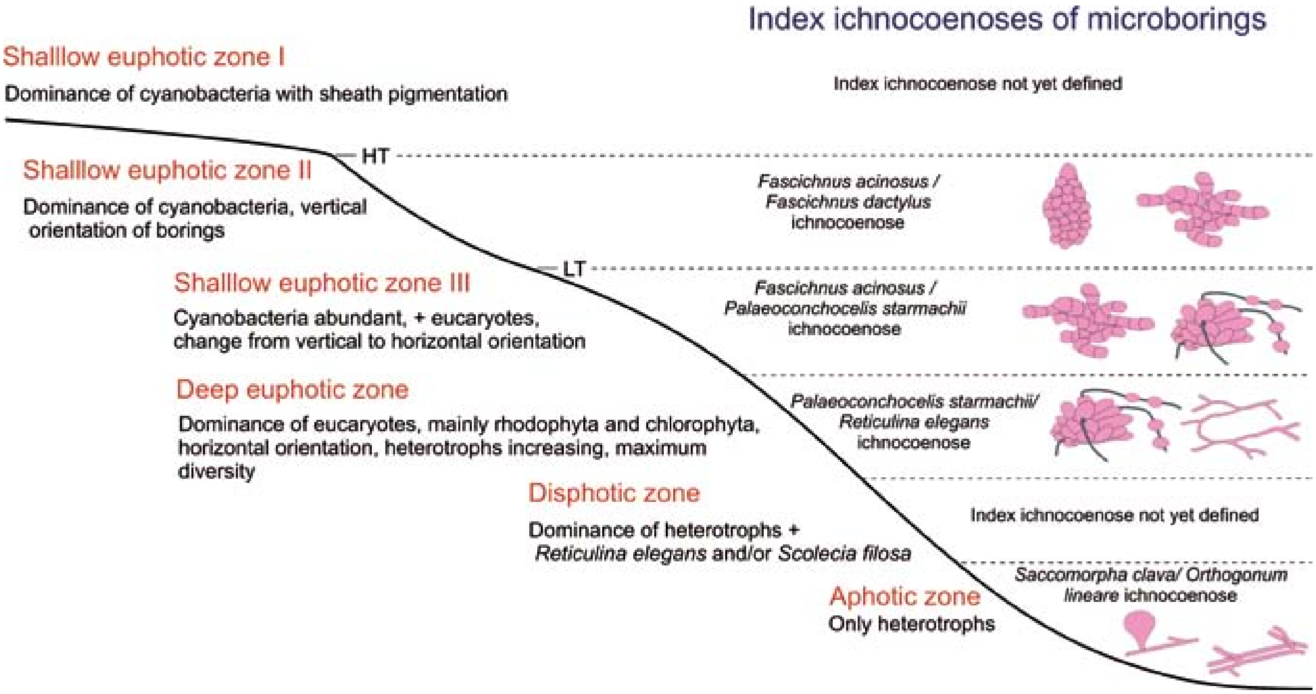

Figure 6.12 Bathymetric zonation based on microborings. HT = High tide. LT = Low tide. Vertical scale greatly exaggerated. Modified from Glaub (2004).

The dysphotic zone extends from the 1% level to approximately 0.01% or 0.001% of surface light. This zone is dominated by chemoheterotrophic endoliths, mostly fungi. However, two traces of photoautotrophs (*Scolecia filosa* and *Reticulina elegans*) are present because their producers can cope with less than 1% of surface light. No index ichnocoenose has been defined from this zone. The aphotic zone is characterized by the lack of light and, therefore, includes heterotrophs only. The index ichnocoenose of this zone is the *Saccomorpha clavata*/*Orthogonum lineare* ichnocoenose.

The bathymetric distribution of macroborings is less well understood. Bromley and D'Alessandro (1990) analyzed the distribution of borings in shallow- and deep-marine coral materials from the Pliocene to the Recent in the Mediterranean Sea. They noted that ichnodiversity is higher in shallow water than in deep water. The sponge boring *Entobia* was dominant in both shallow- and deep-water materials, but the latter are typified by less distinctive forms and greater morphological variability. This may result from areally restricted substrates that lead to constrained development of the boring system with more mature chambers crowded into the corners of the substrate. While the abundance of other borings decreases in deep water, that of sponge borings increases dramatically, with coral substrates locally reduced to a filigree. However, the underlying control in degree of bioerosion is certainly not depth per se, but low rates of sedimentation in deep-sea settings.

Comparative analysis of shallow- to deep-water macrobioerosion in the Pleistocene carbonates of Rhodes also indicates higher ichnodiversity in shallow-marine settings (Titschack *et al*., 2005). The shallowest-water facies is dominated by the bivalve boring *Gastrochaenolites torpedo* and the sponge boring *Entobia goniodes*. With increasing water depth, *Gastrochaenolites* disappears and the association is dominated by several ichnospecies of *Entobia*. The deepest-water ichnofabrics are dominated by the simple borings of polychaetes (*Trypanites*). However, relatively diverse macroboring associations were documented in the deep-water coral *Lophelia* in the Pleistocene of Rhodes (Bromley, 2005). Rasping traces that are dominant in shallow-water corals, such as *Radulichnus* (produced by mollusks) or *Gnathichnus pentax* (produced by regular echinoids), are patchily distributed or absent, supporting an aphotic environment for the *Lophelia* bioerosion association. Associated microborings belong to the *Saccomorpha clavata*/*Orthogonum lineare* ichnocoenose, further supporting aphotic settings.

6.1.8 WATER TURBIDITY

The role of water turbidity is beginning to be recognized as an important controlling factor for benthic faunas (e.g. Gingras *et al*., 1998; MacEachern *et al*., 2005). In coastal areas affected by fluvial discharge, buoyant mud plumes extend in a seaward direction particularly under hypopycnal conditions (Bates, 1953; Wright, 1977; Kineke *et al*., 1996). Because high suspended loads of fine-grained material close to the sediment–water interface clog the filter-feeding apparatus of suspension feeders, this trophic type tends to be inhibited under such conditions (Perkins, 1974). As a result, there is an impoverishment or direct suppression of the *Skolithos* ichnofacies, and associations are dominated by deposit-feeding traces (Gingras *et al*., 1998; MacEachern *et al*., 2005; Buatois *et al*., 2008). However, primary production can be severely affected in settings characterized by high water turbidity, resulting in a general impoverishment of both suspension and deposit feeders (Leithold and Dean, 1998). Therefore, on occasions, water turbidity may be conducive to an overall reduction in ichnodiversity and burrow density (MacEachern *et al*., 2005).

Estuaries are commonly turbid due to the amounts of silt and clay in the water, particularly in the low-energy estuary basin (Vernberg, 1983). Turbidity at the sediment surface typically excludes suspension feeders, which are sensitive to clogging (Rhoads and Young, 1970). Estuary-basin deposits, therefore, tend to be dominated by trace fossils of deposit feeders (Buatois *et al*., 2002b). In particular, turbidity may be extreme in tide-dominated estuaries, with nonbioturbated mudstone typically characterizing the turbidity-maximum zone (Bechtel *et al*., 1994; MacEachern and Gingras, 2007; Lettley *et al*., 2007b).

Water turbidity also plays an important control in microboring distribution (Perry and MacDonald, 2002). The depth-related microboring zonation (see Section 6.1.7) may display some departure from the typical model depending on water turbidity. These authors noted that in turbid waters the euphotic zone is extremely compressed, and elements of the dysphotic zone (mostly fungi microborings) may occur at only 30 m depth.

6.1.9 CLIMATE

The application of ichnology in paleoclimatology is still in its infancy. The first studies were conducted in paleosols, using insect trace fossils (e.g. Genise and Bown, 1994a; Genise *et al*., 2000). These authors noted that insects are extremely sensitive to local ecological constraints, and emphasized the importance of microclimate as an environmental limiting factor. Microclimate includes different aspects, such as temperature, radiation, humidity, and wind speed near the ground (Unwin and Corbet, 1991). In turn microclimate depends on local vegetation, and these two factors are ultimately controlled by climate. Therefore, insect trace fossils are powerful indicators of climate conditions at the time of nest formation. In fact, archetypal and potential paleosol ichnofacies are indicators of paleoclimatic conditions rather than depositional environments (Genise *et al*., 2000, 2010a). In particular, insect nests (calichnia) contain larvae that are provisioned with organic matter by the adults; both larvae and provisions are sensitive to microclimatic conditions, such as moisture and soil temperature (Michener, 1979; Grassé, 1984; Genise, 1999; Genise *et al*., 2004b). Excessive moisture inside cells results in the decay of provisions, while insufficient moisture results in the dehydration of larvae (Genise *et al*., 2000). More recently, Hasiotis *et al*. (2007) addressed the relationship between tiering and availability of water, suggesting that tiers become progressively shallower as a response to increasing humidity.

A close relationship exists between Scarabaeinae dung beetles (producers of *Coprinisphaera*, *Fontanai*, and *Monesichnus*) and herbaceous communities, because these beetles provision their nests with excrement of vertebrate herbivores (Halffter and Edmonds, 1982; Genise *et al*., 2000). The nests of most solitary bees (e.g. *Celliforma*, *Palmiraichnus*) are produced on bare, well-drained, light soil exposed to sun rather than humid tropical areas (Batra, 1984; Michener, 1979; Genise and Bown, 1994a). Clustered bee cells, such as *Corimbatichnus*, *Uruguay*, and *Palmiraichnus*, most likely display similar preferences (Genise and Verde, 2000). This distribution is related to the fact that the larval food is commonly exposed to fungal attack or hygroscopic liquefaction in humid environments (Michener, 1979; Roubik, 1989; Genise *et al*., 2000, 2004b). Bee nesting in poorly drained soils is, therefore, very rare (e.g. Roubik and Michener, 1980). Ants (producers of *Attaichnus*) also favor bare soil, although they may move eggs and larvae from one site to another to avoid submersion during flooding (Hölldobler and Wilson, 1990; Genise *et al*., 2004b). Ecological preferences of dung beetles, bees, and, to a lesser extent, ants explain the association of the *Coprinisphaera* ichnofacies with herbaceous communities that range from dry and cold to relatively humid and warm climates. The climatic affinities of coleopteran pupal chambers (e.g. *Teisseirei*, *Rebuffoichnus*, *Fictovichnus*) are less well understood, although they tend to be associated with bee nests (e.g. Genise *et al*., 2002).

In contrast, termite nests (e.g. *Termitichnus*, *Vondrichnus*, *Fleaglellius*, *Tacuruichnus*) tend to be more abundant in more humid environments, including waterlogged soils (Grassé, 1984). Paleosols dominated by termite nests commonly developed under higher-moisture conditions and more frequent flooding events than those dominated by dung beetle and bee nests (Genise and Bown, 1994b; Genise *et al*., 2000, 2004b). Genise (1997) used the presence of *Tacuruichnus* (a nest very similar to that of the extant species *Cornitermes cumulans*) to infer warm and wet conditions in Pliocene deposits. In some cases, termite nests may be associated with dung beetle nests (e.g. Sands, 1987). However, these termite nests are assigned to the Macrotermitinae, whose distribution ranges from tropical rain forest to semiarid steppes. In the Miocene Pinturas and Santa Cruz formations of Patagonia, the lower paleosols contain abundant termite nests (*Syntermesichnus*), while the upper ones display bee and dung beetle nests (*Celliforma*, *Palmiraichnus*, and *Coprinisphaera*), reflecting increasingly arid conditions and deforestation after ash fall events (Bown and Laza, 1990; Genise and Bown, 1994a). Climatic fluctuations characterized by the presence of relatively wet periods within more permanent semiarid conditions have been inferred from the presence of bee nests and coleopteran pupal nests in Quaternary paleosols of the Canary Islands (Alonso-Zarza and Silva, 2002; Genise and Edwards, 2003).

Tidal-flat environments commonly exhibit rapid changes in temperature related to periodic subaerial exposure that have strong impact on animal–sediment interactions (Mángano *et al*., 2002a). In addition, tidal-flat faunas experience important latitudinal changes in connection to temperature gradients (e.g. Green and Hobson, 1970; Yeo and Risk, 1981; Aitken *et al*., 1988). Upper-intertidal zones in tropical settings are characterized by very high temperatures, long durations of subaerial exposure, and abnormal salinities, representing an extremely inhospitable habitat for marine organisms. As a result, the highest density of biogenic structures in tropical tidal flats is in the lower intertidal zone (Terwindt, 1988). In particular, arid climates cause more extreme upper-intertidal conditions and correspondingly impoverished communities than humid climates. In general, benthic organisms tend to be less specialized in their diet, often being trophic generalists. On the other hand, high-latitude tidal flats commonly exhibit dense concentrations of biogenic structures in the upper-intertidal zone (e.g. Yeo and Risk, 1981). As documented by Reise (1985), bathymetric displacement of certain species along latitudinal gradients is common. For example, Green and Hobson (1970) noted that the bivalve *Gemma gemma* lives in intertidal areas in northern North America and in subtidal areas in the south to avoid high temperatures on tidal flats. Aitken *et al*. (1988) documented a dominance of vertical domiciles of bivalves and polychaetes in modern subarctic tidal flats. These authors compared subarctic and temperate tidal flats in terms of biogenic structures and noted that some species (e.g. *Corophium volutator*) are abundant in temperate tidal flats but are absent from subarctic intertidal areas. Tidal flats that are exposed to regular winter freeze contain lower ichnodiversity than their warmer counterparts (Gingras *et al*., 2006). As noted by Mángano *et al*. (2002a), application of modern observations to the stratigraphic record is complicated. However, these authors extensively documented a Carboniferous equatorial tidal-flat ichnofauna that displays the highest density and diversity of biogenic structures in lower-intertidal deposits close to low tide. Therefore, they concluded that high temperatures and increased desiccation in the upper-intertidal zone were probably major limiting factors.

The topic of climatic controls on shallow-marine ichnofaunas has been explored also by Goldring *et al*. (2004). These authors proposed the existence of three climatic zones: (1) tropical and subtropical with *Ophiomorpha*, echinoid trace fossils as well as other ichnotaxa; (2) temperate with echinoid trace fossils and *Thalassinoides*; and (3) arctic with only molluscan and worm trace fossils. Partial support for this model comes from observations in modern environments by Gingras *et al*. (2006), although they extended the dominance of mollusk and worm burrows to the temperate zone. Burrowing bivalves and worms tend to occur in bare intertidal deposits of temperate to cold climates, while crabs mostly burrow in vegetated intertidal sediments of tropical to subtropical settings (Eisma, 1998). However, both *Ophiomorpha* and *Scolicia* are abundant in Miocene mid-latitude shallow-marine settings under temperate to cold climates, suggesting an anomaly in the proposed pattern (Buatois *et al*., 2003; Carmona *et al*., 2008).

In particular, the ichnogenus *Macaronichnus* tends to occupy cold to temperate zones (Gingras *et al*., 2006; Pemberton *et al*., 2006). Interestingly, *Macaronichnus* has been recently documented in Miocene tropical foreshore deposits, but associated

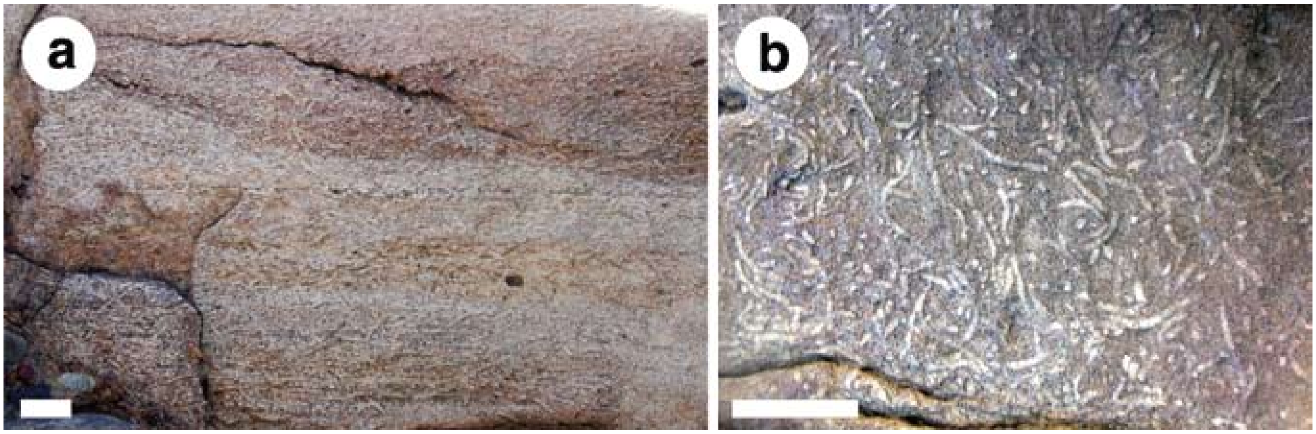

Figure 6.13 *Macaronichnus* in tropical settings, but linked to upwelling conditions, Upper Miocene, Urumaco Formation, Urumaco, northwest Venezuela. See Quiroz *et al.* (2010). (a) Foreshore deposits with *Macaronichnus segregatis* (cross-section). (b) Close-up of specimens showing light colored sand fill that contrasts with the dark colored surrounding mantle (bedding-plane view). Scale bars are 4 cm.

with upwelling conditions (Quiroz *et al.*, 2010) (Fig. 6.13a–b). Preliminary data also suggest an increase in trace-fossil size towards high latitudes (Gingras *et al.*, 2006; Pemberton *et al.*, 2006). In addition, deep-infaunal burrowers tend to be more abundant in mid and high latitudes (Aberhan *et al.*, 2006; Bush *et al.*, 2007; Carmona *et al.*, 2008).

It has long been suggested that the evolution of deep-sea benthic biotas has been influenced by water temperature (Wolf, 1960). Comparative analysis of trace-fossil diversity in the deep sea through the Phanerozoic (Seilacher, 1974; Uchman, 2004a) seems to support this view (see Section 14.2.2). Uchman (2004a) noted that the lowest ichnodiversities tend to occur in times of cold deep-seawaters, such as the late Paleozoic and the Oligocene. The role of the Late Ordovician glaciation is still unclear, but some authors have suggested that there is an associated drop in ichnodiversity (McCann, 1990).

A different dataset comes from carbonate ichnofaunas. Most ichnological studies on carbonates focus on tropical environments, particularly in the Bahamas, Grand Cayman, and Florida (e.g. Pemberton and Jones, 1988; Curran and White, 1991, 2001; Curran, 1992, 1994, 2007). Terrestrial suites in tropical settings include relatively diverse insect ichnofaunas, mostly produced by sphecid wasps and halictid bees, and pervasive root traces as well (Curran and White, 2001; Curran, 2007). Intertidal and subtidal tropical carbonates are dominated by crustacean burrows, including *Ophiomorpha* (Curran, 1994, 2007). However, *Ophiomorpha* is apparently rare in temperate carbonates. Large specimens of *Conichnus* seem to be common in both tropical and temperate carbonates (e.g. Curran and White, 1997).

Bioerosion also displays some specific patterns in response to climate and latitude (Johnson, 2006). While most studies concentrate in tropical and subtropical environments (e.g. Bromley, 1978; Bromley and D'Alessandro, 1983; Bromley and Asgaard, 1993a, b; Vogel *et al.*, 2000; Glaub *et al.*, 2001; Perry and MacDonald, 2002), there is a growing dataset on cold-temperate and polar regions (e.g. Akpan, 1986; Akpan and Farrow, 1984; Glaub *et al.*, 2002; Vogel and Marincovich, 2004; Wisshak *et al.*, 2005; Wisshak, 2006). Some studies (e.g. Glaub *et al.*, 2002; Vogel and Marincovich, 2004) have pointed to overall similarities between microbioerosion in high and low latitudes, indicating a widespread applicability of schemes originally established for tropical and subtropical areas. However, some differences were noted by Wisshak *et al.* (2005) and Wisshak (2006) in their study of bioerosion along the Swedish coast. The index ichnotaxa of the euphotic zone were either rare or absent, and this zone was very compressed in comparison to low latitudes. In fact, the boundary between the euphotic and dysphotic zones occurs at only 15 m. Some ichnotaxa (e.g. *Flagrichnus baiulus*) have been suggested to occur only in non-tropical settings (Wisshak and Porter, 2006).

6.1.10 WATER TABLE

The position of the water table and the degree of substrate humidity is one of the most fundamental controls in trace-fossil formation and preservation in continental environments (Gierlowski-Kordesch, 1991; Hasiotis *et al.*, 1993a; Hasiotis and Honey, 2000; Buatois and Mángano, 2002, 2004a; Genise *et al.*, 2004b). Sediment water content strongly influences the degree of substrate consolidation, which in turn controls trace-fossil morphology and preservation (Buatois and Mángano, 2002, 2004a). In fact, the position of the water table is essential to understand distribution of the *Mermia* and *Scoyenia* ichnofacies. The *Mermia* ichnofacies is formed in subaqueous freshwater environments and, therefore, characterizes a high water table that results in the formation of water bodies, such as lakes and ponds (see Section 4.4.2). In contrast, the *Scoyenia* ichnofacies is formed in transitional settings, such as lake-margin environments (see Section 4.4.1), and corresponds to areas of relatively low water table. This is particularly so in the case of the firmground suite of the *Scoyenia* ichnofacies, which is associated with subaerial desiccated substrates. Links between the architecture of crayfish burrows (*Camborygma*), and the position of the water table have been established (Hobbs, 1981; Hasiotis

Figure 6.14 Roots of a modern quiver tree in arid environment, Gannabos Farm, South Africa. Note horizontally extended root systems to follow the water table generated close to the sediment surface after sporadic torrential rain.

and Mitchell, 1993; Hasiotis *et al*., 1993a, 1998; Hasiotis and Honey, 2000). Complex architectures with many branches and chambers are constructed by primary burrowers in areas with a high water table, while deep simple burrows are dominant in areas with a low and/or highly fluctuating water table.

Genise *et al*. (2004b) reviewed the relationships between different insect nests and the position of the water table in paleosols. Bee and dung beetle nests are commonly associated with low water tables. Hasiotis *et al*. (1993b) explored the links between a fluctuating water table and the scarabeid nest *Scaphichnium* in hydromorphic paleosols developed in a distal floodplain. They noted that the appearance of *Scaphichnium* was coincident with a decrease in gray root traces and meniscate traces, suggesting that the nest was emplaced during periods of low water table. The significance of coleopteran pupal chambers is unclear, but they are definitely constructed in subaerial substrates above the water table (Genise *et al*., 2002). Ant and termite nests are constructed in well-drained to seasonally flooded soils (Genise *et al*., 2004b). In the case of seasonally flooded soils, termites use a series of devices, such as chimneys or special walls, which allow them to deal with a higher water table (Genise *et al*., 2004b). Finally, earthworm burrows (e.g. *Edaphichnium*, *Castrichnus*) commonly occur in moist substrates, such as gleyed paleosols (Genise *et al*., 2004b; Verde *et al*., 2007).

Root traces are particularly useful to evaluate position of the water table (Sarjeant, 1975; Cohen, 1982; Bockelie, 1994; Kraus and Hasiotis, 2006). Roots tend to be shallow and horizontally extended in poorly drained soils with a high water table as a response to lack of aeration (Sarjeant, 1975; Cohen, 1982). These roots are typically filled with carbonaceous material and branch at distinct intervals (Bockelie, 1994). Goethite rims commonly surround root traces formed in poorly drained paleosols; some rhizoliths are preserved as tubular bodies of Fe and Mn oxides and jarosite (Kraus and Hasiotis, 2006). In contrast, environments with a low water table are characterized by penetrative, deep root traces (Cohen, 1982; Bockelie, 1994). These well-drained paleosols are characterized by calcareous rhizocretions, or elongate gray mottles surrounded by hematite rims (Kraus and Hasiotis, 2006). In arid environments affected by sporadic torrential rains, root systems can be horizontally extended to follow the rapidly generated water table close to the sediment surface (Fig. 6.14)

6.2 ROLE OF TAPHONOMY

Parallel to the detailed analysis of the limiting ecological factors, the role of taphonomic aspects should be clarified. Information derived from benthic ecology cannot be directly translated into the fossil record without a careful evaluation of the fossilization barrier (Seilacher, 1967a; Bromley, 1990, 1996), a taphonomic filter that separates the plethora of biogenic structures produced from the few that are preserved in the fossil record (see Section 5.2.2). In addition, different diagenetic processes provide a final overprint that may enhance ichnofossil visibility (see Section 1.3.2).

Savrda (2007b) noted that two factors are involved in trace-fossil taphonomy: completeness of the preserved record of biogenic activity or ichnological fidelity, and degree of ichnofossil preservation or trace-fossil visibility. He noted that these two factors may be independent of one another. For example, some ichnofabrics may have high fidelity, but some or all trace fossils may be difficult to discern, while other ichnofabrics may have low fidelity, but discrete ichnotaxa may be well expressed.

The concept of fossil-lagerstätten has been used extensively for body fossils and refers to "any rock containing fossils that are sufficiently well preserved and/or abundant to warrant exploitation" (Seilacher *et al.*, 1985). Some studies attempt to apply this concept to the ichnological record, stressing the importance of taphonomic aspects in the final shaping of ichnofaunas (Bromley and Asgaard, 1991; Savrda *et al.*, 1993; Savrda and King, 1993; Savrda and Ozalas, 1993; Mángano and Buatois, 1995a; Fornós *et al.*, 2002; Savrda, 2007b). This has resulted in the adaptation of the classification framework of body-fossil lagerstätten of Seilacher *et al.* (1985) to the analysis of ichnofaunas (Mángano and Buatois, 1995a; Savrda, 2007b). Seilacher *et al.* (1985) distinguished concentration and conservation deposits, and divided the latter into obrution and stagnation deposits, these being the categories that can be easily translated into ichnofossil-lagerstätten.

Concentration lagerstätten are characterized by an abundance of fossils that results either from transport, commonly in connection with episodic processes, or from condensation due to sediment starvation. Both situations are detected in connection with concentrations of wood fragments with *Teredolites*. Although transport is exceedingly rare in the case of trace fossils, secondary displacement is common with *Teredolites* logs, and concentration lagerstätten commonly occur in transgressive lags (Savrda *et al.*, 1993) (see Box 12.1). In addition, dense occurrences of logs with *Teredolites* result from the combination of increased rate of wood introduction during transgression and concentration of logs that have drifted via sediment starvation, delineating maximum flooding surfaces (Savrda and King, 1993; Savrda *et al.*, 2005). Other examples of condensation ichnofossil-lagerstätten occur in omission surfaces developed in carbonates. In hardgrounds, very low sedimentation rates and early cementation result in intensely bioeroded surfaces that record ecological succession and changes in the degree of substrate consolidation (Mángano and Buatois, 1995a).

Conservation lagerstätten involve exceptional preservation. Obrution deposits result from the episodic smothering of the sea floor that strongly affects benthic biotas (Seilacher *et al.*, 1985). Obrution ichnofossil-lagerstätten are relatively common. The best example is represented by the delicate preservation of graphoglyptids as predepositional trace fossils on the base of thin-bedded turbidites (e.g. Seilacher, 1962; Uchman, 2007). In continental settings, a similar situation is represented by delicate superficial trails preserved in underflow-current lacustrine deposits (Buatois and Mángano, 1993a).

Stagnation deposits are formed under anoxic conditions that favor delicate preservation of body fossils (Seilacher *et al.*, 1985). Because anoxia prevents the establishment of macrobenthic organisms, the emplacement of biogenic structures is commonly restricted (see Section 6.1.3). However, meiofaunal subsuperficial trails have been recorded in Cambrian conservat lagerstätten. Tiny micrometric to millimetric trails (e.g. *Helminthoidichnites*, *Helminthopsis*, *Cochlichnus*) are directly associated with soft-bodied organisms in the Burgess Shale (Mángano and Caron, 2008; Caron *et al.*, 2010; Mángano, 2010), Sirius Passet (Williams *et al.*, 1996), Chengjiang (Y. Zhang *et al.*, 2006), and Kaili (X. Wang *et al.*, 2009; Lin *et al.*, 2010) biotas. Interestingly, non-mineralized carapaces of *Tuzoia* and other organisms serve as sites of preferential preservation of biogenic structures. Dying trackways (mortichnia) formed under anoxic conditions and associated with the body fossils of their producers have been documented in stagnation fossil lagerstätten of Jurassic lithographic limestone (see Section 6.1.3).

An ichnofossil-lagerstätten analogous to stagnation deposits is represented by a pelletal mixed layer preserved as a result of a deoxygenation event (Savrda and Ozalas, 1993) (see Section 5.2.2). Preservation of mixed-layer biogenic structures is commonly inhibited by the interplay of physical and biological processes, including bioturbation by deep-tier infaunal organisms, and low sediment-shear stress. In the case analyzed by Savrda and Ozalas (1993), deoxygenation led to the cessation of bioturbation and, in the absence of physical and biogenic reworking, mixed-layer traces became part of the historical layer.

Ideally, taphonomic overprints should be analyzed in the context of depositional settings. In an attempt to evaluate the interplay between depositional and taphonomic processes in specific sedimentary environments, the concept of taphonomic pathways has been applied to ichnology (Buatois and Mángano, 2004a, 2007; Desjardins *et al.*, 2010a). Analysis of trace-fossil preservational styles in continental deposits suggests that ichnofaunas result from various taphonomic pathways that reflect depositional conditions (subaqueous versus subaerial) and time spans between flooding events (Buatois *et al.*, 1997b, 2007a; Zhang *et al.*, 1998; Buatois and Mángano, 2002, 2004a, 2007; Minter *et al.*, 2007b). Additionally, taphonomic pathways help to explain the role of substrate and rapid environmental fluctuations as main controlling factors in ichnofacies development and replacement (Buatois and Mángano, 2002, 2004a, 2007). In fluvial systems, a variety of taphonomic pathways results from channel abandonment, overbank deposition, and establishment of ponded areas that may desiccate or be filled by overbank vertical accretion without experiencing desiccation (see Section 10.2). In lakes, taphonomic pathways commonly reflect shoreline fluctuations, and associated changes in substrate consolidation (see Section 10.3). Ichnofaunas formed in subaerially exposed overbank and lake-margin deposits are commonly represented by palimpsest surfaces recording taphonomic pathways due to progressive desiccation. The concept of taphonomic pathways has been applied also to the study of subtidal sand-dune complex dynamics (Desjardins *et al.*, 2010a) and storm-dominated shallow-marine (see Section 7.1) and deep-marine (see Section 9.2.1) enviroments.

6.3 ICHNODIVERSITY AND ICHNODISPARITY

In trace-fossil studies, ichnodiversity simply refers to the number of ichnotaxa present. Most studies use ichnodiversity at ichnogenus rather than at ichnospecies level because trace-fossil taxonomy is more firmly established at the ichnogenus level. As noted by Ekdale (1985), by no means should one establish equivalence between species diversity and ichnodiversity. Because ichnodiversity essentially reflects the different interactions of organisms and the substrate, it depends on factors that are different from those that determine species diversity or, in the case of paleontological studies, body-fossil diversity (Bromley, 1990, 1996). Also, while some of the taphonomic filters that operate in trace-fossil preservation are shared by body fossils, trace-fossil taphonomy has its own peculiarities (see Sections 5.2.2 and 6.2).

However, if used with caution, ichnodiversity may provide some information on general trends in species richness along depositional environments and through geological time (Ekdale, 1988; Buatois *et al.*, 1997b; Mángano and Buatois, 2004b). Low ichnodiversity may be associated with some stress factors (e.g. brackish water, oxygen depletion, high energy). In contrast, high ichnodiversity is commonly linked to stable and predictable environmental conditions. Some ichnofacies as a whole illustrates this principle. While the poorly diverse *Skolithos* ichnofacies develops under unstable conditions (e.g. high energy, fluctuating rates of deposition and erosion), the highly diverse *Nereites* ichnofacies corresponds to the more stable conditions of the deep sea. Accordingly, trends in ichnodiversity may follow the hypothesis put forward by Sanders (1968) for species diversity that states that high stability or predictability of the environment is conducive to high species diversity. However, low ichnodiversity may, in some cases, be a simple taphonomic artifact resulting from intense bioturbation of deep-tier organisms (see Section 5.2.2).

In ecological and macroevolutionary studies, global diversity has been divided in three components: alpha, beta, and gamma (Whittaker, 1972; Sepkoski, 1988). Alpha diversity measures the richness of taxa at a single locality or in a particular community; beta diversity refers to taxonomic differentiation between sites or communities; and gamma diversity records the taxonomic differentiation between regions. Alpha and beta diversity reflect species differentiation of niche and habitat, respectively, while gamma diversity reflects provinciality (Whittaker, 1972; Sepkoski, 1988). Ichnological studies oriented towards macroevolution (see Chapter 14) deal mostly with global diversity, essentially changes in ichnodiversity during certain times of Earth history (e.g. Crimes, 1992, 1994; Orr, 2001; Mángano and Droser, 2004), or in certain ecosystems through geological time (e.g. Buatois *et al.*, 1998c, 2005). However, the three components of global diversity are not commonly discriminated in ichnological studies and, as a result, the term ichnodiversity has been used in more than one sense. This is illustrated by studies dealing with the colonization of deep-marine ecosystems (e.g. Orr, 1996). Seilacher (1974) recorded the ichnodiversity of individual deep-marine trace-fossil associations in a use analogous to that of alpha diversity (Sepkoski, 1988), while Crimes and Crossley (1991) recorded diversity as the total number of ichnotaxa for that same time interval (global ichnodiversity). In that case, alpha ichnodiversity provides information about the structure of individual deep-marine communities, while global ichnodiversity gives evidence of large-scale diversification patterns in the deep sea (Buatois *et al.*, 2001).

An analog to alpha diversity is the most commonly used in ichnological studies dealing with paleoenvironmental characterization, in which ichnodiversity is assessed for individual facies or environmental zones. In turn, changes in alpha ichnodiversity throughout a succession represented by different facies or at different localities are evaluated to detect environmental changes. Conversely, beta ichnodiversity is commonly overlooked although it may provide information about the degree of similarity between ichnofaunas formed along an environmental gradient. For example, beta ichnodiversity could be useful to assess the degree of differentiation between nearshore and offshore trace-fossil associations, commonly represented by the *Skolithos* and *Cruziana* ichnofacies. Application of the notion of gamma diversity to ichnological studies is less evident because few studies deal with paleobiogeographic implications (e.g. Seilacher, 1992a, 1994; Orr, 1996; Systra and Jensen, 2006). However, gamma ichnodiversity may provide information to detect trace-fossil provincialism.

While diversity reflects taxonomic richness, paleontologists have also introduced the concept of morphological diversity or disparity (Gould, 1989, 1991; Foote, 1997; Erwin, 2007). This concept refers to variability in anatomical design, and has been used in current debates on the evolutionary significance of Cambrian faunas (e.g. Gould, 1989, 1991; Briggs and Fortey, 1989; Briggs *et al.*, 1992; Fortey *et al.*, 1996). Gould (1991) stressed the need for developing quantitative techniques to define morphospaces and map their fillings as a way of assessing disparity, a task subsequently undertook in several studies (e.g. Hickman, 1993; Foote, 1993, 1997).

The concept of disparity may be adapted by ichnology, albeit in a qualitative way. While ichnodiversity simply refers to ichnotaxonomic richness, ichnodisparity provides a measure of the variability of morphological plans in biogenic structures (or trace-fossil bauplan *sensu* Bromley, 1990, 1996). The fact that ichnodiversity and ichnodisparity are not necessarily concordant can be illustrated with a series of examples. The *Mermia* ichnofacies is relatively diverse, but ichnodisparity is remarkably low. Very minor behavioral variants result in relatively high ichnodiversity, but the different ichnotaxa mostly belong to a few basic morphological plans represented by simple grazing trails. On the other hand, the *Cruziana* ichnofacies is characterized by both high ichnodiversity and ichnodisparity because it is taxonomically rich and, at the same time, contains a wide variety of trace-fossil bauplans (e.g. branching feeding systems, galleries, spreiten burrows, concentrically laminated structures, bilobate trails). A special situation is recorded by the *Nereites* ichnofacies. The ichnodisparity is relatively high and represented by different basic designs (e.g. networks, meandering systems, branching meandering systems, radial structures).

However, the most diagnostic feature of this ichnofacies is the remarkably high ichnodiversity, which results from small but multiple variations of these basic patterns (e.g. Seilacher, 1977a). Future work on this topic will be essential to attain more refined definitions of ichnodisparity, if possible, including quantitative techniques.

6.4 POPULATION STRATEGIES

The subdivision between r- and K-selection was introduced by MacArthur and Wilson (1967) to explain two different types of natural selection. Subsequently Pianka (1970) explored the concept in further detail, and noted that both types represent, in fact, end members of an r–K continuum. In particular, r-selection characterizes colonization in an ecological vacuum under little competition, typically following an environmental disturbance. It favors rapid reproductive and growth rates, small body size, short lives, wide environmental range, generalized trophic habits, high density of individuals, and low diversity of species. K-selection characterizes stable, specialized populations at equilibrium that have developed due to keen competition. Organisms are slow to colonize a new habitat, but are adaptively superior in the long term. It favors slow reproductive and growth rates, larger body size, long lives, narrow environmental range, specialized trophic habits, low density of individuals, and high diversity of species.

These concepts on population strategies have been successfully adapted to ichnology by distinguishing r-selected ichnotaxa (opportunistic) and K-selected ichnotaxa (equilibrium) (Miller and Johnson, 1981; Ekdale, 1985, 1988). Bromley (1990, 1996) further discussed the application of these concepts in ichnology, and suggested replacing equilibrium by climax trace fossils to avoid confusion with the ethological category equilibrium traces or equilibrichnia. Opportunistic ichnofaunas commonly display low ichnodiversity, high density of trace fossils, simple morphologies that reflect poorly specialized feeding strategies, and production over a short period of time (Ekdale, 1985). Examples of opportunistic ichnofaunas include monospecific suites of *Skolithos* or *Ophiomorpha* in high-energy shorelines and post-event suites in tempestites and turbidites (see Section 6.5). *Spirophyton* has been suggested as an opportunistic ichnotaxa based on its profuse occurrence in Devonian marginal-marine environments (Miller and Johnson, 1981), while *Fuersichnus* may represent another example but in continental environments (Bromley, 1990, 1996). Other ichnotaxa seem to be more controversial. *Chondrites* and *Zoophycos* have been suggested as opportunistic ichnotaxa by Ekdale (1985), but other authors tend to favor a climax strategy based on the fact that sophisticated feeding strategies seem to be involved (e.g. Bromley, 1990, 1996).

Climax ichnofaunas commonly display high ichnodiversity, low density of trace fossils, complex morphologies that reflect sophisticated feeding strategies, and production over a long period of time commonly revealed by permanent structures (Ekdale, 1985). Individual ethological categories in climax ichnofaunas are represented by numerous ichnotaxa. Graphoglyptids are a typical example of climax ichnofaunas. These complex burrow systems flourish under the stable conditions that characterize the deep sea. Graphoglyptid associations are commonly characterized by large diversity, both at ichnogeneric and ichnospecific level (Seilacher, 1977a; Uchman, 1995, 1998). Although graphoglyptids are shallow-tier structures, Bromley (1990, 1996) noted that most climax biogenic structures (e.g. *Zoophycos*) occupy deep tiers.

Bromley (1990, 1996) noticed that subtle modifications in the environment could result in the two communities (opportunistic and climax) alternating in a stratigraphic succession. Fair-weather associations of the *Cruziana* ichnofacies that alternate with storm-related suites of the *Skolithos* ichnofacies represent a classic example of alternating climax and opportunistic ichnofaunas (Pemberton and Frey, 1984a; Pemberton *et al*., 1992c; Pemberton and MacEachern, 1997) (see Section 7.1). Interestingly, the established link between population strategies and time spans involved in bioturbation is at odds with observation from modern shallow-marine environments (Gingras *et al*., 2008b). Measurement of burrowing rates in various suspension and deposit feeders indicates that intensely burrowed examples in the *Skolithos* ichnofacies require longer time spans than in the *Cruziana* ichnofacies!

6.5 RESIDENT AND COLONIZATION ICHNOFAUNAS

The topic of population strategies is directly linked to the notion of resident and colonization ichnofaunas. Recognition of these ichnofaunas is essential in any paleoecological analysis. Resident ichnofaunas record the activity of the indigenous benthic fauna, while colonization ichnofaunas reflect the activity of a pioneer community that becomes established after a major environmental disturbance. In fully marine settings, resident ichnofaunas are commonly highly diverse and tend to be morphologically complex, reflecting the activity of climax communities. As such, they reflect depositional conditions associated with times of stable background sedimentation. In the case of environments affected by episodic sedimentation, resident ichnofaunas are commonly preserved as pre-depositional suites at the base of event sandstones. This is typically illustrated by graphoglyptids on the soles of deep-marine turbidite sandstone (Seilacher, 1962; Leszczyński and Seilacher, 1991). Although these structures are preserved as secondary casts in the turbidite layers, they reflect the activity of the organisms that inhabit the mudstone biotope during interturbidite times (see Section 9.2). Therefore, the *Nereites* ichnofacies, in particular, the *Paleodictyon* subfacies of Seilacher (1974), represents the archetypal resident ichnofauna of the deep sea. In shallow-marine, wave-dominated environments resident ichnofaunas record the activity of fair-weather communities. Resident suites are preserved either at the base of storm deposits or in the intercalated, fair-weather finer-grained deposits (e.g. Mángano and Buatois, 2011). The *Cruziana* ichnofacies typifies the activity of the indigenous biota in this setting.

Colonization ichnofaunas are typically of low diversity and are morphologically simple, reflecting the activity of opportunistic communities. They represent the work of a pioneer community that rapidly invades an ecosystem, and is able to thrive under unstable and stressful conditions. Because colonization ichnofaunas establish immediately after a rapid depositional episode, they are commonly preserved as post-depositional suites in event sandstone. The classic example is the bathymetrically displaced suites of the *Skolithos* ichnofacies (i.e. *Arenicolites* ichnofacies of Bromley and Asgaard, 1991). This ichnofacies occurs in deeper water than that of its archetypal position, colonizing offshore tempestites (Pemberton and Frey, 1984a; Frey, 1990) or deep-marine turbidites (Leszczyński and Seilacher, 1991). Low-diversity suites of simple grazing trails may represent colonization ichnofaunas in lacustrine turbidites (Buatois and Mángano, 1995c).

6.6 ECOSYSTEM ENGINEERING

In the previous sections of this chapter, we have essentially adopted an adaptationist and externalist view of ichnology that is based on the assumption that an ichnofauna is shaped by environmental controls via their influence on the behavior of the tracemakers. However, some organisms modify, maintain, and create habitats, exerting profound changes in the ecosystems. The concept of ecosystem engineering (Jones *et al*., 1994) helps to explain the active role that some organisms play in modifying their environment. This concept refers to the modification of the physical environment by the action of organisms that directly or indirectly modulate the availability of resources to other species (Jones *et al*., 1994; Coleman and Williams, 2002; Berkenbusch and Rowden, 2003; Wright and Jones, 2006). Empirical studies have demonstrated that the loss of key bioturbators is critical in ecosystem performance (e.g. primary productivity) and results in a decrease in biodiversity (Lohrer *et al*., 2004). The impact of burrowing organisms in ecosystem function has been emphasized in studies framed within the perspective of biodiversity and ecosystem function (Solan *et al*., 2008, 2009).

In particular, Jones *et al*. (1994) classified ecosystem engineers into two types: autogenic, or those who change the environment via their own physical structures (i.e. their living and dead tissues), and allogenic, or those who do so by transforming living or non-living materials from one physical state to another via mechanical or other means. For example, by constructing dams, beavers alter the hydrology of an alluvial plain and create water bodies, representing a typical example of allogenic engineers (Naiman *et al*., 1988). It is this latter type that has implications in ichnology, because the process of bioturbation itself physically modifies the environment in a significant way (e.g. Reise and Volkenborn, 2004; Wada *et al*., 2004; Dewitt *et al*., 2004). Although ichnology certainly has not emphasized this aspect of animal activity, the role of bioturbation in ecosystem engineering has long been recognized. In fact, Darwin (1881) provided one of the earliest studies on the effects of bioturbation in his classic book on soil formation through earthworm activity.

For example, infaunal burrowers influence the chemical properties of the substrate by increasing oxygen circulation through the sediment, which in turn has a positive feedback on the biomass of organisms within the sediment, the rate of organic matter decomposition, and the regeneration of nutrients, which is essential for primary productivity (Solan *et al*., 2004a, 2008). The depth and abruptness of the redox potential discontinuity depend on the amount of oxidizable organic matter within the sediment and oxygen flow. Subsurface deposit feeders extend the oxic layer of sediment from close to the surface down to their depth of feeding in modern environments (e.g. Rhoads and Germano, 1982; Reise, 1985).

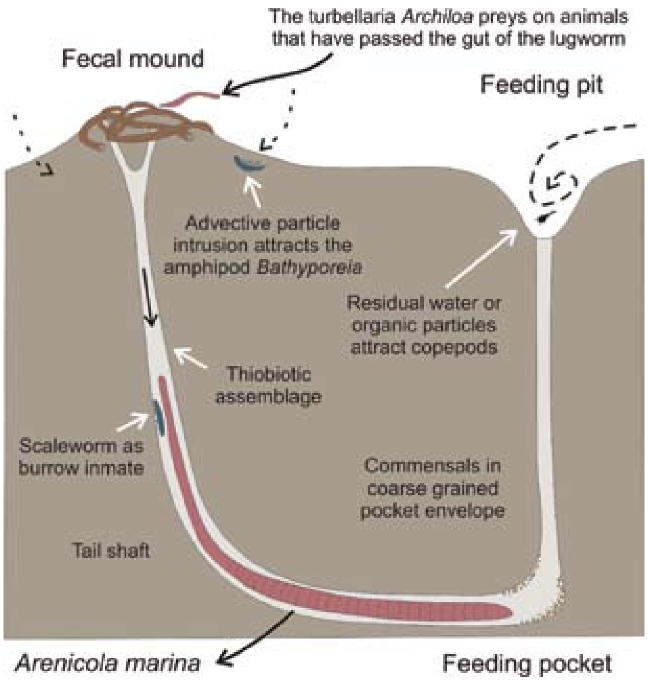

Figure 6.15 The polychaete *Arenicola marina* as an ecosystem engineer. Modified from Reise and Volkenborn (2004).

In addition, burrows may provide habitats for other organisms. Reise and Volkenborn (2004) analyzed the role of the polychaete *Arenicola marina*, which increases diversity on modern sand flats by maintaining a complex burrow in which other animals live (Fig. 6.15). At the surface, feeding pits become water ponds during low tide and serve as refuges for swimming copepods, turbelarians, and juvenile shrimps. Amphipods exploit organic particles that are flushed into the interstitial system associated with the fecal mound, and turbelarians (e.g. *Archiloa*) prey on small animals that have passed through the gut of *A. marina* and can be trapped in the fecal mound itself. Within the coarse-grained sand that envelopes the burrow, several meiofaunal organisms are established, together with small capitellid polychaete, tubificid oligochaetes, nemertines, and amphipods. Up to 173 specimens of the amphipod *Urothoe poseidonis* were counted at a single burrow. Other inhabitants (e.g. copepods, nematodes) live between the bushy gills, the tail shaft, and the sediment enveloping the tail shaft of *A. marina*.

Trace fossils may also provide evidence, albeit indirect, of amensalism (one species is unaffected, and the other one is harmed). Rhoads and Young (1970) proposed that deposit feeders may negatively affect suspension feeders to the point of making life impossible for the affected group. This phenomenon is referred to as trophic-group amensalism and has been subsequently regarded as an example of ecosystem engineering by Jones *et al*. (1994). Mobile, mostly detritus- and deposit-feeder infauna and epifauna, but also some sedentary organisms, whose feeding and defecation activities may provide abundant particles in suspension, destabilize the substrate (Rhoads and Young, 1970; Rhoads, 1974). Physical instability tends to clog the filtering structures of suspension feeders, bury newly settled suspension-feeding larvae or inhibit their settling, and prevent sessile epifauna from attaching to an unstable mud bottom (Rhoads and Young, 1970). In contrast, sedentary organisms that build mucus-lined tubes within the sediment reduce resuspension and erosion, and represent sediment stabilizers. At least in part, this is commonly expressed in the trace-fossil record by the segregation of two distinct associations broadly reflected by the *Skolithos* and *Cruziana* ichnofacies.

Based on observations on an example of the latter in Carboniferous tidal-flat deposits, Mángano *et al*. (2002a) suggested that dense concentrations of mobile detritus-feeding nuculanid bivalves (producers of *Protovirgularia* and *Lockeia*) may have acted as sediment destabilizers, precluding the development of vertical burrows of suspension feeders. The same role may have been played by the worm-like producers of dense associations of *Nereites* that altered the nature of the substrate, encapsulating within the sediment large volumes of defecation products. The intruding up-and-down movements of the *Curvolithus* tracemaker (gastropods or flat worms) may have also played a destabilizing role in some communities.

On a larger scale, bioturbation results in landscape changes. This has been clearly illustrated by ichnological studies documenting pervasive changes in intertidal landscape due to the activity of callianassids (Curran and Martin, 2003) (Box 6.2), and sturgeons (Pearson *et al*., 2007). Bioturbation can also significantly alter continental landscapes. Extensive burrows are dug and excavated by a wide variety of mammals (e.g. rabbits, mole rats, prairie dogs, pocket gophers), creating complex underground gallery systems that are expressed by a complex topography on the surface and provide opportunities for ecological interactions (Whicker and Detling, 1988; Bromley, 1990, 1996; Neal and Roper, 1991; Moloney *et al*., 1992; Whitford, 2002).

Spectacular examples of “ichnolandscapes” are provided by the activity of the South African harvester termite *Microhodotermes viator*, which produces a mounded topography referred to as heuweltjies (Afrikaans for “little hills”) (Lovegrove and Siegfried, 1989; Turner, 2004; Fey, 2010). These mounds are 1–2 m in height above ground level, and 20–30 m in diameter, becoming easily recognizable because they support plant communities that are different from those in surrounding areas (Fig. 6.17a–b). The mounds represent long-term structures that result from successive colonization events by several generations of termites (Milton and Dean, 1990). Mounds produced by the hairy-nosed wombat *Lasiorhinus latifrons* in Australia can cover several hundred square meters and can be seen on LANDSAT images (Löffler and Margules, 1980).

6.7 ORGANISM–ORGANISM INTERACTIONS

Although ichnology is defined as the science of organism–substrate interactions, trace fossils also provide information on organism–organism interactions. As discussed in the previous section, some of these effects result from the impact of ecosystem engineers (see Section 6.6). However, other effects are due to direct interactions between organisms (Abrams, 1987). This commonly occurs when another organism acts as a substrate, suggesting a symbiotic association. Symbiosis refers to relationships between two or more different species, in which at least one of them benefits from the association (Smith and Douglas, 1987; Tapanila and Ekdale, 2007). Three main types of symbiotic relationships can be established: parasitism (one species benefits to the detriment of the other), commensalism (one species benefits and the other one is not affected), and mutualism (both species benefit).

Parasitic infestation may be expressed by bioerosion structures. In order to recognize parasitism, the alternative explanation of post-mortem bioerosion should be ruled out and one should rely on detecting evidence of specific responses by the host organism (e.g. overgrowth, regeneration, or embedment).

Box 6.2 Thalassinidean shrimps as ecosystem engineers in modern tidal flats of San Salvador Island, Bahamas

A spectacular example of ichnolandscapes has been documented in tidal flats of Pigeon Creek, in the Bahamian island of San Salvador (Fig. 6.16a–b). These tidal flats are formed along the margins of a hypersaline lagoon. The tidal flat is characterized by a mounded topography, resulting mostly from the activity of the callianassid shrimp *Glypturus acanthochirus*. This shrimp produces deep, large and complex burrows, with a downward spiraling morphology, generating intense bioturbation. *Glypturus acanthochirus* is an ecosystem engineer that completely transforms the intertidal landscape. Mounds are up to 30 cm high and 1 m wide. The resulting mounds may coalesce forming larger structures that are flattened by tidal action. In addition to the activity of *Glypturus acanthochirus*, microbial mats stabilize the mounds by tending to armor their surfaces. As a result, the mounds are highly resistant to erosion and are long lived. The mounds are also colonized by the shrimp *Upogebia vasquezi* and the fiddler crab *Uca major*. The former produces U-shaped, commonly paired, burrows, while the latter constructs simple vertical burrows with a basal bulbous turnaround.

Reference: Curran and Martin (2003).

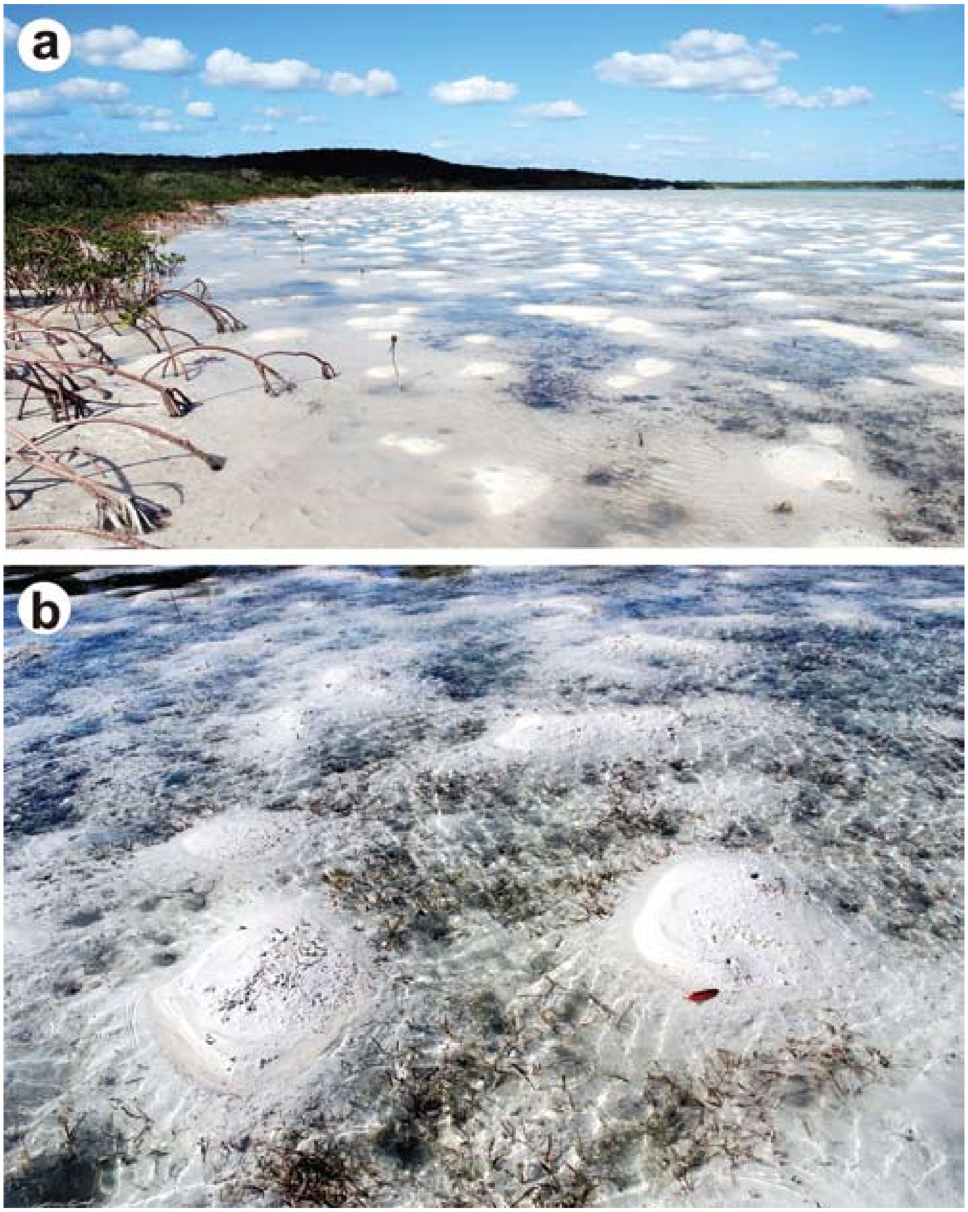

Figure 6.16 Mounded topography resulting from the activity of the thalassinidean shrimp *Glypturus acathochirus*. Pigeon Creek, San Salvador Island, Bahamas. (a) General view. (b) Close-up of mounds. See Curran and Martin (2003).

Neumann and Wisshak (2006) noted that echinoderms favor the recognition of infestation of parasites, because the echinoderm skeleton represents a living tissue capable of reacting to disturbance. These authors documented Late Cretaceous etched attachment scars produced by parasitic foraminifers on the oral surface of a holasteroid echinoid. A specific type of parasitism is revealed by the dual behavior of endosymbionts that is preserved in the ichnological record as bioclaustrations or embedment structures (Bromley, 1970; Tapanila, 2005; Tapanila and Holmer, 2006; Tapanila and Ekdale, 2007). In these cases, a trace-fossil cavity is produced by the growth-interfering behavior of a symbiont living in the growing skeleton of the host. The dual activity of the settler symbiont is revealed by interference of host growth and maintenance of the dwelling structure (Tapanila, 2005). Although less common, parasitism may be expressed by structures that are not strictly due to bioerosion, but preserved in a trace fossil itself. An example is illustrated by beetle nests in paleosols that contain internal galleries formed by cleptoparasites (Mikuláš and Genise, 2003; see Section 1.2.4). Nara *et al*. (2008) documented a Pleistocene bivalve, *Cryptomya busoensis*, with its posterior end attached to the upogebiid burrow *Psilonichnus*, and compared this association with modern examples. They interpreted this as a mild form of parasitism, in which the bivalve used the sediment–water interface on the internal surface of the crustacean burrow, taking food and oxygen, and expelling wastes.

Even less common is ichnological evidence of commensalism in the ichnofossil record, and only very recently have examples been documented. Wisshak and Neumann (2006) documented a commensal association between a spionid polychaete and a

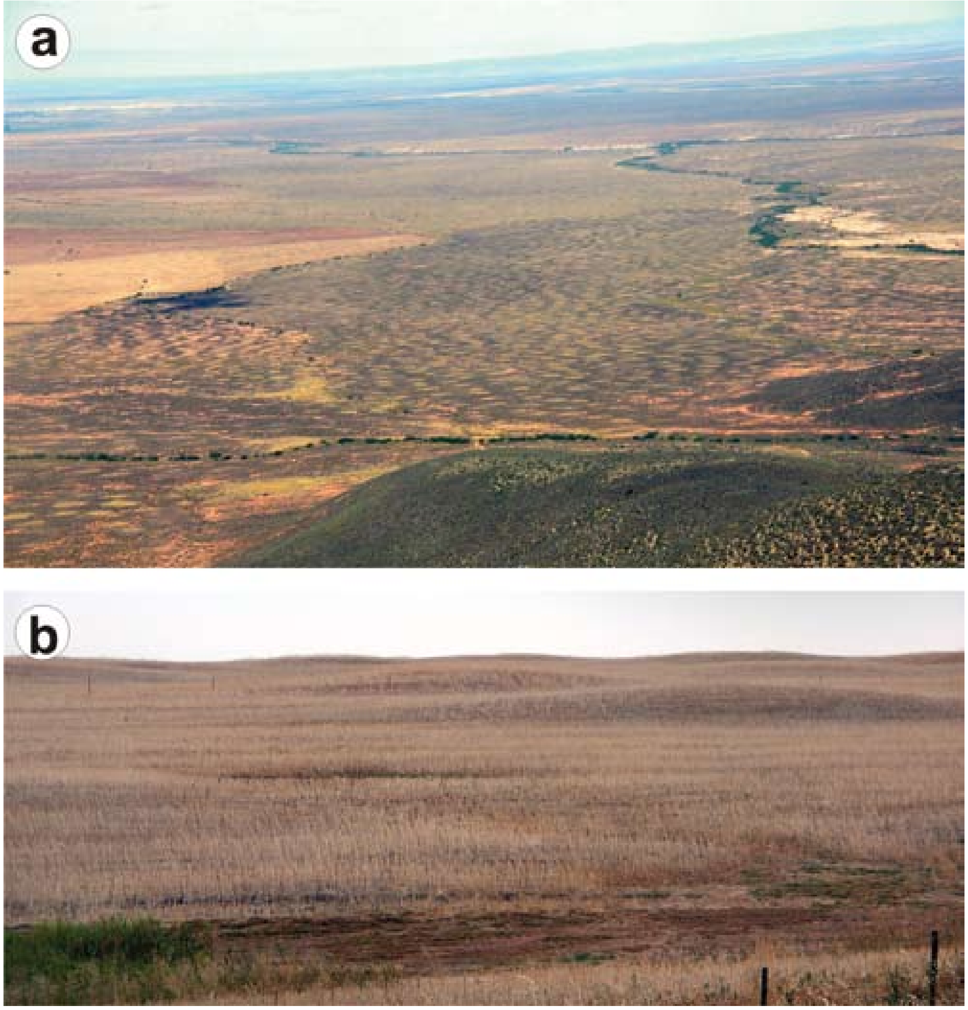

Figure 6.17 Mounded topography (heuweltjies) produced by the harvester termite *Microhodotermes viator*, Matjiesgloof Farm, South Africa. See Fey (2010) (a) General view. (b) Close-up of termite mounds.

holasteroid echinoid from the Late Cretaceous. The interaction is suggested by the presence of abundant specimens of the boring *Caulostrepsis* associated with distinct regeneration textures in the echinoderm. These authors suggested commensalism rather than parasitism, based on the fact that while the polychaete sheltered and fed from organic matter resuspended by the echinoderm, there was no evident harm involved for the latter.

Mutualism is expressed in the ichnological record by farming behavior. For example, some termites (i.e. subfamily Macrotermitinae) build gardens where a symbiotic fungus is cultivated (Sands, 1969). Termites use their own feces to build a structure where the fungus grows (fungus comb). Fossil fungus combs are associated with termite nests in Miocene paleosols, recording the earliest example of symbiotic termite fungiculture (Duringer *et al.*, 2007).

6.8 SPATIAL HETEROGENEITY

Trace fossils commonly display a heterogeneous distribution across an individual sedimentary unit (i.e. they show a deviation from randomness). In fact, any casual observer inspecting an outcrop can find substantial differences in the trace-fossil content along a single bedding plane. However, despite being spatial heterogeneity, a well-known feature in ecological studies (e.g. Schäfer, 1972; Reise, 1985; Gili and Coma, 1998), it has been noted in ichnological analysis relatively recently (Pemberton and Frey, 1984b; Leszczyński, 1991b; Mángano *et al.*, 2002a; Genise *et al.*, 2004b; McIlroy, 2007a; Scott *et al.*, 2007a). In many instances, spatial heterogeneity is produced by the impact of ecosystem engineers (see Section 6.6). Also, computer simulations and experiments seem to indicate that resource patchiness plays a strong control on invertebrate behavior, particularly in foraging organisms (Plotnick and Koy, 2005; Koy and Plotnick, 2010) (see Section 3.4).

Zonation and patchiness of benthic communities is common in modern marine environments, both in shallow-marine (e.g. Schäfer, 1972; Anderson and Meadows, 1978; Newell, 1979; Reise, 1985; Tufail *et al.*, 1989) and deep-marine settings (Gage and Tyler, 1991). Within shallow-marine settings, intertidal areas are particularly heterogeneous as a result of both physical and biotic processes. The tidal cycles, tidal currents, river input, and wind processes lead to a wide variety of salinity changes and hydrodynamic regimes (Meadows *et al.*, 1998). For example, different suspension feeders capture particles of variable sizes, leading to patchy species distribution controlled by the flow rate of the surrounding water (Gili and Coma, 1998). In addition, the complex biogenic interactions of the intertidal zone result in further complexity (Reise, 1985; Bertness, 1999; Little, 2000). In fact, the process of bioturbation itself, which involves particle selective feeding, influences spatial heterogeneity (Murray *et al.*, 2002). Under these conditions, heterogeneity occurs primarily at two scales. At the larger scale, zonational distribution is expressed along the entire tidal range, as illustrated by different animal communities living in different areas within the tidal flat (i.e. tidal channels and tidal flats; upper, middle, and lower tidal flats); these changes are better understood within the framework of facies analysis (see Section 7.2).

Of more interest here are those changes revealed at a smaller scale. Spatial segregation of species may reflect distinct microhabitats and partitioning of energy resources within each environment. A particular spatial array of organisms permits the exploitation of particular food resources within the limits of their tolerance to environmental conditions. This allows maximum utilization of available food resources and minimum interspecific competition (Newell, 1979). The spatial separation of barnacles and limpets within the lower intertidal zone of rocky shorelines represents an example (Lewis, 1961). In the middle- and, particularly, in the lower-intertidal area, food resources are abundant and varied, but, equally, the organisms are bound by other species whose requirements may overlap with their own. In these settings, patchiness commonly results from niche specialization, thereby significantly reducing interspecific competition. Selection commonly favors those behavioral responses that tend to restrict organisms to particular niches at which they convert energy more efficiently than their neighbors (Wolcott, 1973).

Substrate microtopography across the tidal flat exerts a control on spatial heterogeneity because it strongly influences sediment grain size, sorting, and organic richness (Thum and Griffiths, 1977). These authors noted that water enters through ripple troughs and exits through the crests along a pressure gradient. This circulation pattern results in a re-sorting of sediment with small grains and organic debris being drawn into the troughs. Organics are trapped within the sediment to a depth equal to the height of the ripple crest. The localized distribution of organic matter accounts for the aggregation of meiofauna, and invertebrate grazers in ripple troughs (Jansson, 1967; Harrison, 1977, Newell, 1979). Small patches of nematodes may occur in ripple troughs as a response to preferential accumulation of organic detritus (Hogue and Miller, 1981).

The polychaete *Scolecolepsis squamata* constructs vertical shafts on slight topographic rises, while the spiral traps of the paraonid polychaete *Paraonis fulgens* occur in nearby depressions in intertidal areas (Röder, 1971; Bromley, 1990, 1996). Segregation of associations of the amphipod *Corophium volutator*, the polychaete *Arenicola marina*, and the prosobranch *Hydrobia* has been noted in modern sand flats (Reise, 1985). Mounds are stabilized and inhabited by the tube-dwelling amphipods, the prosobranch tends to concentrate at the fringe of the mounds, and the polychaete causes high sediment turnover in the surrounding areas. In this case, heterogeneity most likely reflects trophic amensalism as a result of the mutual exclusion of sediment stabilizers and destabilizers (see Section 6.6). Evaluation of spatial heterogeneity in modern intertidal areas has been quantitatively assessed through the establishment of three transects in intertidal areas of the Clyde Estuary, Scotland (Meadows *et al.*, 1998). The first transect was at right angles to the sand dunes (crest/trough transect), the second and third crossed the crest (crest transect) and trough (trough transect), respectively. Correlation, cluster, and principal component analysis highlighted patterns of spatial patchiness in the microhabitats and the associated macrobenthic community.

Information from marine benthic ecology can be used to understand heterogeneous distribution of biogenic structures in the stratigraphic record. Heterogeneity related to local microtopography, typically bedforms or small positive areas along individual bedding planes, has been detected in Carboniferous tidal flats (Mángano *et al.*, 2002a). In particular, patchiness is revealed by the preferential presence of *Psammichnites implexus* in ripple troughs. Small-scale spatial heterogeneity probably documents the effects of bedform topography on the partitioning of food resources. *Psammichnites implexus* commonly displays a guided meandering pattern in ripple troughs, reminiscent of the hyporelief *Helminthorhaphe* of deep-marine settings. Absence of self-overcrossing suggests phobotaxis. This distribution may reflect food searching in ponded areas of ripple troughs during the low tide (Mángano *et al.*, 2002a, b).

Patchiness in these Carboniferous tidal flats is also represented by mounds characterized by dense aggregations of U-shaped tubes (*Protovirgularia bidirectionalis*) and small vertical burrows. U-shaped, mucus-lined bivalve burrows most likely stabilized the substrate and trapped the sediment to form the mounds on the tidal-flat surface (see Section 6.7). Similar mounds are produced by *Corophium volutator* (Reise, 1985) and tube-building polychaete worms (Jones and Jago, 1993) in modern tidal flats. The reason why the infaunal burrowers chose this particular spot is more difficult to assess, but it may have been related to some particularly attractive feature of the sediment, as site selection is rarely random. Larval preference for settlement in particular sites has been associated with specific substrate features, either physical properties (e.g. grain roundness) or biological components (e.g. organic film induced by bacteria, type of interstitial organisms, presence/absence of seagrass) (Newell, 1979; Reise, 1985). For example, the presence of a film of microorganisms on the surface of sand grains is instrumental in allowing the settlement of the polychaete *Ophelia bicornis* (Wilson, 1954, 1955). Meadow and Anderson (1968) conducted a survey of microorganisms attached to grains of intertidal sand and found an uneven distribution, with microorganisms tending to concentrate in small pits and grooves on the surface. Microbial stabilization is also a major controlling factor in creating topographic irregularities in tidal flats, such as erosive remnants, mounds, and domal upheavals, and projecting bedding planes in tidal flats (Gerdes *et al.*, 1994, 2000; Noffke *et al.*, 1996; Noffke, 1999, 2010; Schieber *et al.*, 2007).

Patchiness in trace-fossil distribution has been systematically analyzed in wave-dominated shallow-marine successions from an ichnofabric perspective (McIlroy, 2007a). Lateral changes in ichnodiversity, proportions of ichnotaxa, and behavioral types are remarkable over short distances (less than 55 m along a depositional strike). In contrast, the size of trace fossils shows less spatial variation. Accordingly, McIlroy (2007a) suggested caution in the use of ichnofabrics for intra-regional correlations.

Heterogeneity is also very common in deep-marine environments (Gage and Tyler, 1991; Leszczyński, 1991b). Observations from modern deep-sea floors indicate that benthic organisms display a heterogeneous distribution as result of a complex interplay of factors (e.g. local environmental changes, larval settlement). One of the most common cases is the concentration of organisms (e.g. ophiuroids, holothurians) forming patches across the sea floor (e.g. Billett *et al.*, 1983; Gage and Tyler, 1991). Examination of turbidite soles reveals lateral variation in the distribution of complex grazing traces and graphoglyptids at different scales (e.g. Leszczyński and Seilacher, 1991; Leszczyński, 1991b). Trace-fossil patchiness seems to be common in thin-bedded turbidites, including radial patches of *Ophiomorpha* and gregarious occurrences of *Scolicia*.

Patchiness is particularly common in the continental realm, where it has been noted in both terrestrial and freshwater settings. Habitat heterogeneity is also common in lakes, as a result of a wide variety of factors, such as food resources, shelter, and breeding opportunities (Cohen, 2003). In particular, hypersaline-lake environments associated with hot springs display heterogeneous distribution of biogenic structures (Scott *et al.*, 2007a). These lakes are very stressful, but may contain local zones where less extreme environmental conditions allow formation, and preservation of biogenic structures (see Section 10.3.1). These so-called oases are commonly present around freshwater point-sourced springs and contain a concentrated view of the biodiversity within the lake (Scott *et al.*, 2007a).

River floodplains are also extremely variable, being characterized by sharp environmental gradients, leading to strong spatial heterogeneity at different scales (Baker and Barnes, 1998; Ward *et al.*, 1999, 2002). Species-rich areas commonly exist as isolated fragments across the channel and overbank landscape. At a smaller-scale, terrestrial–aquatic gradients linked to overbank flooding create local patches that influence formation and preservation of biogenic structures (e.g. Smith, 1993) (see Section 10.2.2). In this respect, proximity to the river channel is directly linked to water availability, which is one of the main controlling factors in alluvial environments (see Section 6.1.10).

Genise *et al.* (2004b) mentioned variable lateral distribution in coleopteran pupation chambers (*Rebuffoichnus*) from Cretaceous paleosol ichnofabrics. This pattern was in sharp contrast with that of meniscate trace fossils present in the same ichnofacies, which display a more homogeneous lateral distribution. Ecological studies in modern soils suggest that heterogeneity may be linked to patchy distribution of populations in response to several factors, such as soil texture and carbon content (Ettema and Wardle, 2002).

In deserts, heterogeneity is linked to both patterns of plants in relationship to soil and topography, and animal-generated disturbances in soil (Whitford, 2002). Vertebrates (e.g. mammals, reptiles) and even arthropods create patches in arid environments (see Section 6.6). Some holes excavated by mammals serve as collection points for seeds and organic matter, having a strong impact in arid ecosystem dynamics. Animal activity affects soil chemistry and vegetation growth, resulting in heterogeneous distribution of root traces in desert environments. Water availability is also highly variable across desert areas controlling distribution of biogenic structures (e.g. dunes versus interdunes, dry versus wet interdunes).

7 Ichnology of shallow-marine clastic environments

> As discussed in other chapters of this book, traces commonly receive a paleontologic or zoologic connotation. Because of this aspect, traces are often given a short shrift by sedimentologists. This situation is unfortunate, and indeed unfair, to the study of sediments because the contained lebensspuren are sedimentary structures (albeit biologically formed) and should receive attention equal to that devoted to structures developed by physical processes. In fact, these traces often supply evidence of sedimentological conditions that is superior to information gained only by the study of physical structures. If the foregoing is not sufficient reason for sedimentologists to be concerned with the study of ichnology, perhaps they can be prodded into it by virtue of the fact that the nefarious beasts creating the biogenic structures have a nasty habit of destroying their beloved physical structures, and they should at least attempt to identify the enemy!
>
> Jim Howard
>
> "The sedimentological significance of trace fossils" (1975)

Historically, one of the major strengths of ichnology is its utility in facies analysis and paleoenvironmental reconstructions. Undoubtedly, marine ichnology has been the main focus of most trace-fossil research in this respect. However, our knowledge of marine ichnofaunas is still uneven. The vast majority of ichnological studies applied to facies analysis and paleoenvironmental reconstruction deals with ichnofaunas from siliciclastic successions, rather than carbonates, mixed carbonates-clastics, or volcaniclastics. In siliciclastic settings, both shallow- and deep-marine ichnofaunas have received similar attention. However, ichnological studies in shallow-marine environments have attained better integration with sedimentological data than those in deep-marine settings. In turn, the ichnology of wave-dominated shallow-marine environments has been explored in more detail than their tide-dominated counterparts. In connection with this, the ichnological content of sandy shores is much better known than that of muddy coasts. In fact, some specific types of muddy shorelines, such as chenier plains (e.g. Augustinus, 1989), remain essentially unrecognized in the geological record. Also, end members, with respect to wave and tidal dominance, are better understood than mixed systems (e.g. Anthony and Orford, 2002). In this chapter, we will review the ichnology of different shallow-marine clastic environments, covering wave-dominated, tide-dominated, mixed systems, and muddy shorelines.

7.1 WAVE-DOMINATED SHALLOW MARINE

Shallow-marine wave-dominated environments host a large number of benthic organisms that interact with the substrate in many different ways. As a result, trace fossils are diverse and abundant in wave-dominated shallow-marine deposits. Alternating and contrasting hydrodynamic energy levels due to repeated storm events are among the most important limiting factors for trace-fossil distribution and preservation (Pemberton and Frey, 1984a; Vossler and Pemberton, 1989; Frey, 1990; Frey and Goldring, 1992; MacEachern and Pemberton, 1992; Pemberton *et al.*, 1992c; Pemberton and MacEachern, 1997; Buatois *et al.*, 2002b, 2007b; Mángano *et al.*, 2005a). These studies demonstrated that storms involve erosion followed by rapid deposition, which in turn is followed by a waning phase and the re-establishment of fair-weather sedimentation under a lower-energy regime (Fig. 7.1). Storms impose a stress factor on the benthic communities inhabiting these wave-dominated environments (see Section 6.1.1).

Storm-dominated successions contain two contrasting trace-fossil suites revealing the response of the benthic fauna inhabiting two successive and different habitats (Pemberton and Frey, 1984a; Pemberton *et al.*, 1992c, 2001; Pemberton and MacEachern, 1997). The resident, fair-weather suite is produced by a benthic community developed under stable and rather predictable conditions. This suite typically illustrates the *Cruziana* ichnofacies, and reflects the activity of populations displaying K-selected or climax strategies (see Section 6.4). Common components of the fair-weather suite are *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Teichichnus*, *Asteriacites*, *Rhizocorallium*, *Asterosoma*, *Dactyloidites*, *Phycodes*, and *Arthrophycus*, among many others. By contrast, the storm-related trace-fossil suite indicates colonization after the storm event. This suite is produced by an opportunistic community displaying r-selected population strategies in an unstable, physically controlled environment. Opportunistic colonizers commonly, though not always, belong to the *Skolithos* ichnofacies (or *Arenicolites* ichnofacies of Bromley and Asgaard, 1991). *Skolithos*, *Ophiomorpha*, and *Arenicolites* are typical components of the storm-related assemblage. Escape trace fossils do not belong to any of these suites, but are produced during the sedimentation event in an attempt to avoid rapid burial (Bromley, 1990, 1996). Extremely dense concentrations of *Chondrites* at the top of tempestites may suggest the burial of high quantities of organic matter during storms (Vossler and Pemberton, 1988a). Also, fair-weather *Chondrites* may rework burrow-fills of the storm-related suite, representing the only evidence of the resident fauna (Fig. 7.2a–b).

Integration of ichnological and sedimentological information has resulted in a detailed paleoenvironmental model that

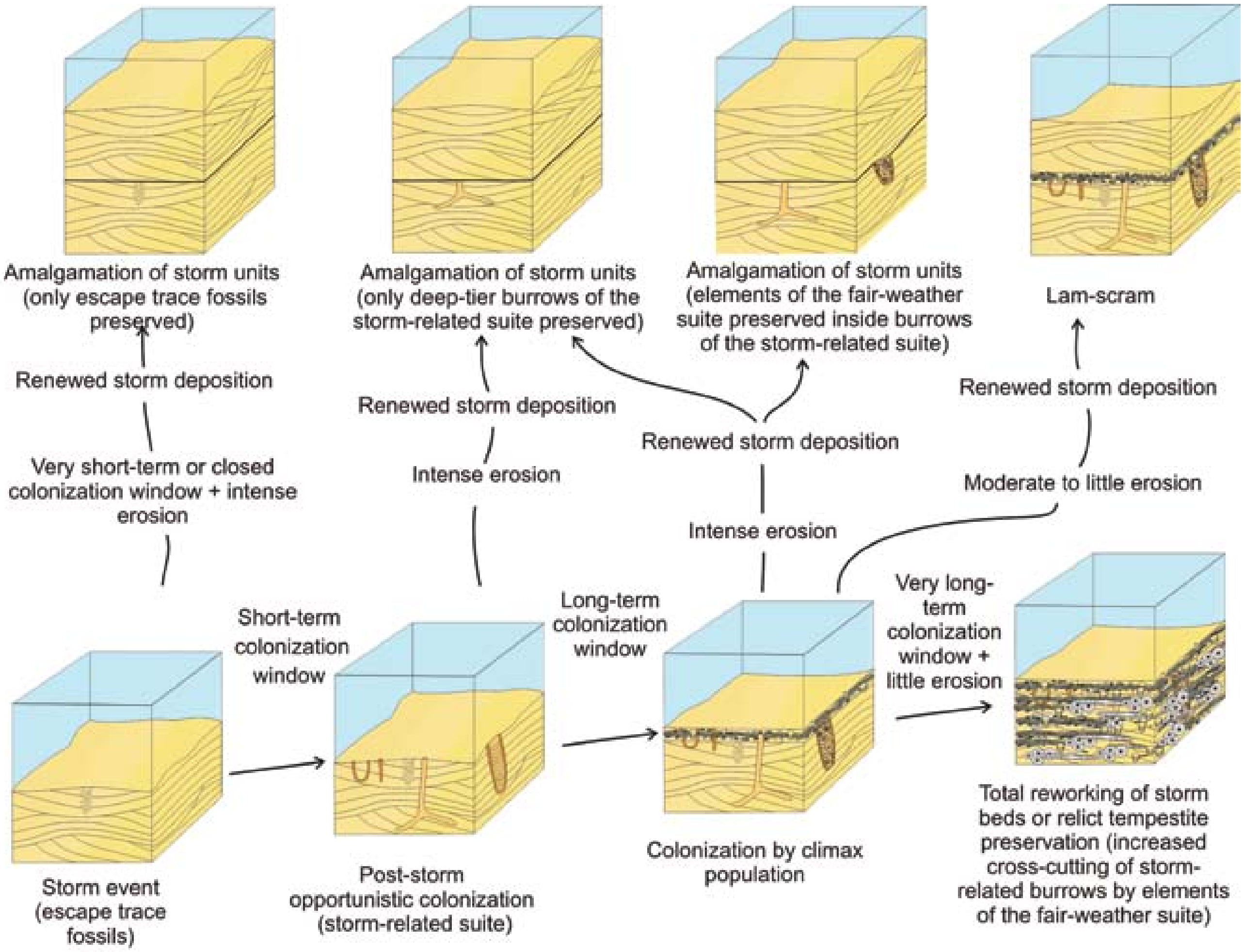

Figure 7.1 Taphonomic pathways of shallow-marine environments affected by storm erosion and deposition. A high frequency of storms results in very short-term to negligible colonization windows. Under these conditions, amalgamated storm deposits are formed. These tempestites are either non-bioturbated, or contain only escape burrows. Under slightly lower frequency of storms, short-term colonization windows allows the establishment of elements of the storm-related trace-fossil suite. Strong erosion due to intense storms results in removal of shallow-tier trace fossils and burrow truncation, allowing preservation of only deep-tier burrows (e.g. *Ophiomorpha*, *Diplocraterion*). Long-term colonization windows allow development not only of the storm-related suite but also establishment of the fair-weather suite. If erosion by a subsequent storm is intense, the latter is removed and only deep-tier burrows of the former are preserved. Alternatively, elements of the fair-weather suite (e.g. *Chondrites*) may be preserved inside burrows of the storm-related suite. Under moderate to little erosion, the fair-weather suite is preserved, resulting in the alternation of intervals preserving the storm primary fabric (plus burrows of the storm-related suite) and bioturbated intervals due to the activity of the fair-weather suite (lam-scram). Very long-term colonization windows accompanied by little erosion results in total obliteration of storm deposits or relict tempestite preservation.

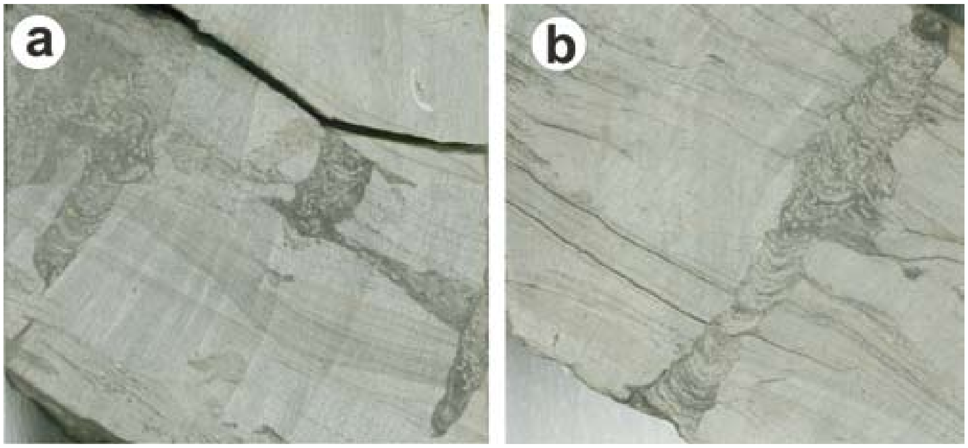

Figure 7.2 Fair-weather *Chondrites* isp. reworking storm-related *Diplocraterion parallelum*. Middle Eocene, Pauji Formation, Motatán Field, Maracaibo Basin, western Venezuela. Core width is 6 cm. (a) General view. (b) Close-up. See Delgado *et al.* (2001).

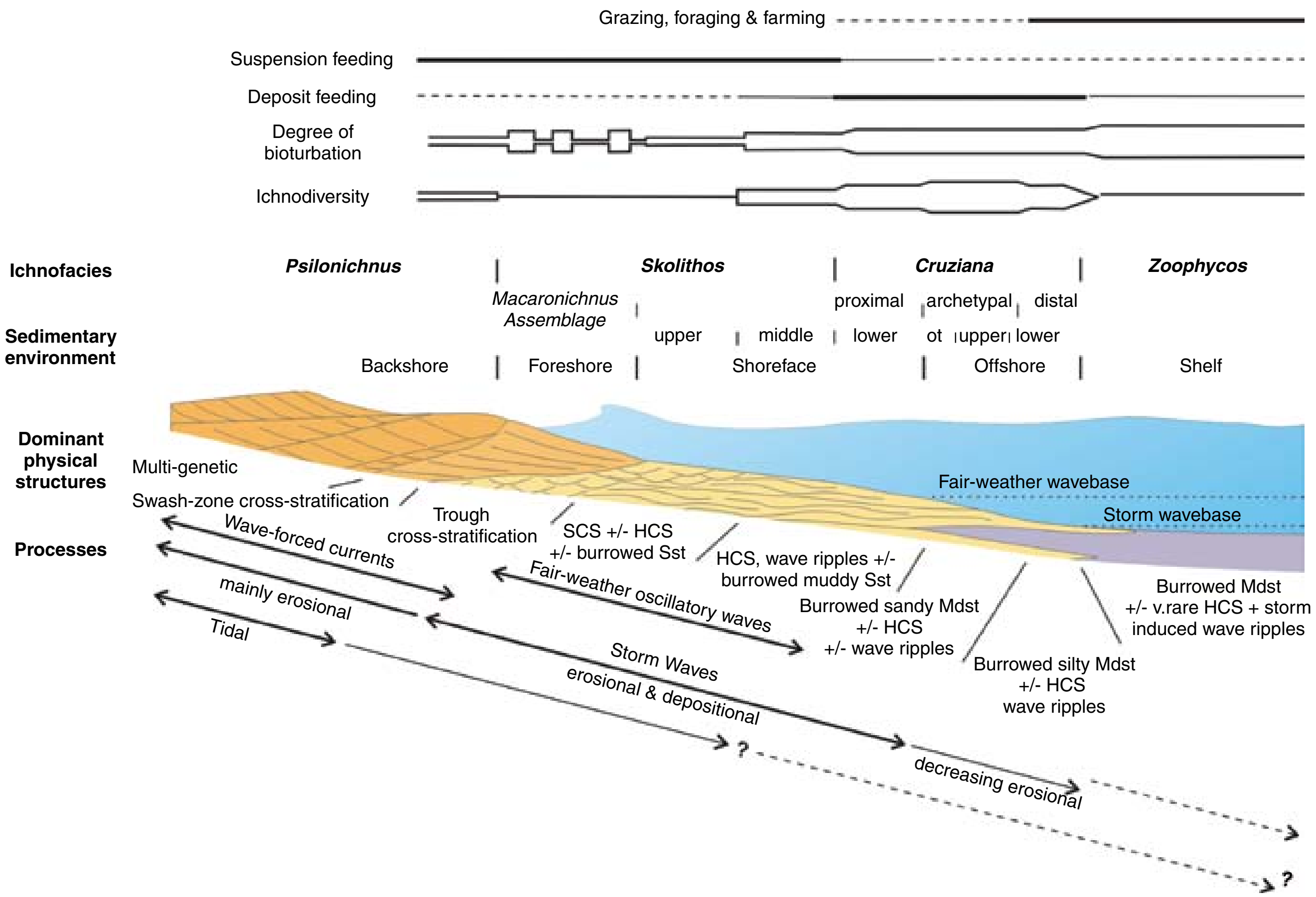

Figure 7.3 Ichnological and sedimentological aspects along a wave-dominated depositional profile. Alternating low and high intensity of bioturbation in the foreshore is due to local patches displaying intense reworking by *Macaronichnus*. HCS, hummocky cross-stratification; SCS, swaley cross-stratification. Distribution of ichnofacies and depositional processes based on MacEachern *et al.* (1999a).

allows delineation of proximal–distal trends along a backshore-nearshore-offshore-shelf transect, referred to as the "shoreface model" (MacEachern and Pemberton, 1992; MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001) (Figs. 7.3 and 7.4). In this model the term "shelf" is used in a more restricted way and separated from the offshore. Observations were originally based on outcrops and cores from the Mesozoic foreland basin of western North America (e.g. Pemberton *et al.*, 1992d), but the database has been subsequently expanded to include information from elsewhere (e.g. Buatois *et al.*, 2002b; Mángano *et al.*, 2005a; Angulo and Buatois, 2009) (Box 7.1).

The proximal–distal energy gradient in open-marine wave-dominated systems is rather straightforward, with a seaward decrease in wave energy (Yoshida *et al.*, 2007). In connection to the energy gradient, other environmental factors change in a predictable way. The energy gradient determines the type of substrate available for benthic colonization. Sand–mud rate decreases seaward and, therefore, wave-dominated environments are represented by sandy shores (Brown and McLachlan, 1990). The distribution of biogenic structures is also controlled by the available food supply (the food resources paradigm of Pemberton *et al.*, 2001). Proximal settings typically contain food particles kept in suspension in the water column by currents and waves, while distal environments are characterized by organic detritus within the sea bed (see Section 6.1.6). Oxygen content usually is not a limiting factor in agitated shallow waters, but dysaerobic and even anoxic conditions may occur in low-energy distal settings, significantly affecting ichnodiversity (see Section 6.1.3).

Analysis of selected case studies documenting shallow-marine clastic ichnofaunas shows that few ichnotaxa are restricted to particular subenvironments of the nearshore to offshore transect. The available information reveals, therefore, the pitfalls of the checklist approach, as previously noted by Howard and Frey (1975). An integrated approach, taking into account several characteristics, such as degree of bioturbation, abundance of individual ichnotaxa, ethological, and ecological significance of the biogenic structures, ichnofabrics, and tiering structure, is more useful to delineate environmental subdivisions of shallow-marine clastic successions (e.g. Buatois *et al.*, 2002b; Mángano *et al.*, 2005a).

7.1.1 BACKSHORE

Backshore environments are characterized by stressful conditions, resulting from a combination of subaerial exposure and rapid variations in substrate types and energy levels, mostly reflecting torrential rains and storm surges (Frey and

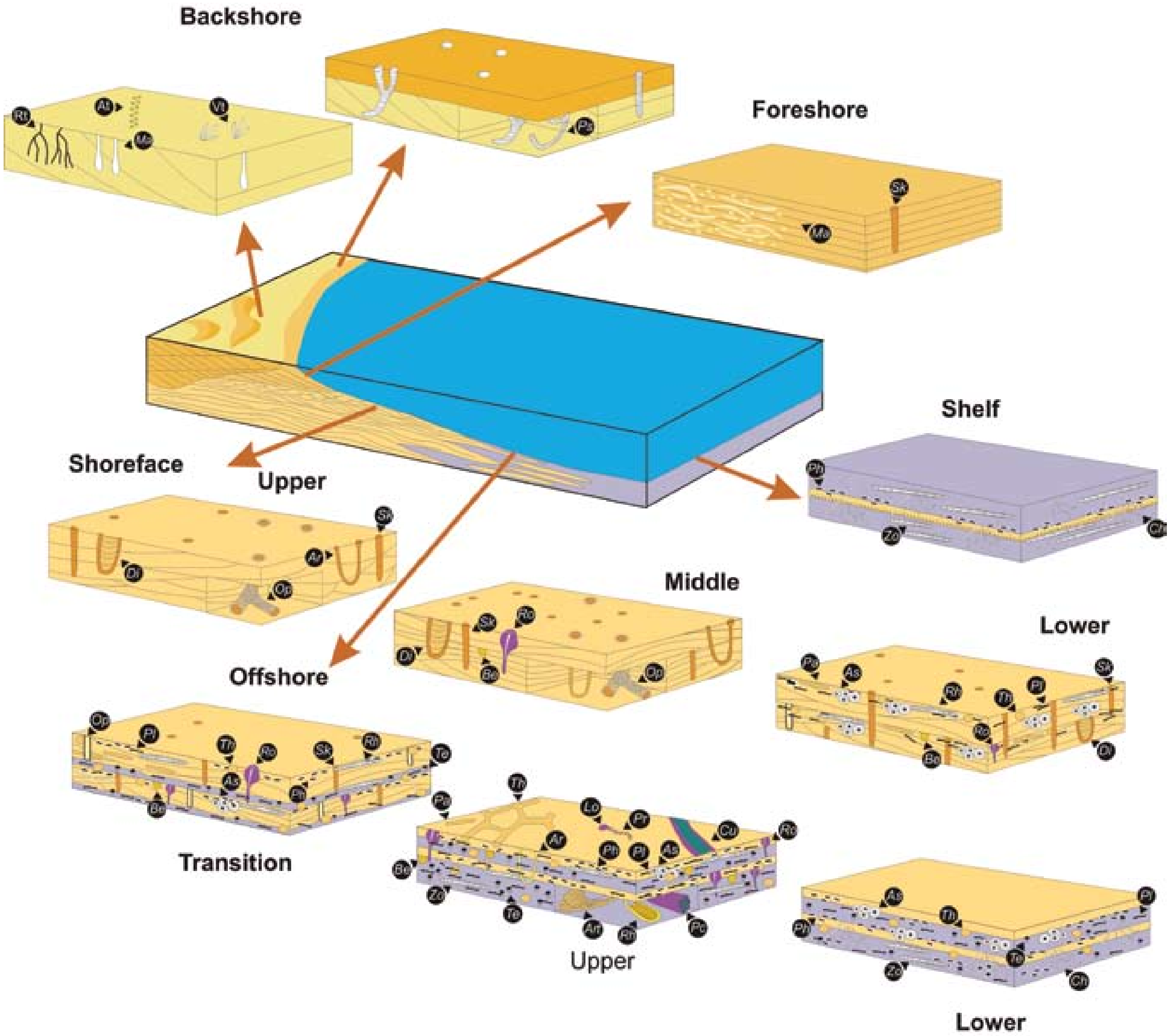

Figure 7.4 Schematic reconstruction of trace-fossil distribution in wave-dominated shallow-marine environments. The proximal zone of the backshore is characterized by vertical dwelling structures with a bulbous basal cell, which are assigned to *Macanopsis* (*Ma*) together with arthropod trackways (At), vertebrate trackways (Vt), and root traces (Rt). The seaward zone of the backshore is dominated by *Psilonichnus* (*Ps*). The foreshore is unbioturbated for the most part, but it may contain *Skolithos* (*Sk*) and high-density occurrences of *Macaronichnus* (*Ma*). The upper shoreface is sparsely bioturbated and may contain vertical burrows, such as *Skolithos* (*Sk*), *Diplocraterion* (*Di*), and *Arenicolites* (*Ar*), as well as crustacean galleries, such as *Ophiomorpha* (*Op*), dominated by vertical components. The middle shoreface is similar to the lower shoreface, but tends to be more bioturbated and other ichnotaxa, such as *Bergaueria* (*Be*) and *Rosselia* (*Ro*), may be added. The lower shoreface is extremely variable with respect to intensity and frequency of storms. *Asterosoma* (*As*), *Bergaueria* (*Be*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Thalassinoides* (*Th*), *Rhizocorallium* (*Rh*), *Rosselia* (*Ro*), *Skolithos* (*Sk*), and *Diplocraterion* (*Di*) are typical components. The offshore transition is similar in taxonomic composition to the lower shoreface, but tends to display higher ichnodiversity and intensity of bioturbation. Ichnogenera, such as *Teichichnus* (*Te*) and *Phycosiphon* (*Ph*), may become abundant. The upper offshore is highly diverse, and may include *Asterosoma* (*As*), *Arenicolites* (*Ar*), *Bergaueria* (*Be*), *Planolites* (*Pl*), *Curvolithus* (*Cu*), *Protovirgularia* (*Pr*), *Lockeia* (*Lo*), *Palaeophycus* (*Pa*), *Arthrophycus* (*Art*), *Phycodes* (*Pc*), *Thalassinoides* (*Th*), *Rhizocorallium* (*Rh*), *Rosselia* (*Ro*), *Teichichnus* (*Te*), *Zoophycos* (*Zo*), and *Phycosiphon* (*Ph*). The lower offshore is less diverse, and tends to be dominated by *Asterosoma* (*As*), *Planolites* (*Pl*), *Thalassinoides* (*Th*), *Chondrites* (*Ch*), *Teichichnus* (*Te*), *Zoophycos* (*Zo*), and *Phycosiphon* (*Ph*). Shelf deposits are intensely bioturbated, but trace-fossil diversity is low. *Chondrites* (*Ch*), *Zoophycos* (*Zo*), and *Phycosiphon* (*Ph*) are typical components.

Pemberton, 1987). Beach-backshore deposits are extremely diverse, including wave and current-rippled cross-laminated sand in ponded areas, and a wide variety of wind-generated structures (e.g. wind ripples and small-scale blowouts) in sand exposed to eolian action. The landward edge of the beach is characterized by eolian dunes, which in the rock record are commonly preserved as planar cross-stratified sandstone commonly displaying steeply dipping foresets.

Box 7.1 Ichnology of lower Paleozoic wave-dominated shallow-marine deposits of northwest Argentina

The Alfarcito Member of the Upper Cambrian–Tremadocian Santa Rosita Formation in northwestern Argentina contains well-preserved and laterally continuous outcrops, recording deposition in a wave-dominated, low-gradient open-marine system. The lower interval of the Alfarcito Member represents a transgressive-regressive cycle, encompassing lower offshore to lower-middle shoreface environments (Fig. 7.5). Benthic fauna and trace-fossil distribution were essentially controlled by alternating and contrasting energy conditions due to repeated storm events superimposed on fair-weather deposition. The fair-weather suite is the most diverse and includes a wide variety of behaviors, such as locomotion (*Archaeonassa fossulata*, *Cruziana semiplicata*, *C. problematica*, *Cruziana* isp., and *Diplichnites* isp.), resting (*Rusophycus moyensis*, *R. carbonarius*, *Rusophycus* isp., and *Bergaueria* aff. *B. hemispherica*), pascichnia (*Dimorphichnus* aff. *D. quadrifidus*), feeding (*Arthrophycus minimus*, ?*Gyrolithes* isp., *Gyrophyllites* isp., ?*Phycodes* isp., and *Planolites reinecki*), and dwelling (*Palaeophycus tubularis* and *P. striatus*). The storm-related suite is monospecific and consists of *Skolithos linearis*, preserved as relatively deep, endichnial structures that penetrate into sandstone tempestites. While the fair-weather suite is represented by the *Cruziana* ichnofacies, the storm-related suite illustrates the *Skolithos* ichnofacies. Integration of ichnological and sedimentological data allows ichnological proximal–distal trends along a nearshore-offshore transect to be established (Fig. 7.5). High energy prevailed in lower-and middle-shoreface environments, and bioturbation is restricted to vertical burrows (*Skolithos linearis*), recording colonization after storm events. Environmental conditions in the offshore transition and the upper offshore are more variable as a result of the alternation of high-energy storm events and low-energy fair-weather mudstone deposition. The storm-related *Skolithos* ichnofacies is present, but alternates with the fair-weather suite (*Cruziana* ichnofacies) which reaches a diversity maximum in the upper offshore. Trace fossils are scarce in lower-offshore deposits, mostly being restricted to *Palaeophycus tubularis*. Shoreface deposits are of the strongly storm-dominated type.

Reference: Mángano *et al*. (2005a).

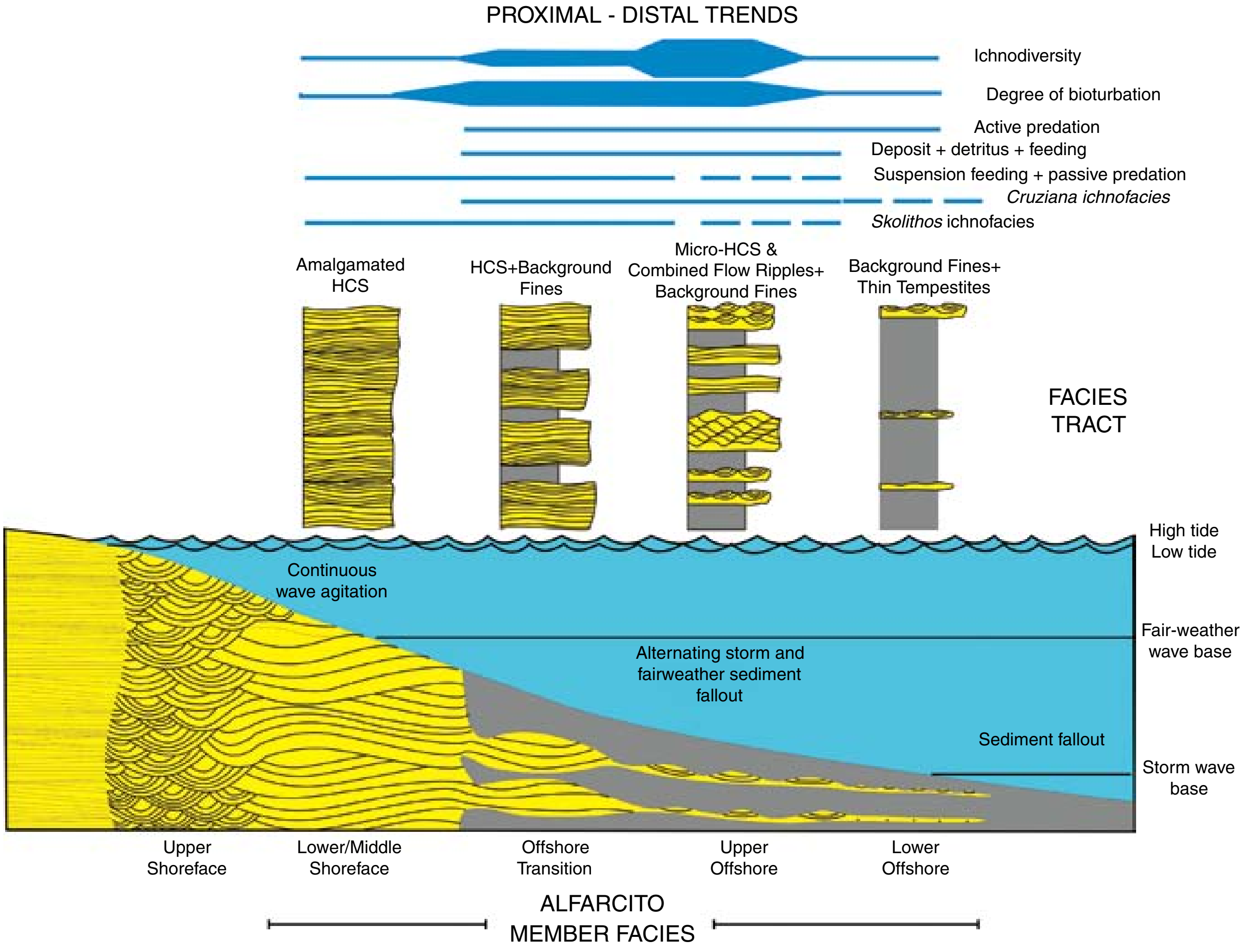

Figure 7.5 Ichnological and sedimentological model of the Alfarcito Member of the Upper Cambrian–Tremadocian Santa Rosita Formation of northwest Argentina (after Mángano *et al*., 2005a). HCS, hummocky cross-stratification.

As a result of harsh conditions, few animals are able to survive in supralittoral areas and, therefore, ichnofaunas are characterized by low ichnodiversity and abundance. Backshore areas contain a mix of structures produced by terrestrial and marine animals, as well as plant-generated structures (Frey and Pemberton, 1987). Terrestrial elements occur in dune areas, while the marine components are present in the beach. A link between both settings occurs, mostly represented by exchange of sand, groundwater, salt spray, and living and dead organic material (Brown and McLachlan, 1990).

The terrestrial component is represented by invertebrate, vertebrate, and plant traces. Terrestrial invertebrate structures include vertical domiciles of insects and spiders, commonly with a bulbous basal cell, and horizontal locomotion and grazing tracks and trails of insects. However, these horizontal traces have minimum preservation potential. The vertebrate ichnofauna consists of different trackways produced by amphibians, reptiles, birds, and mammals (Frey and Pemberton, 1986). Coprolites may also be abundant. Plant traces are represented by root structures mostly generated by halophytic vegetation (adapted to conditions of high salinity) in seaward areas and by other types of plants landward. In particular, foredunes, relict foredunes, and parabolic dunes are extensively vegetated by aggressive pioneer plants and relatively robust plants (Brown and McLachlan, 1990).

Marine organisms are mainly represented by ghost crabs of the family Ocypodidae (e.g. *Uca pugilator* and *Ocypode quadrata*), including both detritus feeders and scavengers. Ghost crabs construct vertical J-, Y-, and U-shaped dwelling structures assigned to the ichnogenus *Psilonichnus* (Radwański, 1977; Fürsich, 1981; Curran, 1984; Frey *et al*., 1984a; Nesbitt Campbell, 2006). In siliciclastic settings, ghost crabs extend from the beach to the eolian dune area (Frey *et al*., 1984a; Curran and White, 1991). Crawling traces of crabs, although extremely common in modern shorelines, have a very low preservation potential (Curran, 1984; Frey *et al*., 1984a). Other locomotion and grazing horizontal traces are produced by limulids, amphipods, bivalves, and gastropods in modern examples, but remain virtually unknown in fossil examples of backshore environments.

Collectively these structures are included in the *Psilonichnus* ichnofacies (Frey and Pemberton, 1987). Backshore areas grade landwards into a wide variety of terrestrial environments characterized by different trace-fossil assemblages that mostly belong to the *Scoyenia* and *Coprinisphaera* ichnofacies, as well as other potential terrestrial ichnofacies (Buatois and Mángano, 1995b; Genise *et al*., 2000).

7.1.2 FORESHORE

The foreshore is characterized by high-energy conditions due to intense swash and backwash processes in the intertidal area. Foreshore deposits mostly consist of well-sorted, coarse- to medium-grained sandstone with subparallel to low-angle cross stratification, known as swash-zone stratification. Parting lineation is common. In some cases, foreshore deposits consist of clast-supported pebble to cobble conglomerate displaying clast imbrication (Buscombe and Masselink, 2006).

Because of high energy, foreshore deposits tend to be sparsely bioturbated and of low ichnodiversity (MacEachern and Pemberton, 1992; Pemberton *et al*., 2001). Locally, zones intensely bioturbated by *Macaronichnus* are common (see Section 6.1.1), representing the *Macaronichnus* assemblage of Pemberton *et al*. (2001) (see also Seike, 2008, 2009) (Fig. 7.6a–b). Deep-tier vertical dwelling structures of suspension feeders, such as *Skolithos* (Fig. 7.6c) and *Ophiomorpha*, are typical elements, reflecting abundant organic particles kept in suspension by energetic wave-forced currents. Middle-tier horizontal to inclined dwelling traces (e.g. *Palaeophycus* and *Schaubcylindrichnus*) involving other trophic groups, such as passive predators and deposit feeders, have lower preservation potential (Pemberton *et al*., 2001). The foreshore ichnofauna is ascribed to the *Skolithos* ichnofacies. In any case, most foreshore deposits are unburrowed.

7.1.3 UPPER SHOREFACE

The upper shoreface occurs below the low-tide line, and is subjected to multidirectional current flows in the build up and surf zones (Clifton *et al*., 1971; Komar, 1976; Walker and Plint, 1992). As in the foreshore, high-energy conditions are predominant. Upper-shoreface deposits typically consist of trough and planar cross-stratified well-sorted, coarse- to medium-grained sandstone. Locally, pebble conglomerate and pebbly sandstone beds may occur.

Continuous migration of large bedforms results in sparse colonization by the benthic fauna. Accordingly, it is not uncommon to find upper-shoreface deposits that are unburrowed. As a result of overall high-energy conditions, upper-shoreface ichnofaunas resemble those from the foreshore in their sparse distribution, low diversity, dominance of vertical domiciles of the *Skolithos* ichnofacies (e.g. *Skolithos*, *Ophiomorpha*, and *Diplocraterion*), and local abundance of *Macaronichnus* (MacEachern and Pemberton, 1992; Pemberton *et al*., 2001). Although *Macaronichnus* is more common in the upper shoreface–foreshore transition, in reflective shorelines it may occur down in the upper shoreface (Pemberton *et al*., 2001). In addition, *Conichnus* may occur locally. Although shallow-tier biogenic structures may be emplaced, deep-tier elements have much higher preservation potential. As a result, upper-shoreface ichnofabrics are overwhelmingly dominated by deeply penetrating vertical burrows (Fig. 7.7a).

7.1.4 MIDDLE SHOREFACE

The middle shoreface is located in the area of shoaling and initial breaking of waves (Reinson, 1984; Clifton, 2006). High energy due to migration of longshore bars is predominant. Middle-shoreface deposits consist of swaley cross-stratified, well-sorted, medium- to fine-grained sandstone. Locally, trough cross-stratification, combined-flow ripples and, more rarely, hummocky cross-stratification may occur. Storm-induced

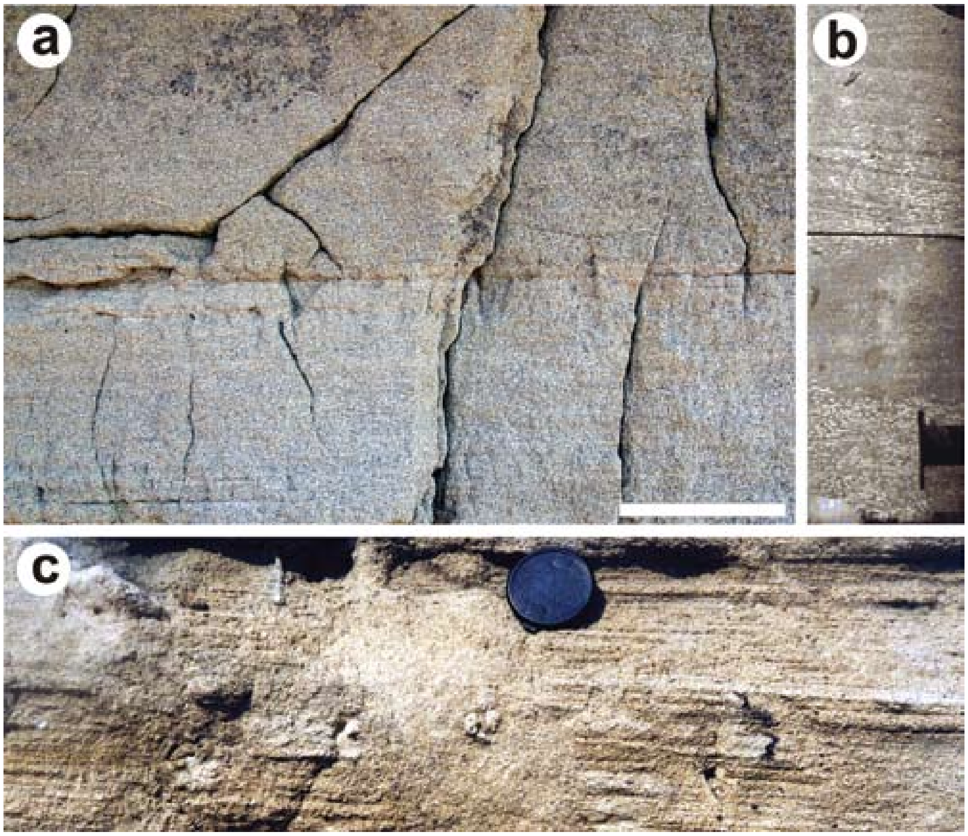

Figure 7.6 Ichnofaunas from foreshore deposits. (a) Low-angle cross-stratified sandstone with a monospecific dense assemblage of *Macaronichnus segregatis*. Upper Cretaceous, Horseshoe Canyon Formation, Drumheller, Alberta, western Canada. Scale bar is 10 cm. See Pemberton *et al.* (2001). (b) Core expression of similar deposits containing *Macaronichnus segregatis*. Upper Oligocene-Lower Miocene, Naricual Formation, El Furrial Field, Eastern Venezuela Basin. Core width is 8 cm. See Quiroz *et al.* (2010). (c) Sparsely bioturbated parallel-laminated sandstone showing low density of *Skolithos linearis*. Pleistocene, Tablazo Formation, Ballenita, Pacific coast, Ecuador. Lens cap is 5.5 cm.

scouring is particularly intense in the middle shoreface (Aigner and Reineck, 1982).

Because of overall high-energy conditions, middle-shoreface deposits are typified by the *Skolithos* ichnofacies (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001). However, in contrast to the foreshore and upper shoreface, ichnodiversity and intensity of bioturbation is somewhat higher. *Ophiomorpha* (Fig. 7.7b), *Skolithos* (Fig. 7.7e), *Diplocraterion*, *Arenicolites*, *Conichnus*, and *Bergaueria* are common components. *Thalassinoides* with dominantly vertical components may occur (Fig. 7.7c). Escape trace fossils may also be present. The frequency and intensity of storms play a major role on patterns of substrate colonization by the benthic fauna (see Section 7.1.5). Under weak and infrequent storms, some elements of the *Cruziana* ichnofacies, such as *Rosselia* (Fig. 7.7d and f) and *Asterosoma* (Fig. 7.7g), may be present. Under increased storm influence nearly all the components are vertical burrows of suspension feeders and passive predators (Pemberton *et al.*, 2001). If the intensity and frequency of storms is high, deposits are unburrowed or only dominated by a few deep-tier forms, resembling upper-shoreface ichnofabrics.

7.1.5 LOWER SHOREFACE

The lower shoreface occurs immediately above the fair-weather wave base (Reinson, 1984; Walker and Plint, 1992). Wave action is the most important process in this zone. Lower-shoreface deposits consist of thick hummocky cross-stratified fine- to very fine-grained sandstone. Wave and combined-flow ripples are locally common at the top of hummocky beds. Individual sandstone beds generally pinch out, but bedsets are commonly laterally persistent (Brenchley *et al.*, 1993). Millimetric partings may occur locally between some hummocky cross-stratified units.

MacEachern and Pemberton (1992) noted that lower-shoreface deposits display strong ichnological variability as a result of contrasting regimes in terms of intensity and frequency of storm events. The weakly storm-affected lower shorefaces (low energy) are characterized by relatively minor amounts of tempestites. These deposits are dominated by fair-weather trace-fossil assemblages, and thin storm beds are commonly obliterated by biogenic reworking or thoroughly bioturbated (e.g. Buatois *et al.*, 2002b, 2003; Carmona *et al.*, 2008). In addition, ichnodiversity is high, and assemblages tend to be dominated by feeding traces of infaunal deposit feeders, such as *Phycosiphon* (Fig. 7.8a), *Teichichnus* (Fig. 7.8e), *Phycodes*, *Asterosoma* (Fig. 7.8a–b), *Schaubcylindrichnus* (Fig. 7.8a–b and f), *Taenidium* (Fig. 7.8d and f), *Helicodromites*, and *Rhizocorallium* (Fig. 7.8h). Grazing trails of deposit feeders, including *Planolites*, *Nereites* (Fig. 7.8b–c) and *Scolicia* (Fig. 7.8a–b,e–g), feeding traces of chemosymbionts (*Chondrites*) and dwelling traces of suspension feeders (e.g. *Palaeophycus*) and deposit or detritus feeders (e.g. *Cylindrichnus* and *Rosselia*) are also present. Crustacean burrow networks, such as *Thalassinoides* (Fig. 7.8f) and *Ophiomorpha* may be abundant. Equilibrium structures, mostly *Diplocraterion* (Fig. 7.8h), may occur locally. *Asterosoma*, *Diplocraterion*, and

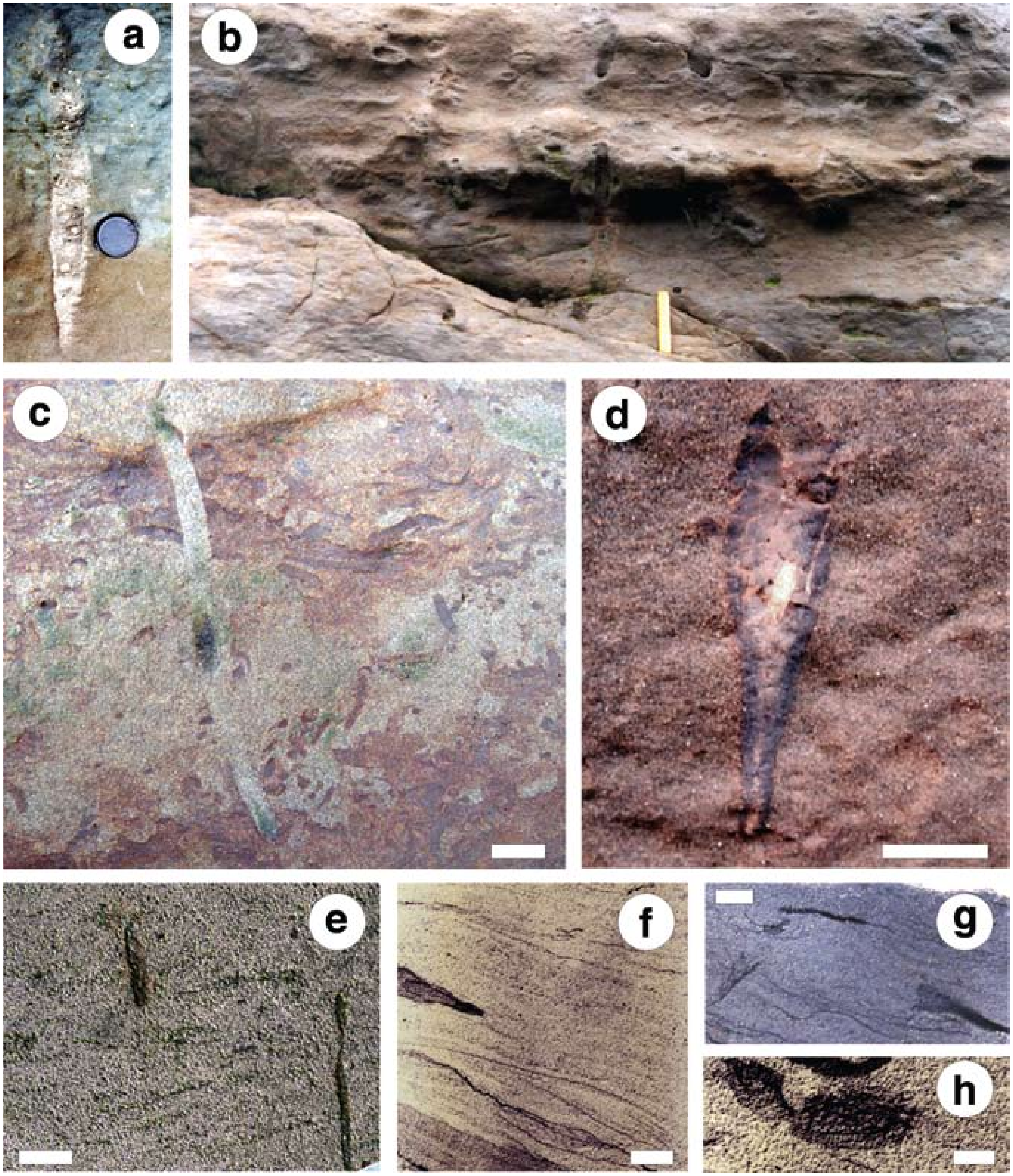

Figure 7.7 Ichnofaunas from upper- to middle-shoreface deposits. (a) Vertical *Ophiomorpha nodosa* in upper-shoreface deposits. Lower Miocene, Chenque Formation, Playa Alsina, near Comodoro Rivadavia, Patagonia, Argentina. Lens cap is 5.5 cm. See Carmona *et al*. (2008). (b) Several vertical specimens of *Ophiomorpha* isp. in middle-shoreface deposits. Lower Miocene, Chenque Formation, Punta Delgada, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 20 cm. See Carmona *et al*. (2008). (c) Vertical *Thalassinoides* isp. cross-cutting variably oriented *Planolites beverleyensis* in middle-shoreface deposits. Pliocene, Lacui Formation, Cucao, Chiloé Island, southern Chile. Scale bar is 1 cm. (d) Sideritized *Rosselia socialis* in middle-shoreface deposits. Pliocene, Lacui Formation, Cucao, Chiloé Island, southern Chile. Scale bar is 1 cm. (e) Core expression of *Skolithos linearis* in middle-shoreface, planar cross-bedded medium-grained sandstone. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b). (f) Core expression of middle-shoreface, planar cross-bedded medium-grained sandstone with reworked *Rosselia* isp. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b). (g) Core expression of *Cylindrichnus concentricus* in middle-shoreface deposits. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b). (g) Core expression of *Asterosoma* isp. in middle-shoreface sandstone. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b).

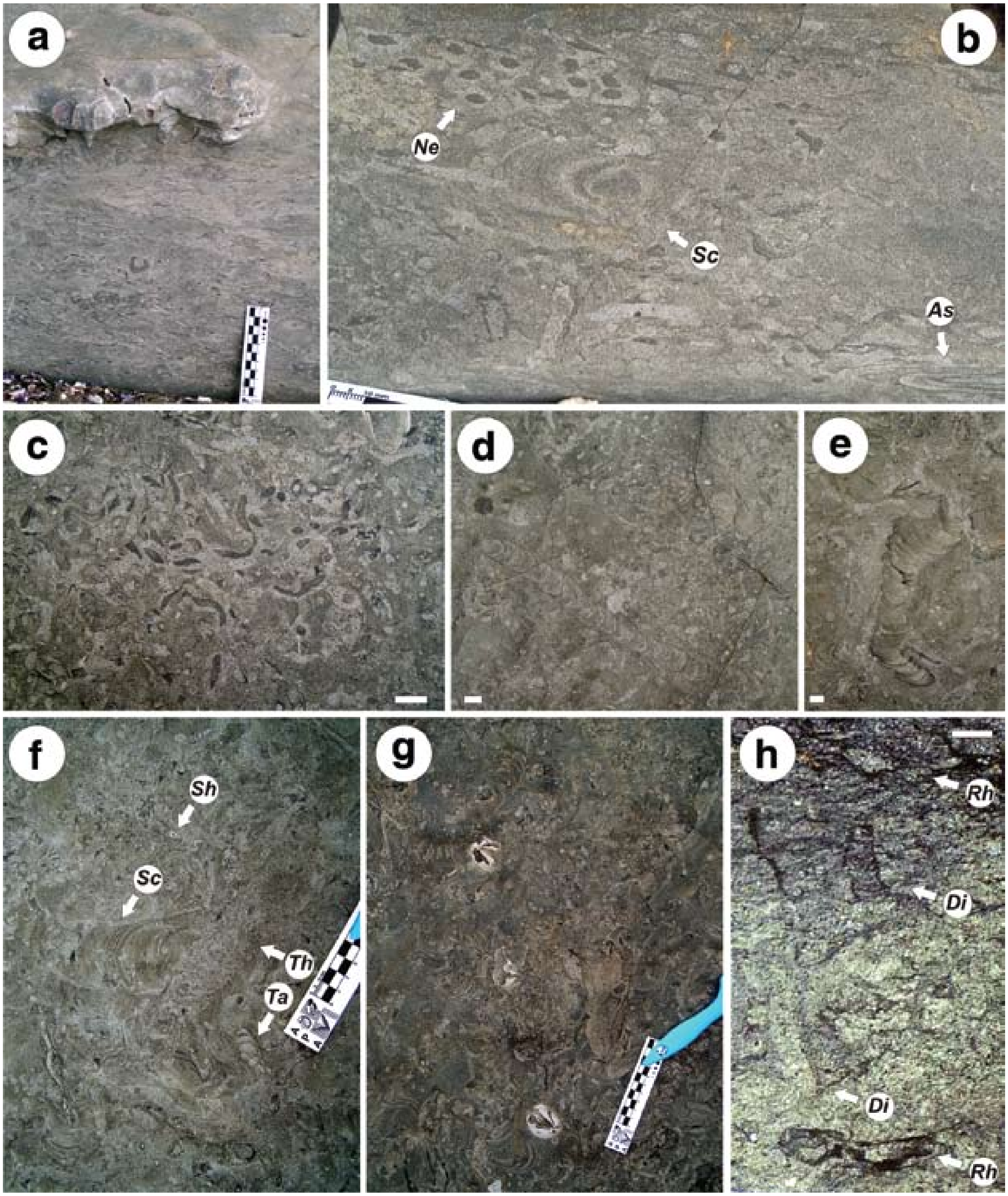

Figure 7.8 Ichnofaunas from weakly storm-affected lower-shoreface deposits (low energy). (a) Cross-section view of intensely bioturbated very fine-grained sandstone below a horizon with *in situ* specimens of *Pinna* sp. containing *Nereites missouriensis*, *Schaubcylindrichnus freyi*, *Asterosoma* isp., *Scolicia* isp., and *Phycosiphon incertum*. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 10 cm. See Carmona *et al*. (2008). (b) Close-up showing of *Nereites missouriensis* (*Ne*), *Asterosoma* isp. (*As*), and *Scolicia* isp. (*Sc*). Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale shows 1 cm division. See Carmona *et al*. (2008). (c) Bedding-plane view of *Nereites missouriensis*. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 1 cm. See Carmona *et al*. (2008). (d) Bedding-plane view of *Taenidium* isp. cross-cutting a background ichnofabric. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 1 cm. See Carmona *et al*. (2008). (e) Oblique view of *Teichichnus zigzag* cross-cutting *Scolicia* isp. and overprinted on a background ichnofabric. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 1 cm. See Carmona *et al*. (2008). (f) Bedding-plane close-up view of intensely bioturbated very fine-grained sandstone containing *Taenidium* isp. (*Ta*), *Schaubcylindrichnus freyi* (*Sh*), *Thalassinoides* isp. (*Th*), and *Scolicia* isp. (*Sc*). Note complex cross-cutting relationships. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale shows 1 cm divisions. See Carmona *et al*. (2008). (g) Bedding-plane view of abundant *Scolicia* isp. (and their echinoid producers) overprinted on a background ichnofabric. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 10 cm. See Carmona *et al*. (2008). (h) Core expression of intensely bioturbated fine-grained sandstone containing *Rhizocorallium* isp. (*Rh*) and *Diplocraterion* isp. (*Di*) overprinted on a background mottling ichnofabric. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b).

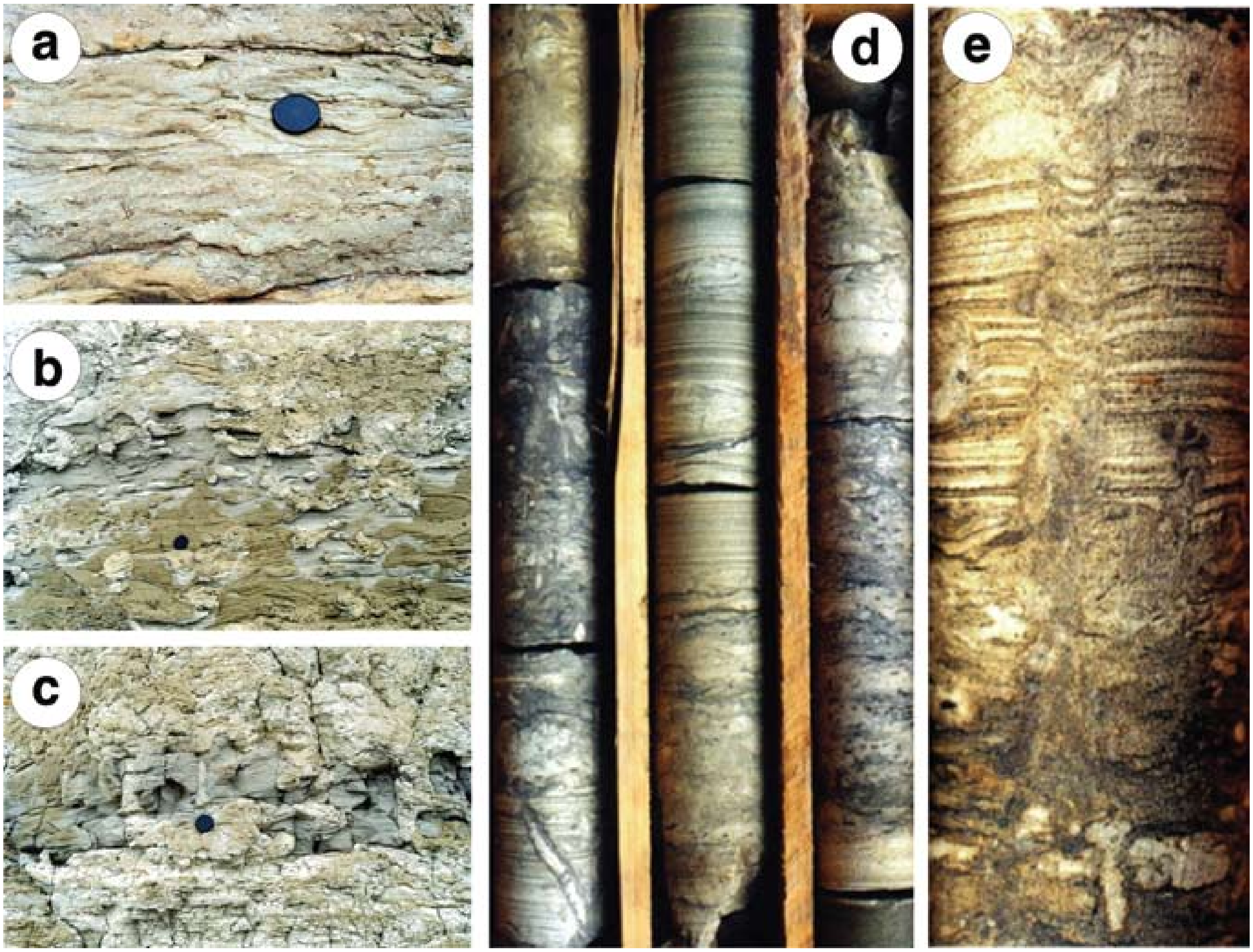

Figure 7.9 Ichnofaunas from moderately storm-affected lower-shoreface deposits (intermediate energy), displaying the typical "lam-scram" pattern. (a) Sparsely bioturbated to non-bioturbated hummocky cross-stratified sandstone zone interbedded with intensely bioturbated sandstone. Note deeply penetrating *Diplocraterion* into hummocky sandstone. Lower Jurassic, Staithes Sandstone Formation, Hartle Loup, North Yorkshire Coast, England. Lens cap is 5.5 cm. See Taylor and Pollard (1999). (b) Alternating hummocky cross-stratified and burrowed zones. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Scasso and Bellosi (2004). (c) Intensely burrowed sandstone with hummocky zones preserved as relict lenses. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Scasso and Bellosi (2004). (d) Alternating hummocky cross-stratified and burrowed zones. Base is on the lower left and top on the upper right. Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al*. (2007b). (e) Close-up showing deep *Diplocraterion* penetrating throughout the whole hummocky sandstone into the underlying bioturbated zone. Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al*. (2007b).

Ophiomorpha tend to be more abundant towards the proximal edge of the lower shoreface. Ichnofabrics from weakly affected lower shorefaces typically display complex tiering structures, revealing finely tuned, climax communities displaying vertical niche partitioning (Buatois *et al*., 2003). A transition from the *Cruziana* to the *Skolithos* ichnofacies is coincident with the lower to middle shoreface transition in this type of shoreface. An archetypal *Cruziana* ichnofacies characterizes weakly affected lower-shoreface deposits.

The moderately storm-affected shorefaces (intermediate energy) show an alternation of laminated storm beds and bioturbated fair-weather deposits, resulting in the so-called "lam-scram" pattern (Howard, 1978; MacEachern and Pemberton, 1992) (see Section 6.1.5). These deposits commonly display the alternation of elements of the *Skolithos* ichnofacies as opportunistic pioneers colonizing sandstone tempestites and the *Cruziana* ichnofacies recording the activity of the fair-weather resident community (e.g. MacEachern and Pemberton, 1992; Buatois *et al*., 2007b) (Fig. 7.9a–e). The laminated storm beds either are totally unburrowed or contain a few deeply penetrating burrows (e.g. *Ophiomorpha*, *Diplocraterion*, and *Skolithos*). The fair-weather deposits are moderately to strongly bioturbated, and contain *Asterosoma*, *Helminthopsis*, *Planolites*, *Palaeophycus*, *Rhizocorallium*, and *Thalassinoides*, among other ichnotaxa. Escape trace fossils are locally present. Tiering structure is less developed than in the weakly affected lower shorefaces. Moderately storm-affected lower-shoreface deposits display an alternation of the *Skolithos* and proximal *Cruziana* ichnofacies.

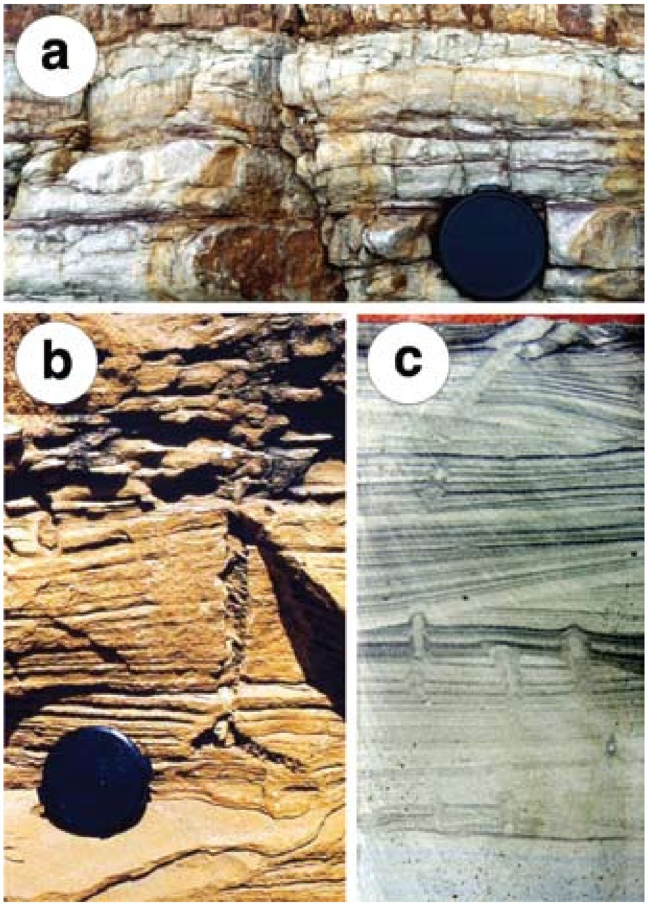

Figure 7.10 Ichnofaunas from strongly storm-dominated lower/middle shoreface deposits (high energy). (a) *Skolithos linearis* forming a pipe rock. Upper Cambrian-Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada Casa Colorada, Alfarcito Range, northwest Argentina. Lens cap is 5.5 cm. See Mángano *et al.* (2005a). (b) *Ophiomorpha nodosa* in hummocky cross-stratified sandstone. Lower Miocene, Capiricual Formation, El Anfiteatro, Serranía del Interior, Eastern Venezuela. Lens cap is 5.5 cm. (c) Escape trace fossils in amalgamated hummocky cross-stratified sandstone. Lower Permian, San Miguel Formation, Mallorquín #1 well, Paraguay. Core width is 8 cm.

The strongly storm-dominated shorefaces (high energy) commonly consist of amalgamated hummocky sandstone showing little or no bioturbation (Fig. 7.10a–c). High-energy conditions prevailed, commonly precluding the preservation of biogenic structures. Only the deepest components of the post-storm *Skolithos* ichnofacies (e.g. *Skolithos* and *Ophiomorpha*) are present. Shallow- to mid-tier biogenic structures were most likely removed by erosion due to deep scouring. Repeated storm-wave erosion either precluded the establishment of fair-weather suites, or limited their preservation in these high-energy settings (MacEachern and Pemberton 1992; Pemberton and MacEachern 1997; Buatois *et al.*, 2007b; Mángano *et al.*, 2005a). The absence of fair-weather suites in strongly storm-dominated shorefaces precludes distinction between the middle and the lower shoreface based on ichnological aspects (MacEachern and Pemberton 1992).

7.1.6 OFFSHORE TRANSITION

The offshore transition occurs immediately below the fair-weather wave base (Pemberton *et al.*, 2001). Environmental conditions in the offshore transition are more variable, and reflect the alternation of high-energy storm events and low-energy fair-weather mudstone deposition. Accordingly, offshore-transition deposits consist of regularly interbedded, parallel-laminated to burrowed mudstone, and thin to thick erosive-based, fine- to very fine-grained sandstone with hummocky cross-stratification, and combined-flow and wave ripples at the top (Fig. 7.11a). Gutter casts, flute casts, tool marks, and load casts may occur at the base of sandstone beds (e.g. Myrow, 1992; Mángano *et al.*, 2005a). Sandstone beds are laterally extensive, but commonly display important thickness variation.

The storm-related *Skolithos* trace-fossil suite is present in the offshore transition, but alternates with the fair-weather suite illustrating an archetypal *Cruziana* ichnofacies (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001). Although the degree of bioturbation is somewhat lower than in offshore deposits, some hummocky sandstone may have intensely bioturbated tops (e.g. Mángano *et al.*, 2005a) (Fig. 7.11b–c). These sandstone tops are palimpsest surfaces, recording a storm-related assemblage overprinted by the subsequent fair-weather assemblage. If the frequency and intensity of storms is low to moderate, the mudstone intervals will be thoroughly bioturbated. The resident biota is represented by a wide variety of ichnotaxa, such as *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Diplichnites* (Fig. 7.11d), *Gyrophyllites* (Fig. 7.11b), *Arthrophycus*, *Scolicia* (Fig. 7.11e), *Cylindrichnus*, *Rosselia* (Fig. 7.11f–g), *Phycosiphon* (Fig. 7.11a), *Lockeia*, *Protovirgularia*, *Siphonichnus*, *Teichichnus* (Fig. 7.11f), *Phycodes*, *Asterosoma*, *Schaubcylindrichnus*, *Taenidium*, *Helicodromites*, *Rhizocorallium*, *Thalassinoides* (Fig. 7.11h), *Chondrites* (Fig. 7.11h), *Palaeophycus* (Fig. 7.11f–g), *Planolites* (Fig. 7.11f), and *Nereites* (Fig. 7.11i). The colonizers are recorded by a few ichnotaxa, mostly *Skolithos*, *Ophiomorpha*, and *Arenicolites* (Fig. 7.11f). Escape trace fossils are also present.

7.1.7 UPPER OFFSHORE

The upper offshore occurs between the offshore transition and the lower offshore. As in the offshore transition, the upper offshore is subjected to the alternation of high-energy, short-term storm events and longer periods of suspension fallout during fair-weather. Compared with the lower offshore and offshore transition, upper-offshore deposits are commonly the most variable. Due to its bathymetric position, the upper offshore experiences a lesser degree of storm-wave influence than the offshore transition. Upper-offshore deposits consist of bioturbated mudstone intervals interbedded with thin, laterally extensive, erosionally based, very fine-grained silty sandstone layers with parallel lamination, combined-flow ripples, and wave ripples (Fig. 7.12a). Thin beds with micro-hummocky cross-stratification, hummocky cross-stratification, and planar lamination may occur.

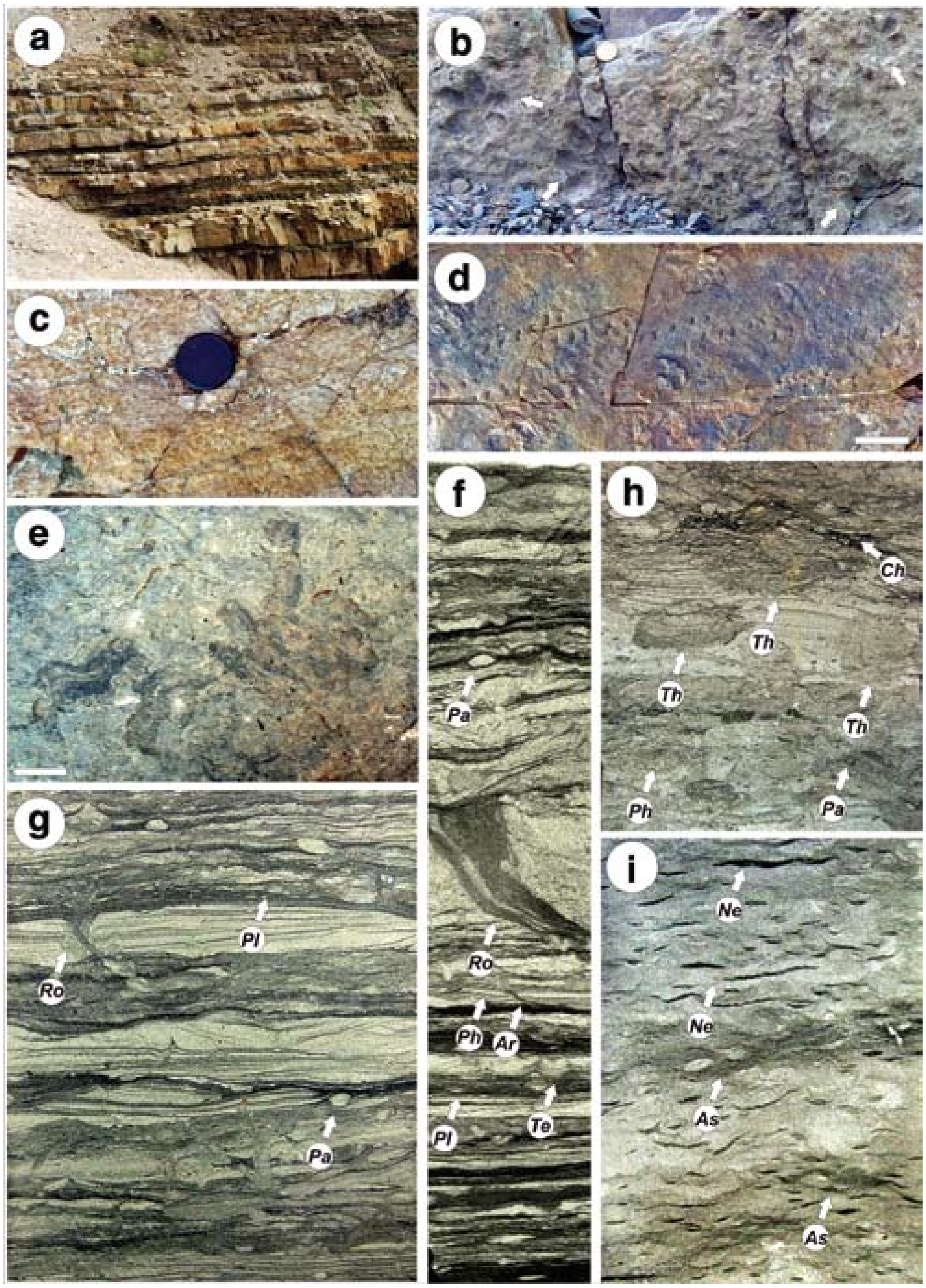

Figure 7.11 Ichnofaunas from offshore–transition deposits. (a) General outcrop view of offshore–transition deposits showing regular intercalation of very fine-grained hummocky cross-stratified sandstone and mudstone. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada de Moya, northwest Argentina. Length of hammer is 33.5 cm. See Mángano *et al*. (2005a). (b) Close-up of the top of a hummocky cross-stratified sandstone, displaying high density of the radial feeding trace fossil *Gyrophyllites* isp. (arrows). Upper Cambrian–Lower Ordovician, Humacha Member, Santa Rosita Formation, Quebrada de Humacha, near Huacalera, northwest Argentina. Coin (upper center) is 1.8 cm. See Mángano *et al*. (2005a). (c) Bedding-plane view of intensely bioturbated very fine-grained sandstone tempestite with high-density circular cross-sections of *Skolithos linearis*. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Arroyo Pintado, northwest Argentina. Lens cap is 5.5 cm. See Mángano *et al*. (2005a). (d) *Diplichnites* isp. at the top of a hummocky cross-stratified sandstone. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Arroyo Pintado, northwest Argentina. Scale bar is 2 cm. See Mángano *et al*. (2005a). (e) Fair-weather deposits containing *Scolicia* isp. Upper Cretaceous, Panther Tongue Member, Star Point Formation, Kennilworth Wash, Book Cliffs, Utah, United States. Scale bar is 2 cm. See Bhattacharya *et al*. (2007). (f) Offshore–transition deposits showing alternation of fair-weather mudstone and thin- to moderately thick-bedded very fine-grained sandstone tempestites. Ichnofauna represented by *Rosselia* isp. (*Ro*), *Arenicolites* isp. (*Ar*), *Teichichnus rectus* (*Te*), *Palaeophycus* isp. (*Pa*), *Planolites* isp. (*Pl*), and *Phycosiphon incertum* (*Ph*). Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al*. (2007b). (g) Interbedded fair-weather mudstones and discrete layers of very fine-grained sandstone tempestites. Note small *Rosselia* isp. (*Ro*) in sandstone layer, and abundant *Palaeophycus* isp. (*Pa*) and *Planolites montanus* (*Pl*) in fair-weather deposits. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (h) Partially preserved storm sandstone layer interbedded with intensely bioturbated deposits with *Thalassinoides* isp. (*Th*), *Chondrites* isp. (*Ch*), *Phycosiphon incertum* (*Ph*) and *Palaeophycus* isp. (*Pa*). In some cases, *Chondrites* is reworking *Thalassinoides* burrow fills. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (i) Intensely bioturbated offshore-transition deposits showing diffuse layers of very fine-grained sandstone emplaced by storms interbedded with fair-weather mudstone. Sandstone is dominated by *Nereites missouriensis* (*Ne*). *Asterosoma* isp. (*As*) tends to be more common in fair-weather deposits. Upper Devonian–Lower Mississippian Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2009, 2010).

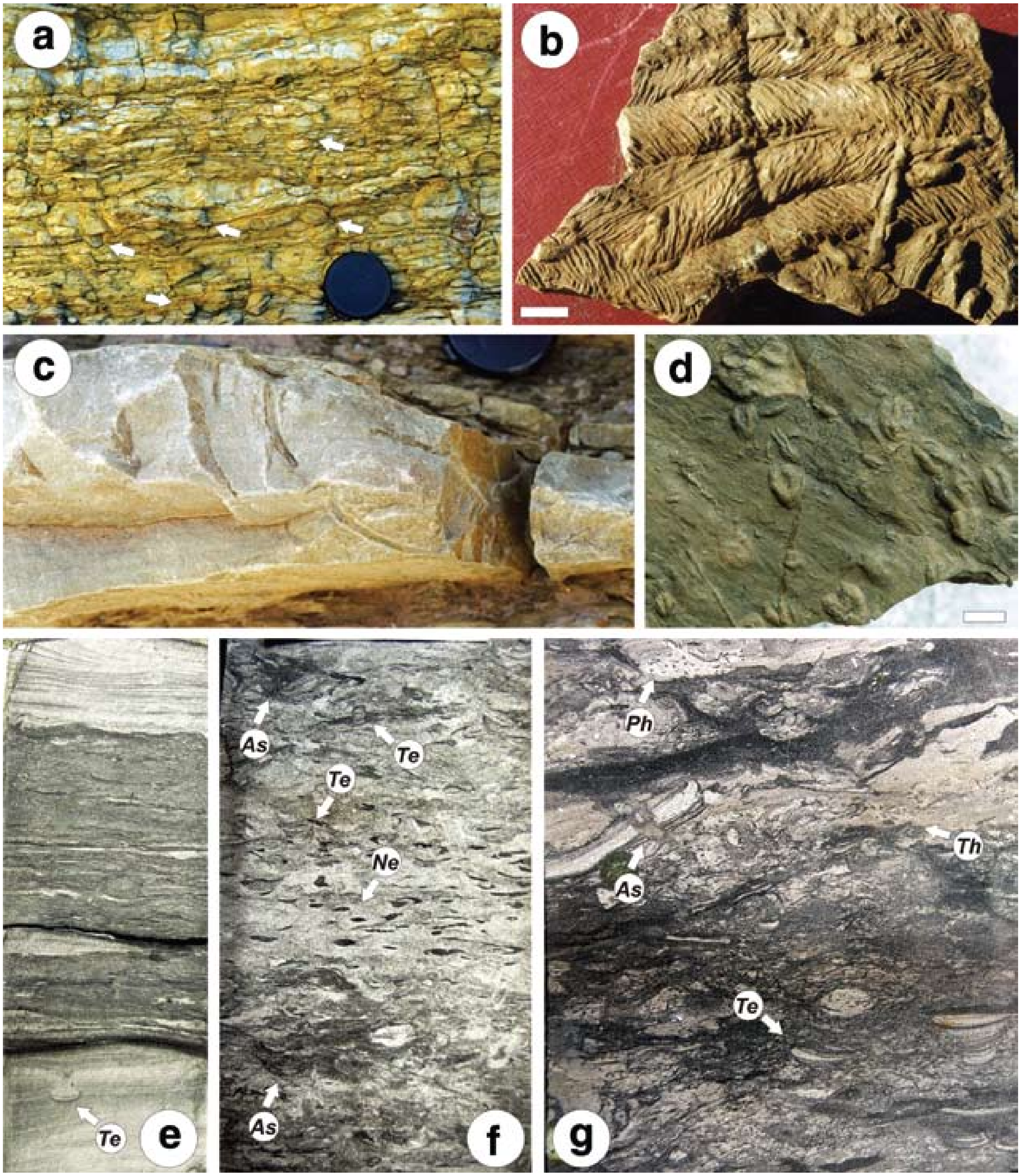

Figure 7.12 Ichnofaunas from upper-offshore deposits. (a) General outcrop view of upper-offshore deposits showing thinly bedded mudstone and very fine-grained sandstone with combined-flow and oscillatory ripples. The ichnofabric is dominated by *Trichophycus venosus* (arrows). Lower Ordovician, Rupasca Member, Santa Rosita Formation, Angosto del Ferrocarril, Chucalezna, northwest Argentina. Lens cap is 5.5 cm. See Mángano and Buatois (2011). (b) Close-up of base of a sandstone tempestite, displaying high density of *Cruziana semiplicata* cross-cut by *Palaeophycus tubularis*. Upper Cambrian, Lampazar Formation, Angosto del Moreno, northwest Argentina. Scale bar is 1 cm. See Mángano and Buatois (2003a). (c) *Arenicolites* isp. colonizing a very-fine grained sandstone tempestite. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada del Arenal, near Huacalera, northwest Argentina. Lens cap is 5.5 cm. See Mángano and Buatois (2003a). (d) Base of a sandstone tempestite, displaying abundant *Rusophycus moyensis*. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada de Moya, northwest Argentina. Scale bar is 1 cm. See Mángano *et al.* (2002c). (e) Moderately bioturbated fair-weather offshore-transition deposits intercalated with discrete very fine-grained sandstone layers emplaced by storms displaying sparse bioturbation by *Teichichnus rectus* (*Te*). Overall moderate bioturbation degree and presence of discrete storm layers suggest relatively high frequency and intensity of storms. Upper Devonian–Lower Mississippian, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (f) Intensely bioturbated fair-weather deposits showing diffuse layers of very fine-grained storm sandstone. Sandstone is dominated by *Nereites missouriensis* (*Ne*). *Asterosoma* (*As*) isp. tends to be more common in fair-weather deposits, while *Teichichnus rectus* (*Te*) occurs in both fair-weather and storm deposits. Overall high bioturbation degree and presence of diffuse storm layers suggest relatively low frequency and intensity of storms. Upper Devonian–Lower Mississipian, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2009, 2010). (g) Partially preserved storm sandstone layer interbedded with intensely bioturbated deposits having *Asterosoma* isp. (*As*), *Phycosiphon incertum* (*Ph*) and *Teichichnus rectus* (*Te*). Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm.

Upper-offshore deposits display the alternation of the resident fair-weather and storm-related colonization trace-fossil suites. The fair-weather suite commonly reaches a diversity maximum in the upper offshore, and represents the archetypal *Cruziana* ichnofacies (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001) (Fig. 7.12b,d,f–g). This ichnofacies is represented by a wide variety of morphological patterns and ethological groups. Its composition tends to be similar to that of the offshore transition. The fair-weather mudstone is commonly completely bioturbated, and the sandstone tempestites may be moderately to intensely bioturbated. In the case of weakly storm-affected settings, bioturbation is intense, and thin storm layers may be completely homogenized or only recorded by remnant lamination (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001) (Fig. 7.12f–g). Under greater intensity and frequency of storms, the degree of bioturbation in both fair-weather and event deposits may be lower (Fig. 7.12e). The less-erosive nature of these more distally emplaced tempestites coupled with the overall lower energy of the upper offshore favor development and preservation of the fair-weather suite (Mángano *et al.*, 2005a). The storm-related suite is less distinctive, with some sandstone beds recording small and dispersed vertical burrows, most commonly *Skolithos*, *Arenicolites* (Fig. 7.12e), and *Ophiomorpha.*

7.1.8 LOWER OFFSHORE

The lower offshore occurs immediately above the storm wave base (MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001). Suspension fallout is the dominant process and, therefore, lower-offshore deposits are mudstone-dominated. However, because sedimentation occurs above the storm wave base, bioturbated mudstone background deposits are locally punctuated by laterally extensive, sharp-based, erosive storm-emplaced, very fine-grained silty sandstone with combined-flow ripples and parallel lamination.

Bioturbation is commonly very intense in lower-offshore deposits (Fig. 7.13). Background mudstone is thoroughly bioturbated, while bioturbation patterns in the associated distal tempestites are more variable. Thin tempestites are commonly represented by remnant lamination, while thick sandstone beds show better preservation of the primary fabric, and trace fossils are commonly restricted to the top (Pemberton *et al.*, 2001). The storm-related trace-fossil assemblage is commonly poorly developed and the fair-weather assemblage represents the distal *Cruziana* ichnofacies (MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001). Typical components are *Phycosiphon* (Fig. 7.13a–f), *Helminthopsis*, *Nereites* (commonly *N. missouriensis*), *Chondrites* (Fig. 7.13e, and f), *Zoophycos* (Fig. 7.13g), *Planolites* (Fig. 7.13f), *Teichichnus* (Fig. 7.13e), *Palaeophycus*, *Asterosoma* (Fig. 7.13f), *Scolicia*, *Schaubcylindrichnus* (Fig. 7.13a–b and d) and *Thalassinoides* (Fig. 7.13c). The tiering structure is commonly complex, displaying multiple ichnoguilds. Although the degree of bioturbation and ichnodiversity are typically high, more impoverished suites may be present under oxygen-depleted conditions (Mángano *et al.*, 2005a). In addition, the scarcity of sandstone interbeds may have inhibited preservation and visibility of biogenic structures in the field.

7.1.9 SHELF

The shelf extends from the storm wave base to the slope break. Therefore, suspension-fallout sedimentation is the dominant process and bioturbated mudstone is the typical facies. Locally, thin normally graded siltstone layers, representing storm-induced turbidites, may occur.

Shelf deposits are typically pervasively bioturbated, and feeding and grazing traces of deposit feeders dominate, illustrating the *Zoophycos* ichnofacies (MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001). Typical components are *Zoophycos*, *Chondrites*, and *Phycosiphon*. *Trichichnus* and *Planolites* may also be present. Ichnofabrics tend to be dominated by deep-tier structures that commonly obliterate shallowly emplaced biogenic structures. However, under certain conditions, the shelf may lie within the oxygen minimum zone and, therefore, deposits may be scarcely bioturbated or even totally unburrowed. In the latter case, parallel laminated black shales represent the typical facies (e.g. Buatois *et al.*, 2006a; Angulo and Buatois, 2009).

7.2 TIDE-DOMINATED SHALLOW MARINE

Our present knowledge of the ichnology of tidal depositional systems lags behind that of wave-dominated environments. However, a number of contributions have outlined some of the most relevant characteristics of ichnofaunas from tidal-flat, subtidal-sandbar complexes and tidal dunes (e.g. Mángano and Buatois, 1999b; Mángano *et al.*, 2002a; Desjardins *et al.*, 2010a). While wave-dominated systems display a clear onshore–offshore trend in energy conditions (see Section 7.1), the energy gradient in tide-dominated shallow-marine environments is not straightforward (Yoshida *et al.*, 2007).

Despite all these complexities, Klein (1971, 1977) proposed a facies model for tide-dominated shorelines based on the integration of observations from modern and ancient deposits. In this model, tide-dominated shorelines are subdivided into a supratidal region, the upper-, middle-, and lower intertidal zones, and the subtidal area (see summary in Dalrymple, 1992). Within this setting, tidal energy increases seaward reaching a maximum in the proximal-subtidal zone and then decreases towards the distal shelf. Accordingly, tidal flats in general coarsen seaward, in contrast to wave-dominated shorelines that coarsen landward. Therefore, a typical tidal-flat profile in a landward direction comprises a lower-intertidal sand flat, a middle-intertidal mixed (sand and mud) flat, and an upper-intertidal mud flat. As a result, many tide-dominated shorelines are represented by muddy coasts (Wang *et al.*, 2002). Landward of the mud flat, supratidal salt marshes are typically present under temperate conditions, while mangroves may occur in tropical to subtropical settings (see Section 8.1.2). The subtidal zone is present seaward of the sand flat.

The intertidal zone represents a harsh ecosystem where marine organisms often approach the survival boundaries of

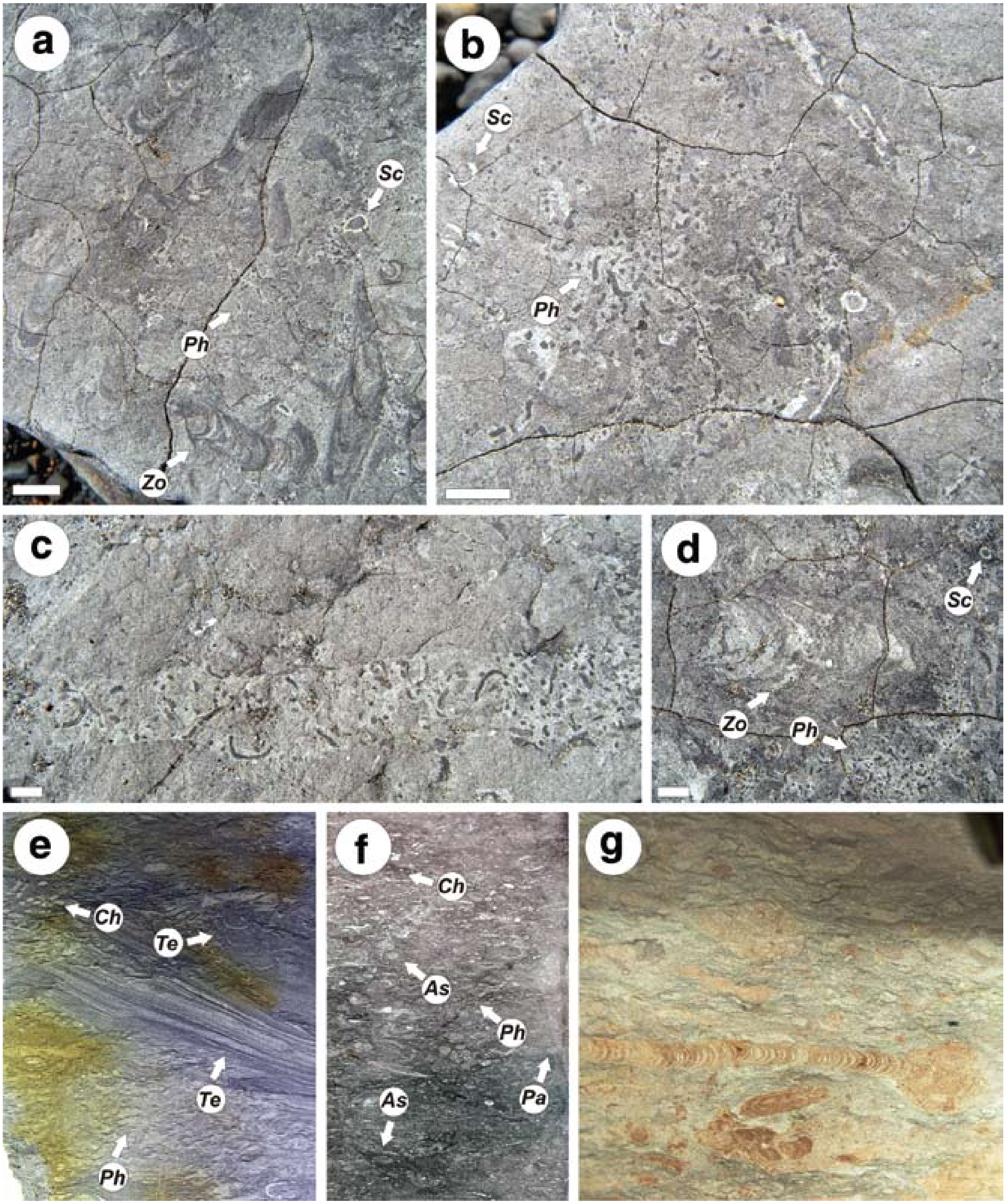

Figure 7.13 Ichnofaunas from lower-offshore deposits. (a) Bedding-plane surface view of intensely bioturbated deposits containing *Phycosiphon incertum* (*Ph*), *Zoophycos* isp. (*Zo*), and *Schaubcylindrichnus freyi* (*Sc*). Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (b) Close-up showing *Phycosiphon incertum* (*Ph*) and *Schaubcylindrichnus freyi* (*Sc*). Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (c) *Thalassinoides* isp. reworked by *Phycosiphon incertum*. Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (d) Close-up of intensely bioturbated deposits with *Phycosiphon incertum* (*Ph*), *Zoophycos* isp. (*Zo*), and *Schaubcylindrichnus freyi* (*Sc*). Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (e) Evenly distributed *Phycosiphon* (*Ph*) cross-cut by *Chondrites* (*Ch*) and *Teichichnus* (*Te*). Note longitudinal view of *Teichichnus* spreiten that may be confused with primary sedimentary lamination. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al*. (2011). (f) Intensely bioturbated deposits dominated by distinctive deep-tier *Chondrites* isp. (*Ch*). Shallow-tier *Asterosoma* isp. (*As*), *Phycosiphon incertum* (*Ph*), and *Planolites* isp. (*Pl*) form the background ichnofabric. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (g) Deep-tier *Zoophycos* isp. overprinted on a background ichnofabric. Lower Cretaceous, Muderong Shale Formation, Pluto Field, Carnavon Basin, offshore northwestern Australia. Core width is 10 cm.

their tolerance range to environmental extremes. Only a very few species are able to inhabit the entire tidal range (Reise, 1985). Zonational distribution of organisms is, therefore, the rule. Accordingly, different animal communities live in different areas within the tidal flat, where various environmental parameters differ substantially. Although tidal flats are primarily a marine habitat, they are subject to the extremes of terrestrial climate, heating, frost, desiccation, and rain (Reise, 1985). Temperature, time of exposure to subaerial conditions, salinity, hydrodynamic energy, and substrate are effective limiting factors. In the upper-intertidal zone, environmental conditions are not only more extreme; high temporal instability and unpredictability resulting in a decrease in species diversity are the norm. Physical factors, such as heating, frost, and water loss, play a crucial role in benthic communities. In general, biological diversity and biomass decrease toward the level of high tide (Newell, 1979; Reise, 1985). Although primary production by benthic microalgae increases in a landward direction, benthic consumers do not show a corresponding increase, most likely due to the difficulties for marine organisms to adapt to prolonged low-tide emersion (Reise, 1985).

Periodic emersions and submersions of the intertidal zone are matched by periodic fluctuations in salinity. In addition, seasonal rains and drainage from the continent strongly control the salinity and position of the water table. Changes in salinity, together with subaerial exposure and temperature, are more drastic in the upper-intertidal area, diminishing towards the lower-intertidal zone (Newell, 1979; Reise, 1985). In general, euryhaline species tend to be more abundant in the upper-intertidal zone (Newell, 1979). Complex hydrological conditions of the tidal flat promote particular behavioral strategies for protection, such as infaunalization. Inhabiting a burrow or temporary refuge in the sediment is an effective strategy in avoiding salinity variations (see Section 6.1.4). In low-energy settings, close to the low-water mark, surface salinity changes have little effect on the salinity of interstitial water below a depth of about 2 cm (Sanders *et al.*, 1965; Johnson, 1967).

Many organisms of the intertidal zone have developed biological rhythms (e.g. circa-tidal and circa-semilunar rhythms) of vertical or horizontal migration controlled by tide cyclicity (Palmer, 1995). Many species (e.g. the modern crab *Sesarma reticulatum*) hide in their burrows during low tide and are active during high tide (Palmer, 1967, 1995; Seiple, 1981). Horizontal migration is another strategy to minimize the dramatic salinity shifts in the upper-intertidal zone. For example, the modern predator isopod *Eurydice pulchra* lives buried in the sand flat during emersion, but rises into the water column with flood tides to swim at the water's edge and feed on epifauna, infauna, and debris. Subsequently, it retreats seaward with ebb tide and reburies itself for protection (Warman *et al.*, 1991). Marine invertebrate surface activity on the tidal flat tends to be more intense during high tide (Vader, 1964; Pieńkowski, 1983). In contrast, many semi-terrestrial and terrestrial animals (e.g. terrestrial crabs and the modern intertidal beetle *Thalassotrechus barbarae*) typically display a peak of activity during low-tide emersions (Palmer, 1995). Other adaptations to stressful salinity conditions involve protection by organic substances (e.g. mucus) and osmoregulation (Kinne, 1964). Some animals combine several strategies for better protection. For example, the modern *Corophium* is a good osmoregulator and a well-known burrower that can tolerate salinities between 2‰ and 47‰.

In contrast to the more stressful conditions of the upper-intertidal zone, lower-intertidal invertebrate communities resemble contiguous communities that inhabit environments below the fair-weather wave base (Schäfer, 1972; Reise, 1985; Swinbanks and Murray, 1981). The higher predictability of the middle- to lower-intertidal zones results in high species diversity containing species that are particularly adapted to utilize the resources of specific microhabitats (Sanders, 1968, 1969; Slobodkin and Sanders, 1969).

An integrated ichnological and sedimentological model has been proposed for tidal flats and related settings (Mángano and Buatois, 2004a) (Figs. 7.14 and 7.15) (Box 7.2). This model attempts to address patterns of distribution of biogenic structures in tide-dominated shorelines which, albeit sheltered, developed under fully or near-fully marine salinity conditions. Therefore, the model does not address ichnofaunas from tidal flats formed in more restricted, marginal-marine settings, such as estuaries or interdistributary bays, which are typically of lower diversity in brackish-water environments or contain freshwater trace fossils in the case of fluvio-estuarine transitions (see Chapter 8). Although the early observations were based on Paleozoic outcrops (Mángano and Buatois, 1999b; Mángano *et al.*, 2002a), the model was subsequently expanded to encompass the rest of the Phanerozoic (Mángano and Buatois, 2004a).

The ichnofacies gradient in tide-dominated shorelines is opposite to that in wave-dominated shoreface environments. As overall tidal energy increases from supratidal to subtidal settings, the *Skolithos* ichnofacies tends to occur seaward of the *Cruziana* ichnofacies (Mángano *et al.*, 2002a). This shoreward decrease of energy parallels a decrease in oxygenation, sand content, amount of organic particles in suspension, and mobility of the substrate. This gradient is consistent with information from modern tide-dominated environments, where the highest faunal diversity is present around mid-tide level (Beukema, 1976). In fact, similar ichnological trends have been detected in modern tidal flats (Bajard, 1966; Howard and Dorjes, 1972; Swinbanks and Murray, 1981; Ghare and Badve, 1984; Gerdes *et al.*, 1985; Frey *et al.*, 1987a, b; Aitken *et al.*, 1988; Larsonneur, 1994). For example, Swinbanks and Murray (1981) recognized five zones in the tidal flats of British Columbia, each characterized by different associations of biogenic structures. Similar zonations have been established in tidal flats of South Korea (Frey *et al.*, 1987a, b) (Box 7.3).

7.2.1 SUPRATIDAL MARSH AND MANGROVES

The supratidal area may be vegetated forming salt marshes or mangroves, depending on the predominant climatic conditions (see Section 8.1.2). Sporadically the supratidal zone may be affected by storm surges (Wang *et al.*, 2002). In supratidal

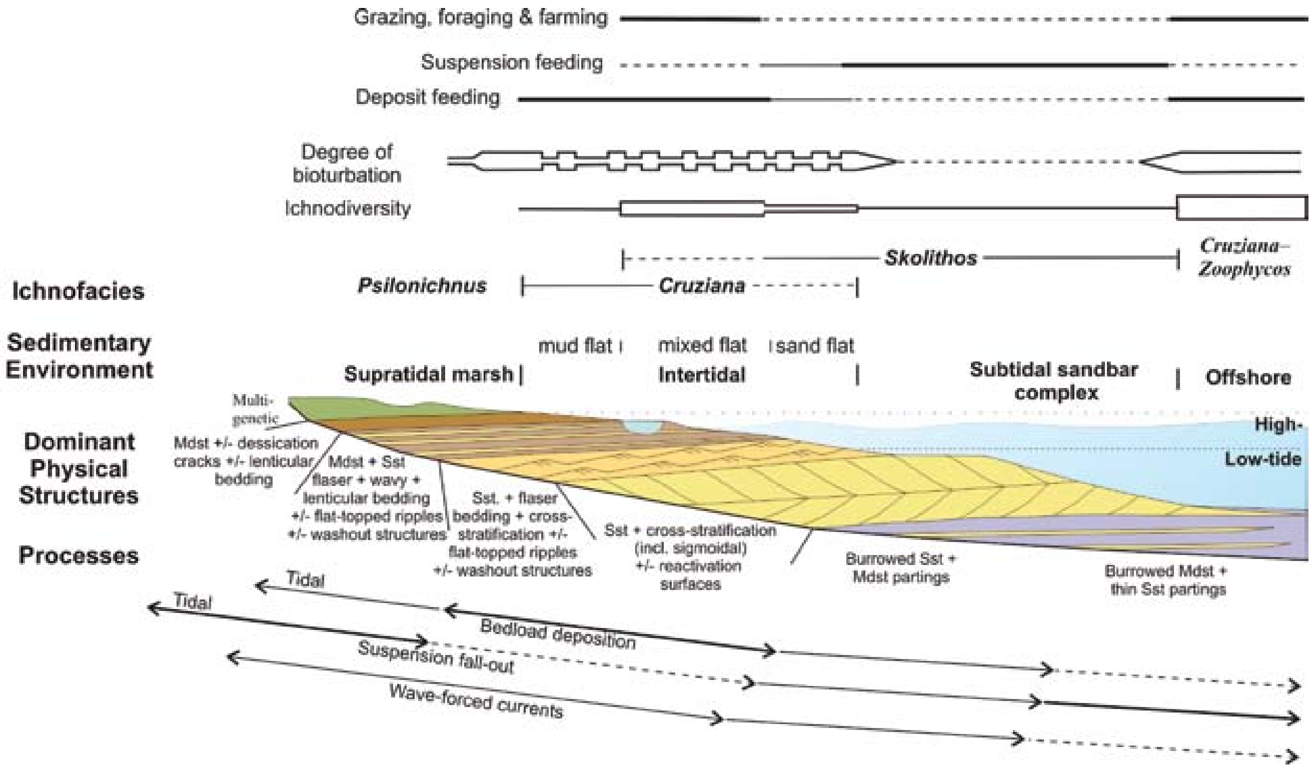

Figure 7.14 Ichnological and sedimentological aspects along a tide-dominated depositional profile. High intensity of bioturbation in supratidal areas is due to plant root traces. Irregular pattern of intensity of bioturbation in the tidal flat reflects spatial heterogeneity. Distribution of ichnofacies and depositional processes based on Mángano and Buatois (1999b, 2004a).

Box 7.3 Ichnology of modern tidal flats in South Korea

Extensive macrotidal flats near the mouth of the Yellow River, in South Korea, span from the shore to approximately 4 km seaward. Analysis of biogenic structures across these low-energy tidal flats allows recognition of ichnofaunal gradients across a tide-dominated depositional profile. Three different ichnocoenosis (brachyuran, molluscan, and holothurian assemblages) have been distinguished. The brachyuran ichnocoenose occurs from 0 to 900 m from the shore, in the muddiest, most landward reaches of the tidal flat. It is dominated by dwelling, locomotion, and grazing traces of crabs, with secondary presence of gastropod locomotion traces and polychaete dwelling traces. The molluscan ichnocoenose is present from 900 to 2100 m from the shore, in mid-flat deposits consisting of sandy and clayey silt. It is dominated by dwelling traces of bivalves and locomotion traces of gastropods, with subordinate occurrences of dwelling traces of polychaetes and grazing and locomotion traces of crabs. The holothurian ichnocoenose is present from 2100 to more than 3900 m from the shore, corresponding to the sandiest, most seaward end of the tidal flat. This ichnocoenose is dominated by feeding and grazing traces of synaptid holothurians; gastropod locomotion traces and bivalve dwelling structures are also present. All the ichnocoenoses belong to the *Cruziana* ichnofacies, demonstrating the presence of this archetypal association in tidal flats.

Reference: Frey *et al*. (1987a, b).

deposits, the sedimentary fabric is commonly obliterated by root traces. The cordgrass *Spartina* is by far the most widespread plant in many supratidal marsh settings, and its root traces are pervasive (e.g. Edwards and Frey, 1977; Basan and Frey, 1977; Pomeroy *et al*., 1981; Montague *et al*., 1981). In mangroves, root networks of *Avicennia*, *Rhizopora*, and *Sonneratia* are extremely widespread (Cadée, 1998). Animal traces include elements of the *Psilonichnus* ichnofacies (Frey and Pemberton, 1987). Gastropods and crustaceans (mainly crabs) are among the most important marine representatives. The supratidal zone grades landwards into a wide variety of terrestrial environments characterized by different trace-fossil assemblages that are mostly included in the *Scoyenia* and *Coprinisphaera* ichnofacies, being insects the most important tracemakers (Buatois and Mángano, 1995b; Genise *et al*., 2000) (see Section 7.1.1). Vertebrates, mostly mammals, reptiles and birds, also produce a wide variety of structures (Frey and Pemberton, 1986).

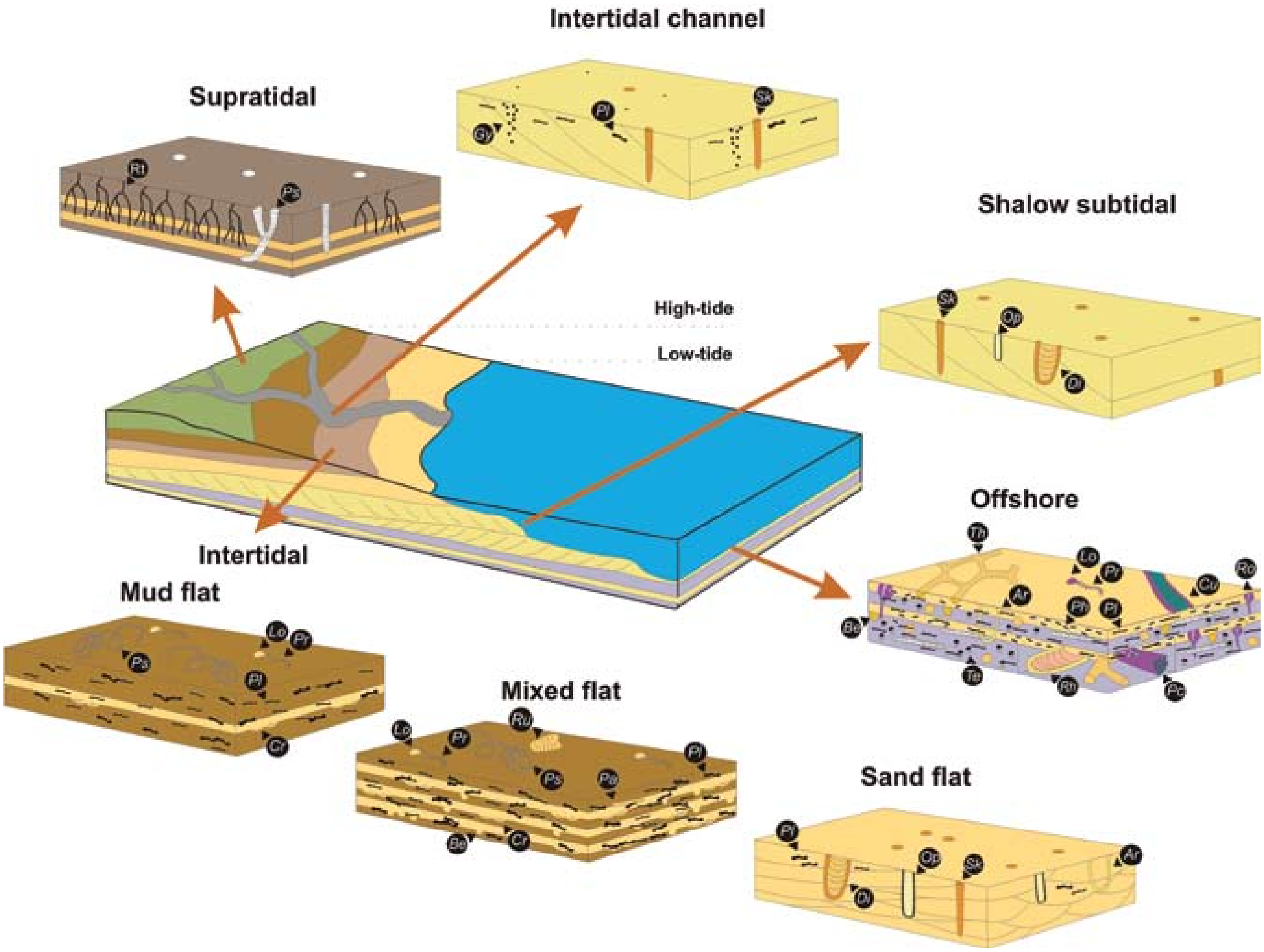

Figure 7.15 Schematic reconstruction of trace-fossil distribution in tide-dominated shallow-marine environments. The supratidal marsh may be intensely bioturbated by root traces (Rt). *Psilonichnus* (*Ps*) may be present also. Deposit-feeder traces, such as *Planolites* (*Pl*), *Psammichnites* (*Ps*), *Cruziana* (*Cr*), *Protovirgularia* (*Pr*), and *Lockeia* (*Lo*) tend to dominate in the mud flat. The mixed flat is similar to the mud flat, but other ichnotaxa may be added mostly along mudstone–sandstone interfaces, including *Rusophycus* (*Ru*), *Palaeophycus* (*Pa*), and *Bergaueria* (*Be*). The sand flat is highly variable depending on the tidal regime. *Ophiomorpha* (*Op*), *Arenicolites* (*Ar*), *Diplocraterion* (*Di*), *Skolithos* (*Sk*), and *Planolites* (*Pl*) are common. Associated intertidal channel deposits are less bioturbated and display less ichnodiversity, *Planolites* (*Pl*), *Gyrolithes* (*Gy*), and *Skolithos* (*Sk*) being common forms. Shallow-subtidal sandbodies typically contain vertical burrows, such as *Ophiomorpha* (*Op*), *Diplocraterion* (*Di*), and *Arenicolites* (*Ar*). These sandbodies tend to grade seaward into fine-grained offshore deposits containing diverse ichnofaunas. Typical components are *Arenicolites* (*Ar*), *Bergaueria* (*Be*), *Planolites* (*Pl*), *Curvolithus* (*Cu*), *Protovirgularia* (*Pr*), *Lockeia* (*Lo*), *Phycodes* (*Pc*), *Thalassinoides* (*Th*), *Rhizocorallium* (*Rh*), *Rosselia* (*Ro*), *Teichichnus* (*Te*), and *Phycosiphon* (*Ph*).

7.2.2 MUD FLAT

The upper zones of the tidal flat, referred to as the mud flat, are dominated by deposition of fine-grained suspended sediment. Mud deposition is also promoted by clay flocculation and biodeposition in the form of the production of fecal pellets and pseudofeces (de Boer, 1998; Augustinus, 2002; Potter *et al.*, 2005). Mud-flat deposits consist of laminated or massive mudstone with rare siltstone and very fine-grained sandstone interbeds and interlaminae. Lenticular bedding is the dominant bedding style. Scarcity of sandstone layers commonly precludes preservation of biogenic structures. Discrete trace fossils are relatively rare, and an indistinct mottled texture (most likely *Planolites*) is common instead. However, interface trace fossils of the *Cruziana* ichnofacies, such as *Cruziana*, *Rusophycus*, *Psammichnites*, *Lockeia*, and *Protovirgularia*, can be preserved in the sporadic sandstone intercalations (e.g. Mángano *et al.*, 2002a). These occurrences may record either a wide environmental range of the producers, or short-term incursions into this zone. High-density trace-fossil assemblages produced by vagile organisms most likely reflect landward migrations from the lower-intertidal zone, rather than upper-intertidal inhabitants (Mángano *et al.*, 2002a). These migrations are probably regulated by tidal cyclicity in connection with the search for food. Also, simple grazing trails, such as *Helminthopsis* and *Helminthoidichnites*, may occur in connection with microbial mats. Vertebrate trackways are also common in tide-dominated shorelines, particularly in supratidal to upper-intertidal zones. Vertebrate trackway assemblages in tidal flats typically illustrate some of the ichnocoenoses of the *Brontopodus* and *Batrachichnus* ichnofacies (Hunt and Lucas, 2007).

Box 7.2 Ichnology of Lower to Middle Cambrian tide-dominated shallow-marine deposits of northwest Argentina

The Campanario Formation of the upper Lower to Middle Cambrian Mesón Group of northwest Argentina records deposition in tide-dominated shallow-marine environments characterized by extensive tidal-flat areas flanked seawards by subtidal-sandbar complexes. Shallow-subtidal and intertidal sand-flat deposits are dominated by vertical domiciles of suspension feeders and passive predators, such as *Skolithos linearis*, *Arenicolites* isp., and *Diplocraterion parallelum*, illustrating the *Skolithos* ichnofacies. Sand-flat deposits also contain high-density occurrences of the ichnogenus *Syringomorpha*, commonly forming monospecific assemblages. Clusters of *Rusophycus leifeirikssoni* are locally present. Although vertical burrows (*Skolithos linearis*, *Syringomorpha nilssoni*) are present in the mixed-flat facies, the dominant form is *Rusophycus leifeirikssoni*. Other ichnotaxa include *Cruziana problematica*, *Rusophycus carbonarius*, large *Rusophycus* isp., *Diplichnites* isp., *Planolites* isp., *Palaeophycus tubularis*, *Helminthoidichnites tenuis*, and *Bergaueria* cf. *B. perata*. In contrast to the sand flat, the mixed flat is dominated by horizontal feeding, locomotion and resting trace fossils, recording a relatively low-diversity *Cruziana* ichnofacies. Trace fossils are rare in the mud-flat deposits, mostly represented by *Planolites* isp. and indistinct mottling. The six ichnoguilds (*Cruziana problematica*, *Palaeophycus*, *Bergaueria*, *Rusophycus leifeirikssoni*, *Syringomorpha*, and *Skolithos*) defined show a preferential palaeoenvironmental distribution following proximal–distal trends (Fig. 7.16). Although there is some superimposition, deep-tier ichnoguilds tend to occur in the higher-energy, seaward distal portions (i.e. shallow-subtidal to intertidal transition and sand flat). Middle- and shallow-tier ichnoguilds are dominant in the moderate- to low-energy, proximal regions (i.e. mixed flat). This resultant pattern of distribution of biogenic structures is shaped by the interplay of key environmental parameters (hydrodynamic energy, substrate and food supply) overprinted by a strong taphonomic control.

Reference: Mángano and Buatois (2004b).

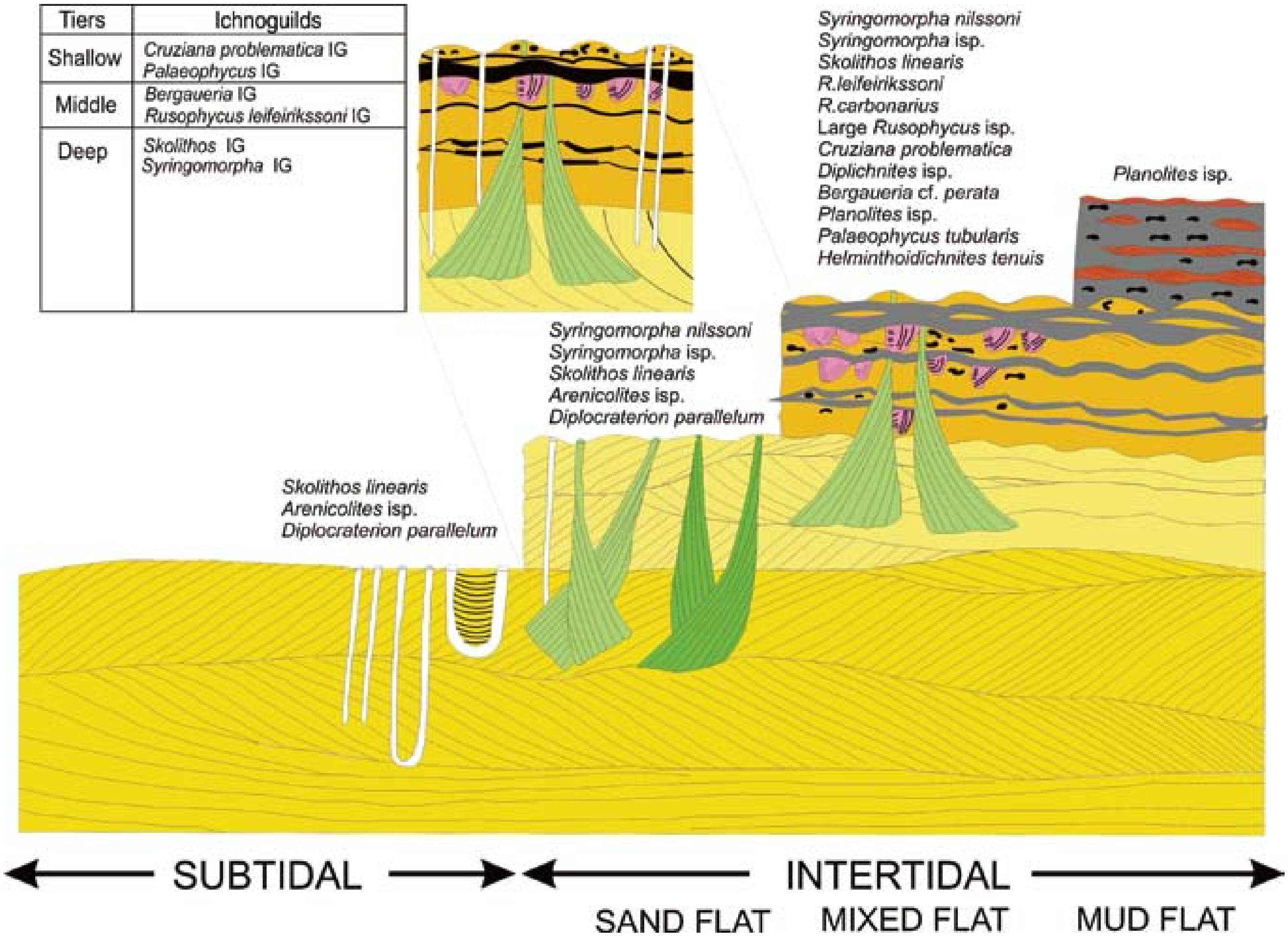

Figure 7.16 Ichnological and sedimentological model of the Campanario Formation of the Lower to Middle Cambrian Mesón Group of northwest Argentina (after Mángano and Buatois, 2004b).

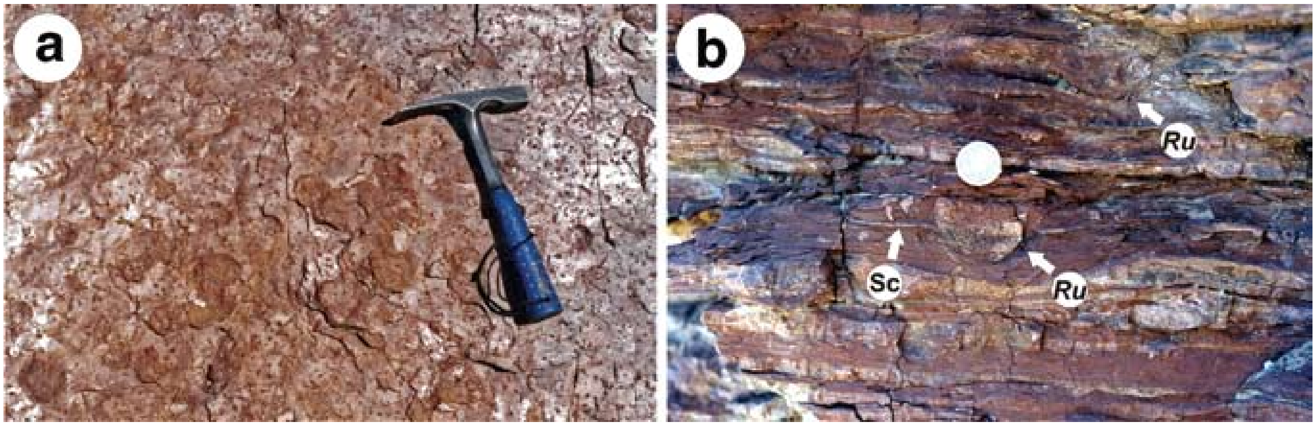

Figure 7.17 Invertebrate ichnofaunas from mixed-flat deposits from the Lower to Middle Cambrian Campanario Formation of the Mesón Group. See Mángano and Buatois (2004b). (a) Bedding plane view (top) of a cluster of *Rusophycus leifeirikssoni* in mixed-flat deposits. Angosto del Morro de Chucalezna, Quebrada de Huamahuaca, northwest Argentina. Length of hammer is 33.5 cm. (b) Cross-section view of *Rusophycus leifeirikssoni* (*Ru*) in mixed-flat deposits. Note associated synaeresis cracks (*Sc*). Angosto del Morro de Chucalezna, Quebrada de Huamahuaca, northwest Argentina. Coin is 2.3 cm.

7.2.3 MIXED FLAT

Middle-intertidal areas (mixed flat) are typified by sedimentation from traction alternating with fallout from suspension. Deposits consist of thinly interbedded wave- and current-ripple cross-laminated very fine-grained sandstone and massive or parallel-laminated mudstone. Heterolithic bedding is typical, mostly represented by flaser and wavy bedding. Wrinkle marks associated with relict troughs are locally common (e.g. Mángano *et al.*, 2002a). Flat-topped ripples and washout structures may occur. Elements of the *Cruziana* ichnofacies are characteristic of the mixed flat (Fig. 7.17a–b). Alternation of sandstone and mudstone layers enhances preservation of horizontal interface traces, such as those that typify the *Cruziana* ichnofacies. Common components are *Cruziana*, *Rusophycus*, *Psammichnites*, *Protovirgularia*, *Lockeia*, *Palaeophycus*, *Planolites*, *Helminthopsis*, *Helminthoidichnites*, and *Bergaueria*. Clusters of *Rusophycus* are common in lower Paleozoic tidal-flat deposits (Mángano and Buatois, 2004b) (Fig. 7.17a). Vertebrate trackways are commonly preserved in sandy layers of the middle-intertidal zone. Mesozoic examples include spectacular dinosaur tracks, commonly forming megatracksites (e.g. Lockley *et al.*, 1992; Avanzini *et al.*, 2006) (Fig. 7.18a–d).

7.2.4 SAND FLAT

Sedimentation in the lower zones of the tidal flat, referred to as the sand flat, is dominated by bedload traction of sand-sized sediment. As is the case of the lower shoreface in wave-dominated shorelines (MacEachern and Pemberton, 1992), the sand flat is the most variable intertidal zone in terms of both sedimentary facies and trace-fossil content. Whereas the character of deposits in the lower shoreface mostly depends on the intensity and frequency of storms (see Section 7.1.5), those of the lower tidal flat are essentially controlled by the intensity of tidal currents (Mángano and Buatois, 2004a). Macrotidal and megatidal regimes are characterized by high current speeds and, therefore, migration of large-scale bedforms (i.e. two-dimensional and three-dimensional dunes) is the dominant process (Dalrymple, 1992; Dalrymple and Rhodes, 1995; Boyd *et al.*, 2006). Deposits consist of thick-bedded, through and planar cross-bedded coarse- to fine-grained sandstone. Medium- to very fine-grained sandstone with upper-flow regime horizontal planar parallel lamination and rare current ripples also occurs in macrotidal and megatidal regimes (Dalrymple *et al.*, 1990; Dalrymple, 1992; Dalrymple and Choi, 2007). Under macrotidal and megatidal conditions, the lower-intertidal zone is very difficult to distinguish from subtidal areas. High energy and rapidly migrating bedforms generally preclude the establishment of a mobile epifauna and shallow infauna, inhibiting development of the *Cruziana* ichnofacies. Bioturbation typically consists of vertical burrows of suspension feeders or passive predators, such as *Skolithos* (Fig. 7.19a), *Ophiomorpha*, *Arenicolites* (Fig. 7.19b), and *Diplocraterion* (Fig. 7.19c), representing the *Skolithos* ichnofacies. In Cambrian examples, the ichnogenus *Syringomorpha* may occur in high densities (Fig. 7.19d). Assemblages reflect short-term colonization windows along reactivation surfaces (Pollard *et al.*, 1993; Mángano *et al.*, 1996b; Mángano and Buatois, 2004b). If mud drapes formed during slack water are preserved, they may contain *Planolites*.

Under tidal currents of lower intensity, the migrating bedforms are small current ripples. Deposits consist of current-ripple cross-laminated fine- to very-fine grained sandstone. Flat-topped ripples, washout structures, and wrinkle marks are common. Low energy coupled with short periods of subaerial exposure allows development of a diverse resident fauna. As a result, these tidal flats contain high-diversity assemblages of the *Cruziana* ichnofacies (Mángano et al., 2002a; Mángano and Buatois, 2004a). A wide variety of ethological groups and trophic types are represented. Common elements are *Cruziana* (Fig. 7.20a), *Rusophycus*, *Asteriacites* (Fig. 7.20a), *Pentichnus*, *Psammichnites*, *Curvolithus* (Fig. 7.20b), *Nereites*

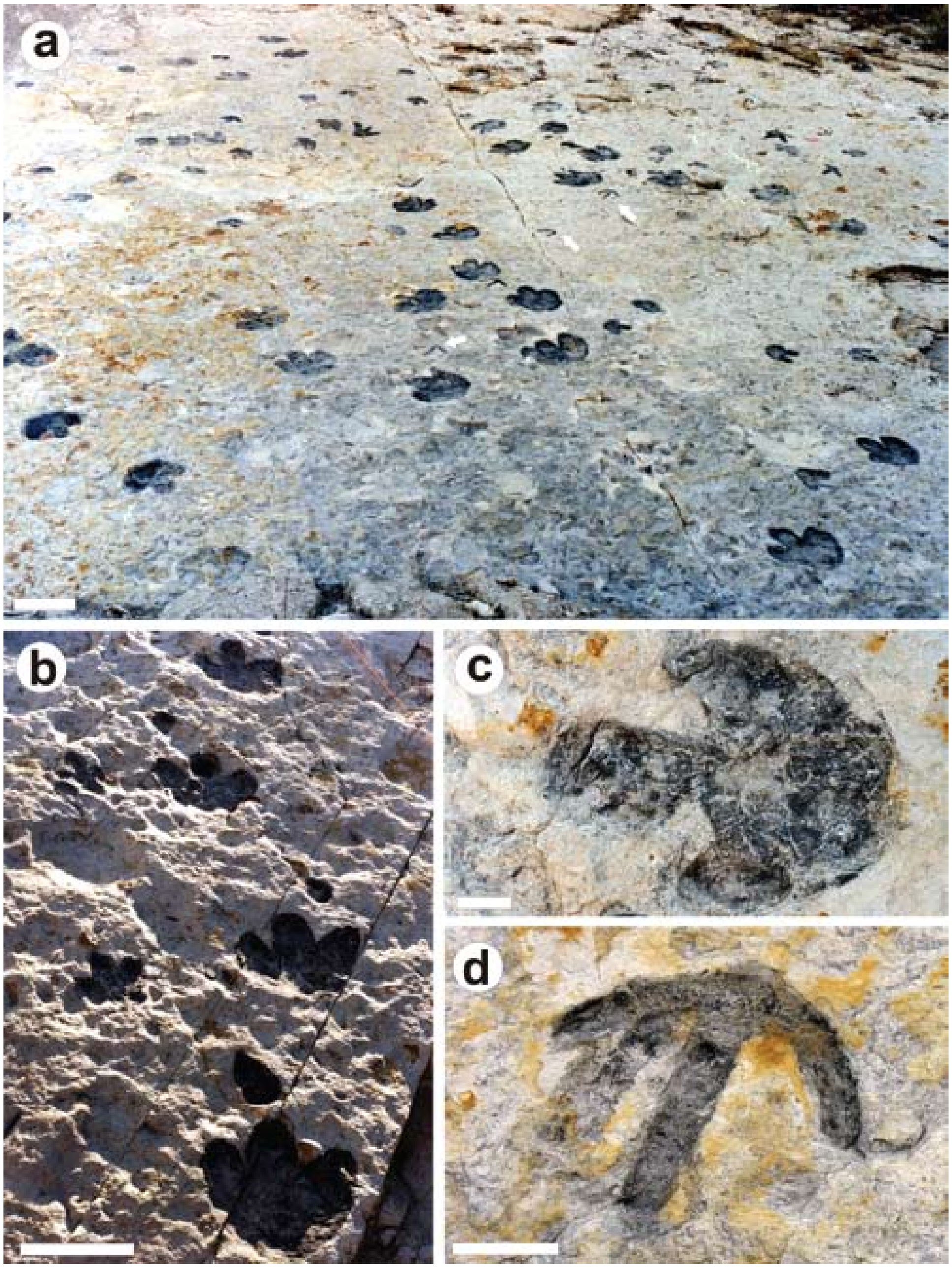

Figure 7.18 Dinosaur tracks in tidal-flat deposits. Lower Cretaceous, Dakota Group, Alameda Avenue, west of Denver, Colorado, United States. (a) General view of a sandstone top with large ornithopod trackways (*Caririchnium leonardii*) and small theropod trackways (*Magnoavipes loewi*, arrowed). Scale bar is 50 cm. (b) The ornithopod trackway *Caririchnium leonardii*. Scale bar is 50 cm. (c) Close up of an ornithopod track (*Caririchnium leonardii*). Scale bar is 5 cm. (d) Close up of a theropod track (*Magnoavipes loewi*). Scale bar is 5 cm. See Lockley (1987, 2001, 2003) and Lockley *et al*. (2001).

(Fig. 7.20c), *Lockeia* (Fig. 7.20d), *Protovirgularia* (Fig. 7.20e–f), *Palaeophycus*, and *Planolites*.

7.2.5 TIDAL CHANNELS AND CREEKS

Tidal-flat deposits are commonly dissected by a network of meandering tidal channels and creeks that migrate across the intertidal zone, producing lateral accretion in point bars (Reineck, 1958; Bridges and Leeder, 1976; Weimer *et al*., 1981; de Mowbray, 1983; Thomas *et al*., 1987; Dalrymple, 1992; Gingras *et al*., 1999b). This process results in the formation of inclined heterolithic stratification (Thomas *et al*., 1987). In the muddy upper-intertidal zones, channels are small to medium size, but in the lower sandy areas, they tend to coalesce forming wider and deeper channels (Dalrymple, 1992). The degree of bioturbation is lower in the point bars than in tidal flats, most likely reflecting higher rates of sedimentation along unstable channel margins (cf. Gingras *et al*. 1999b; Mángano *et al*. 2002a) (see Section 8.1.2).

7.2.6 SUBTIDAL SANDBARS AND TIDAL DUNES

The subtidal zone of tide-dominated shallow-marine environments is characterized by maximum energy with high-current velocities (Dalrymple, 1992). Large-scale bedforms, such as dunes and compound dunes, migrate across the subtidal areas, forming sandbars in the form of sheets and ridges. Deposits

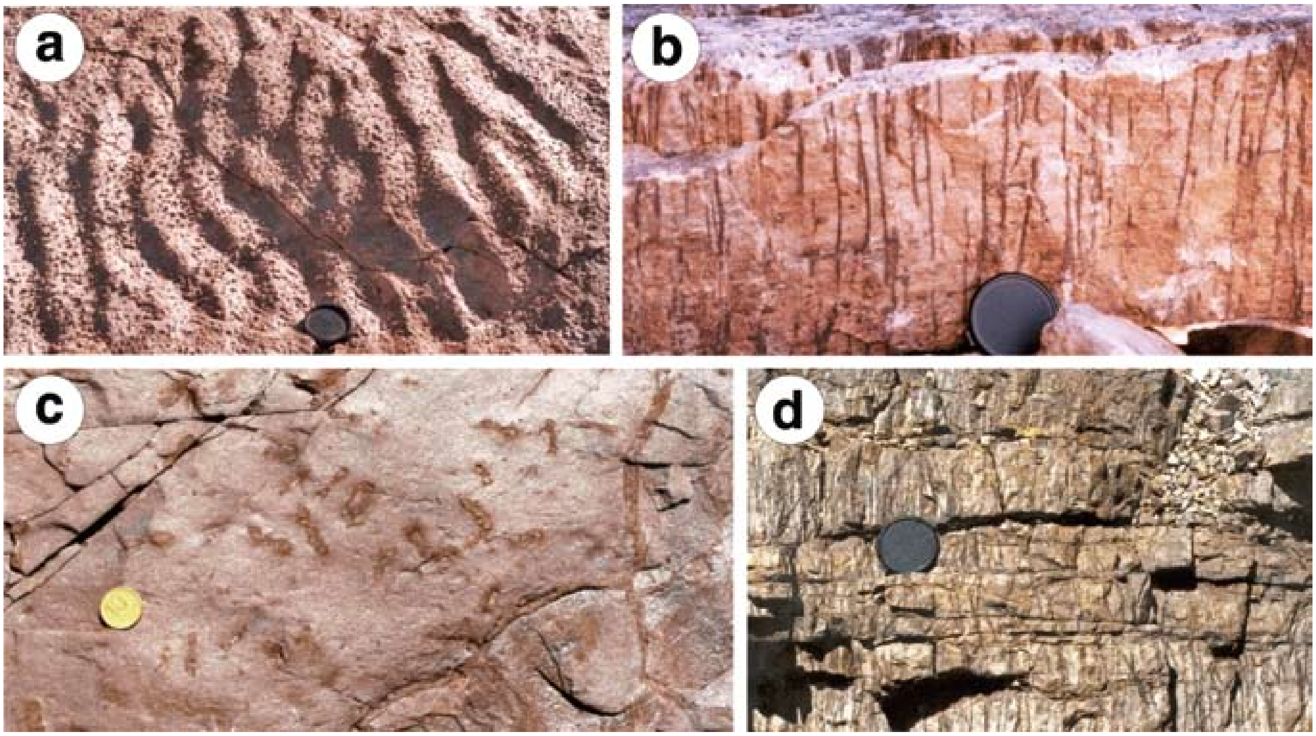

Figure 7.19 Ichnofaunas from high-energy sand-flat deposits from the Lower to Middle Cambrian Campanario Formation of the Mesón Group. See Mángano and Buatois (2004b). (a) Bedding-plane view of a high-density assemblage of *Skolithos linearis* (pipe rock) at a rippled sandstone surface. Angosto de Perchel, Quebrada de Huamahuaca, northwest Argentina. Lens cap is 5.5 cm. (b) Deep *Arenicolites* isp. Angosto de Perchel, Quebrada de Huamahuaca, northwest Argentina. Lens cap is 5.5 cm. (c) General view of the top of a rippled sandstone showing high density of *Diplocraterion parallelum*. Note associated cracks. Quebrada de Moya, northwest Argentina. Coin is 1.8 cm. (d) *Syringomorpha* isp. pipe rock. Angosto del Morro de Chucalezna, Quebrada de Huamahuaca, northwest Argentina. Lens cap is 5.5 cm.

consist of erosionally based, laterally extensive, well-sorted, planar to trough cross-stratified coarse- to fine-grained sandstone. Reactivation surfaces are common, while herringbone cross-stratification and mud drapes may be locally present. In modern subtidal areas, few benthic species are able to survive in zones of actively migrating bedforms (Wilson, 1982, 1986). Accordingly, faunal diversity increases toward areas with smaller bedforms, and in the outer regions where dunes are replaced by small ripples and increasing amounts of mud. Studies of marine benthic ecology also show that suspension feeding is the dominant trophic type in high-energy subtidal environments (Wilson, 1982).

As in the case of high-energy sand flats, vertical trace fossils of the *Skolithos* ichnofacies, such as *Arenicolites* (Fig. 7.21a and d), *Skolithos* (Fig. 7.21b–d) and *Diplocraterion*, are dominant, commonly extending down into the sediment from reactivation surfaces (e.g. Pollard *et al*., 1993; Desjardins *et al*., 2010a). The ichnogenus *Rosselia* (Fig. 7.21d) may occur as a response to prolonged periods of sandbar inactivity and suspended mud in the water column (Desjardins *et al*., 2010a). Vertical burrows are preferentially preserved in high-energy subenvironments, while shallow-tier horizontal traces have low preservation potential, providing a biased picture of the ecology of subtidal sandbars and dunes (Desjardins *et al*., 2010a). Feeding and locomotion traces of deposit feeders, such as *Teichichnus*, *Planolites*, and *Rusophycus*, tend to be preserved in those deposits formed at the toe of the subtidal sandbar complex (Desjardins *et al*., 2010a). Subtidal sandbars and tidal dunes grade seaward into lower-offshore or shelf muds, commonly characterized by the *Cruziana* or the *Zoophycos* ichnofacies.

7.3 MIXED TIDE- AND WAVE-INFLUENCED SHORELINES

While integrated sedimentological and ichnological models have been established for wave- and tide-dominated shorelines, our knowledge of intermediate cases in which both tides and waves influence deposition is much more limited. However, a growing literature on sedimentological aspects of modern mixed tide- and wave-influenced shorelines is beginning to accumulate (e.g. Short, 1991; Masselink and Short, 1993; Masselink and Hegge, 1995; Anthony and Orford, 2002; Yang *et al*., 2005, 2006, 2008a, b; Dashtgard *et al*., 2009, 2011). Still, no detailed ichnological accounts of these deposits have been produced and their recognition in the stratigraphic record remains a challenge. In addition, the distinction between tide- and wave-dominated systems gets further complicated because many systems show seasonal alternations of wave and tidal dominance. For example,

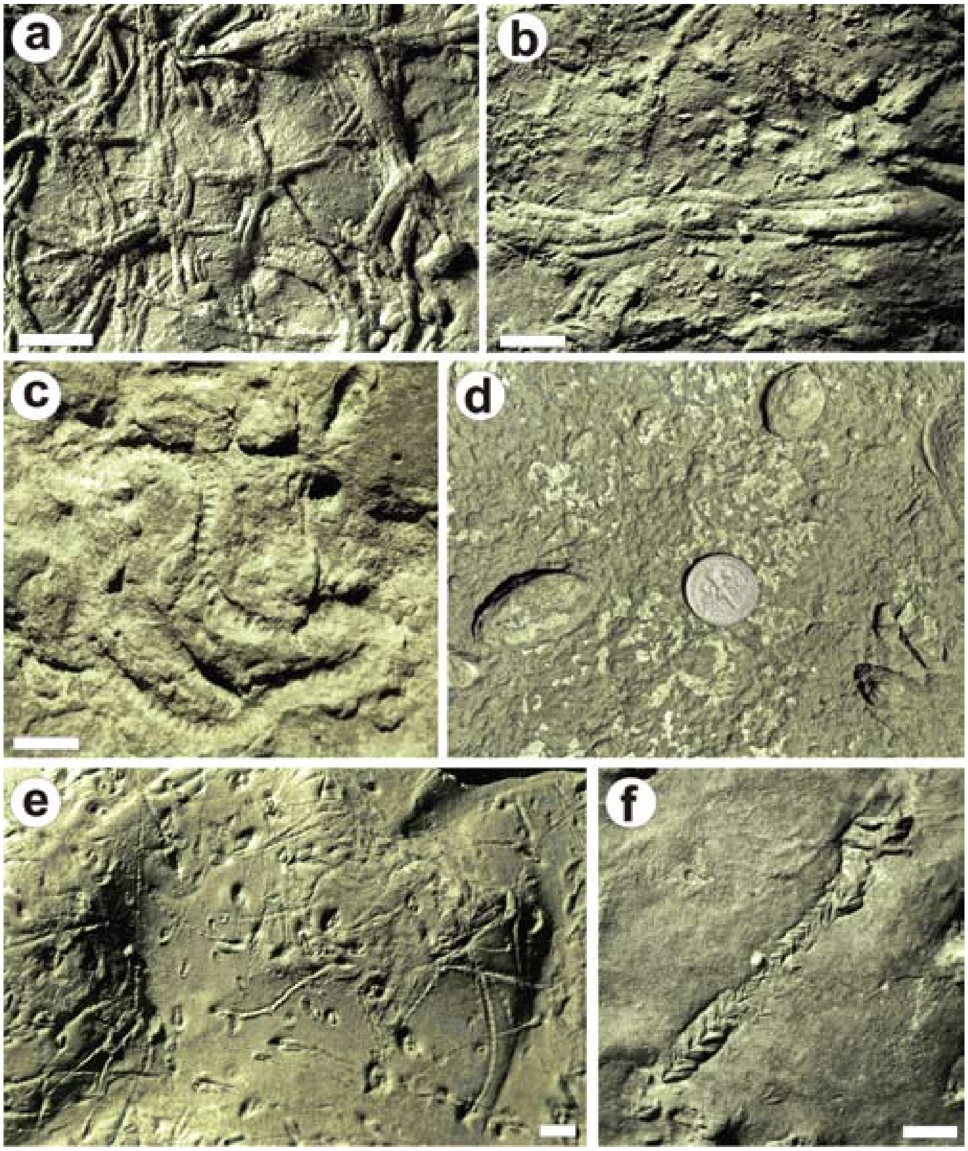

Figure 7.20 Ichnofaunas from low-energy sand-flat deposits in the Upper Carboniferous, Stull Shale of the Kanwaka Formation, Waverly fossil site, Kansas, central United States. See Mángano *et al.* (2002a). (a) Sandstone base showing *Asteriacites lumbricalis* displaying lateral repetition and high density of *Cruziana problematica*. (b) Sandstone top with *Curvolithus simplex*. (c) Sandstone top with *Nereites missouriensis*. (d) Base of sandstone bed containing *Lockeia siliquaria*. Coin is 1.8 cm. (e) Dense assemblage of *Protovirgularia rugosa* and associated resting traces (*Lockeia* isp.) on the upper surface of a sandstone bed. Note preservation as negative epireliefs in *Chevronichnus*-like fashion. (f) Base of sandstone layer containing *Protovirgularia bidirectionalis* display V-shaped markings with opposite directions meeting at a central point. Note that the direction of movement is from the center to the ends. All scale bars are 1 cm.

Yang *et al.* (2005) documented modern coastlines that alternate between tide dominated during summer and wave dominated during winter. Mixed tide- and wave-influenced shorelines can be subdivided into wave-dominated tidal flats (i.e. open-coast tidal flats) and tidal beaches (i.e. tidally modulated shorefaces), with the latter showing increased influence of wave processes (Boyd *et al.*, 1992; Yang *et al.*, 2005; Dashtgard *et al.*, 2009). In these mixed systems, storm sedimentation is tidally modulated (Yang *et al.*, 2008a).

7.3.1 WAVE-DOMINATED TIDAL FLATS

Wave-dominated tidal flats have been mostly described from the central west coast of Korea, which is relatively straight and macrotidal (Yang *et al.*, 2005, 2006, 2008a), in contrast to the typical tidal flats of the north and south west coast which occur in embayed coasts (Frey *et al.*, 1987a, b). In contrast to classic, more sheltered tidal flats (see Section 7.2), wave-dominated tidal flats only locally display mud flats and salt marshes, and typically fine seaward. The central west coast is tide dominated during summer and wave dominated during winter, with wind seasonality controlled by a monsoonal regime (Yang *et al.*, 2005).

In the locally developed inner mud flat, thin storm sand units form during winter and early spring, while mud accumulates during summer and fall. Bioturbation during the summer and fall intensely affects mud-flat deposits, including the winter and spring sandy layer, displaying a lam-scram pattern, but ichnodiversity levels are low (Yang *et al.*, 2008a). The shallower part of the sand flat is dominated by ripple-cross lamination and low-angle inclined lamination during the winter. Mud drapes may form during slack water in the spring. Vertical burrows, such as *Skolithos*, *Lingulichnus*, and *Siphonichnus*, are dominant, locally displaying moderate bioturbation intensities;

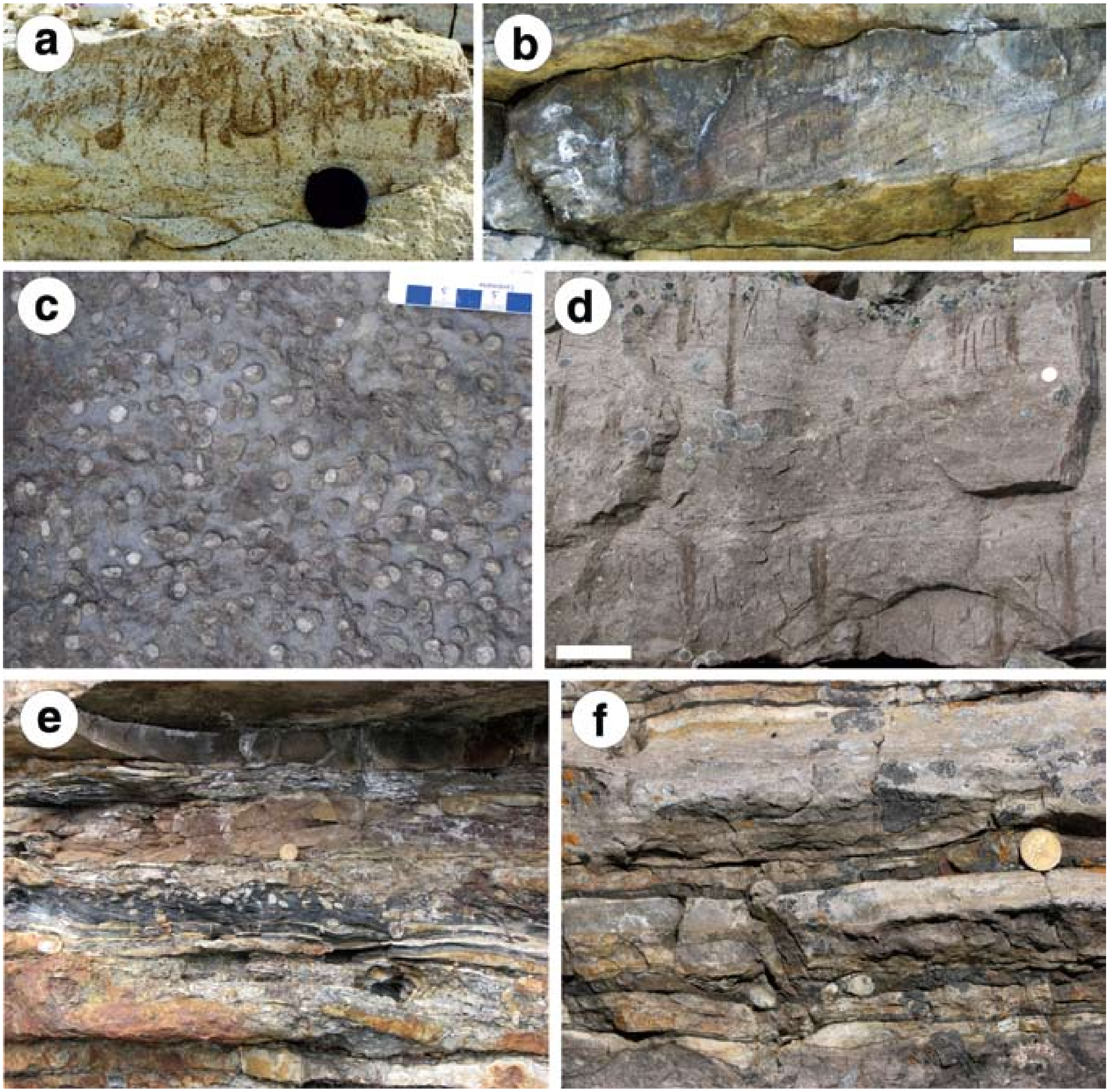

Figure 7.21 Ichnofaunas from subtidal-sandbar deposits. (a) *Arenicolites* isp. penetrating a medium-grained sandstone interpreted as a subtidal-sandbar deposit. Middle Cambrian, Flathead Formation, Absaroka Range, northwest Wyoming, north-central United States. Lens cap is 5.5 cm. (b) *Skolithos linearis* penetrating from a colonization surface at the foreset of a sandbar. Lower Cambrian, Fort Mountain Formation, Gog Group, Mount Assiniboine, Canadian Rockies, western Canada. Scale bar is 10 cm. See Desjardins *et al.* (2010a). (c) Bedding surface view of a high-density association of *Skolithos linearis* at the front of a subtidal sandbar. Lower Cambrian, Fort Mountain Formation, Gog Group, Mount Assiniboine, Canadian Rockies, western Canada. See Desjardins *et al.* (2010a). (d) *Rosselia* isp., *Skolithos linearis*, and *Arenicolites* isp. associated with various colonization surfaces in a subtidal sandbar. Lower Cambrian, Wiwaxi Peaks Member, St. Piran Formation, Gog Group, Larch Valley, Canadian Rockies, western Canada. Scale bar is 5 cm. See Desjardins *et al.* (2010a). (e) Moderately bioturbated subtidal sandbar-toe heterolithic deposits with *Planolites* and synaeresis cracks. Lower Cambrian, St. Piran Formation, Gog Group, Lake O'Hara, Canadian Rockies, western Canada. Coin is 2.6 cm. See Desjardins *et al.* (2010a). (f) Close up of subtidal sandbar-toe heterolithic deposits showing sparse *Planolites*. Lower Cambrian, St. Piran Formation, Gog Group, Lake O'Hara, Canadian Rockies, western Canada. Coin is 2.6 cm. See Desjardins *et al.* (2010a).

Macaronichnus may be present locally, as well as *Ophiomorpha* and *Thalassinoides*. Hummocky cross-stratification and parallel lamination are the dominant structures in the winter sandy beds of the middle and outer part of the sand flat. Bioturbation is extremely rare in the winter beds and typically restricted to sparse polychaete vertical burrows and escape traces. Landward migrating climbing ripples tend to characterize the spring interval, while summer layers are typified by wave-ripple cross-laminated sands and muds. Summer deposits are sparsely bioturbated, containing *Conichnus*, *Palaeophycus*, *Siphonichnus*, *Asterosoma*, and local high densities of *Macaronichnus*.

The overall intensity of bioturbation increases in a landward direction because of decreasing wave energy (Yang *et al*., 2005). However, bioturbation levels across the whole tidal flat are generally low as a result of high rates of sedimentation and episodic high-energy conditions (Yang *et al*., 2008a). On the other hand, a landward decrease in ichnodiversity, most likely as a result of increased duration of exposure, has been proposed. Also, the alternation of storms and fair-weather periods is conducive to a bimodal style of bioturbation characterized by unburrowed intra-storm mud drapes and more bioturbated fair-weather deposits. These authors noted that the bioturbation style in the lower sand flat is similar to that of the upper shoreface of wave-dominated shorelines. In addition, they suggested that the inner sand flat contains a mixed *Skolithos*–*Cruziana* ichnofacies, but of lower diversity than that of offshore environments.

The absence of further case studies prevents any attempt at generalization. However, it seems that ichnologically wave-dominated tidal flats share aspects of both wave-dominated shorefaces and tide-dominated tidal flats. The alternation of unburrowed or sparsely bioturbated intervals with intensely bioturbated units is typical of the former due to the effects of storms (Pemberton and Frey, 1984a). On the other hand, the intense bioturbation in the inner mud zone and the presence of a *Skolithos* ichnofacies seaward of an assemblage containing elements of the *Cruziana* ichnofacies is characteristic of typical tidal flats (Mángano and Buatois, 2004a). As a result of intense wave erosion on the high-tide beach face, the *Glossifungites* ichnofacies may occur, cross-cutting previously emplaced softground trace-fossil suites (Yang *et al*., 2009). Additional studies are necessary to delineate a set of criteria that allow recognition of wave-dominated tidal flats in the fossil record.

7.3.2 TIDAL BEACHES

Tidal beaches have been mostly documented from the central Queensland coast of Australia (Short, 1991; Masselink and Hegge, 1995), and more recently from Waterside Beach in the Bay of Fundy of Eastern Canada (Dashtgard *et al*., 2009). In contrast to wave-dominated shorefaces, sediments of tidal beaches deposited in water depths equivalent to the upper, middle, and lower shoreface are regularly subjected by different wave processes and, in the case of macrotidal and megatidal regimes, the shoreface may be exposed during low tides (Dashtgard *et al*., 2009). In contrast to tide-dominated tidal flats, tidal beaches show a seaward decrease in grain size.

Backshore deposits consist of eolian sand dunes and washover fan sands and gravels, and are characterized by elements of the *Psilonichnus* ichnofacies (Dashtgard *et al*., 2009). Foreshore deposits of tidal beaches are typically unburrowed and dominated by gravels and sands with subparallel to low-angle cross stratification formed due to swash and backwash processes in the upper-intertidal area; eolian processes may also play a role (Masselink and Hegge, 1995; Dashtgard *et al*., 2009). The upper shoreface corresponds to the middle-intertidal zone, and may contain both sand and gravel with through and planar cross-bedding as the dominant structures, as a result of swash and surf processes. Bioturbation is moderate and dominated by elements of the *Skolithos* ichnofacies (Dashtgard *et al*., 2009). The lower shoreface of tidal beaches corresponds to the lower-intertidal to shallow-subtidal zone, and is extremely variable with respect to grain size and physical sedimentary structures. It is essentially dominated by surf zone and shoaling wave processes (Masselink and Hegge, 1995). Fine-grained deposits consist of fine- and very fine-grained sand and silt with abundant oscillatory structures (e.g. hummocky cross-stratification, wave ripples). Coarse-grained deposits consist of medium-grained sand to gravel in which evidence of oscillation alternates with current-generated structures (e.g. trough and planar cross-bedding). Although the *Cruziana* ichnofacies dominates the lower shoreface of tidal beaches, its diversity is reduced and no elaborate grazing or feeding structures occur, illustrating the proximal subdivision of this ichnofacies (Dashtgard *et al*., 2009). The offshore in this type of system falls within the subtidal zone, and is controlled by shoaling wave processes (Masselink and Hegge, 1995). Deposits are fine-grained, mostly consisting of parallel-laminated silt and sand, being characterized by a proximal *Cruziana* ichnofacies (Dashtgard *et al*., 2009).

As in the case of the wave-dominated tidal flats, the scarcity of case studies prevents generalizations. In addition, the more detailed ichnological and sedimentological analysis of a tidal beach corresponds to Waterside Beach in the Bay of Fundy of Eastern Canada (Dashtgard *et al*., 2009) and, therefore, factors other than those typical of open-marine coasts may have influenced the benthic fauna (e.g. salinity dilution), further complicating the proposal of a more general model. While wave-dominated tidal flats share aspects of both wave-dominated shorefaces and tide-dominated tidal flats from an ichnological perspective, tidal beaches seem to have little in common with the latter and mostly resemble wave-dominated shorefaces. The proximal–distal ichnofacies gradient in tidal beaches follows that of wave-dominated shorefaces rather than tide-dominated tidal flats (Mángano and Buatois, 2004a). However, and in contrast to wave-dominated shoreface, no archetypal *Cruziana* is present in tidal beaches, and diversity levels and degree of bioturbation are reduced (Dashtgard *et al*., 2009).

7.4 MUDDY SHORELINES

Muddy shorelines typically form in protected regions, such as bays and lagoons (see Section 8.2). Also, they occur along the open coast forming extensive mud flats in tide-dominated shallow-marine environments (see Section 7.2.2). However, they may also form along open coasts if the supply of suspended sediment is enough to dampen inshore wave power and tidal currents (Potter *et al*., 2005). These muddy coasts are particularly common downcurrent from fine-grained delta systems. However, because muddy shorelines may extend far away from the delta mouth (e.g. 1600 km northwest of the Amazon mouth), they will be addressed herein in the context of shallow-marine open environments rather than in the delta section.

Open-coast mudbelts are relatively well documented in modern environments, such as Surinam (Augustinus, 1978; Rine and Ginsburg, 1985; Allison and Nittrouer, 1998) and western Lousiana (Beall, 1968; Penland and Suter, 1989). Most of the muddy shoreline fauna most likely derived from offshore softground biotopes (Fortes, 2002). Biotic interactions, particularly competition among species, may be quite severe along muddy coasts, although this is not necessarily conducive to reduced diversity, which is essentially a function of physical stress (Fortes, 2002). Information from modern environments indicates that organisms living on muddy shorelines are typically calm-water species, and are affected by a number of stress factors, such as soupy substrates and rapid deposition of mud (Potter *et al.*, 2005). As a result, the diversity of biogenic structures is rather low and bioturbation tends to be sparse. Interestingly, muddy shorelines seem to display significant spatial heterogeneity. On the Surinam muddy coast, rapidly migrating mudbanks oriented obliquely to the shore are formed by fluid mud whose low strength essentially precludes bioturbation (Potter *et al.*, 2005). Between these banks, more consolidated mud is formed and more intense bioturbation occurs.

Although relatively widespread in modern environments, muddy shorelines have remained almost unnoticed in the fossil record and, therefore, palichnological information is virtually absent. A notable exception is that of Hovikoski *et al.* (2008), who documented ichnological and sedimentological aspects of Cretaceous deposits interpreted as being formed in a muddy shoreline based on core data. These authors set up a number of preliminary criteria that may help in the recognition of ancient muddy coasts, including (1) high content of terrestrially derived organic matter; (2) soupy substrates and fluid-mud intervals, which are unburrowed or contain highly deformed trace fossils; (3) high and/or variable depositional rates, resulting in low and/or fluctuating intensity of bioturbation; (4) reduced ichnodiversity and trace-fossil size; (5) dominance of monospecific suites; (7) morphologically simple trace fossils; (8) micro-laminated shale; and (9) abundant erosional features, such as shale-on-shale erosional contacts and scour-and-fill structures.

8 Ichnology of marginal-marine environments

> "Is there any other point to which you would wish to draw my attention?"
> "To the curious incident of the dog in the night-time."
> "The dog did nothing in the night-time."
> "That was the curious incident," remarked Sherlock Holmes.
> Sir Arthur Conan Doyle
> "Silver Blaze" (1892)

Marginal-marine environments represent one of the most successful areas of ichnological research. These environments comprise a wide variety of coastal settings characterized by rapid environmental perturbations, typically salinity changes, but also increased sediment discharge and extreme clay flocculation, among many other controls. These different factors generate stressful conditions that strongly affect benthic biotas, imparting clearly detectable signals in the ichnological record (e.g. Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Buatois *et al.*, 1997b; Mángano and Buatois, 2004a; MacEachern and Gingras, 2007). Ichnology is a powerful tool to differentiate deposits formed under marginal-marine conditions from those that accumulated in fully marine settings. In this chapter we review the ichnology of different marginal-marine environments, visiting estuaries, bays, deltas, and fjords.

8.1 ESTUARIES

Dalrymple *et al.* (1992) defined an estuary as "the seaward portion of a drowned valley system which receives sediment from both fluvial and marine sources and which contains facies influenced by tide, wave, and fluvial processes. The estuary is considered to extend from the landward limit of tidal facies at its head to the seaward limit of coastal facies at its mouth". In this definition, the term estuary is restricted to incised valley systems (see Section 12.5.2). However, in subsequent work a wider definition was adopted, allowing consideration of abandoned areas of the delta plain (destructive phase of deltas during transgression) as estuaries (Dalrymple, 2006).

The distinction between open-marine deposits of regional scale and marginal-marine deposits occupying estuarine systems is one of the areas of applied ichnology in which trace fossils have been most extensively used. Integrating ichnological information, and sedimentological and stratigraphic evidence is critical in discriminating between both types of environments. Several recent studies have led to reinterpretation of a great number of successions that were previously regarded as open-marine successions but are now considered to be estuarine in nature (e.g. Buatois *et al.*, 1999). Ichnological data have proved decisive for new interpretations as the key to the identification of these environments lies in recognizing particular ichnofossil assemblages developed under stress conditions resulting from the dilution of seawater, resulting in the brackish-water model, extensively applied in the oil industry. These characteristics allow identification of anomalous ichnofaunas (typical of marginal-marine brackish environments), which, in contrast to open-sea associations, usually exhibit a lower variety and abundance of forms (see Section 6.1.4). Also, the presence of typical marine ichnotaxa (e.g. *Teichichnus*, *Asteriacites*, *Psammichnites*) has been successfully used to detect marine influence in coastal-plain successions (e.g. Hakes, 1976, 1985; Miller and Knox, 1985; Ranger and Pemberton, 1988; Miller and Woodrow, 1991; Mángano *et al.*, 1999).

It should be noted, however, that brackish-water conditions are not exclusive of estuarine systems, being also present in other depositional settings (e.g. delta plains, distributary mouth bars) (Dalrymple and Choi, 2007). On the other hand, the inner zone of estuarine systems is commonly characterized by freshwater conditions (Buatois *et al.*, 1997b). Trace-fossil analysis aids not only in the recognition of estuarine deposits, but also delineation of different clastic facies within the estuarine valley. Estuaries have been classified into two main groups, wave-dominated and tide-dominated estuaries (Dalrymple *et al.*, 1992); the latter is a partial equivalent to the riverine estuarine valleys of MacEachern and Gingras (2007). Here, we address the ichnology of wave- and tide-dominated estuaries.

8.1.1 WAVE-DOMINATED ESTUARIES

Wave-dominated estuaries are characterized by a well-defined tripartite style of sand-to-mud-to-sand fill due to a pronounced spatial distribution of total energy (e.g. Zaitlin and Shultz, 1990). Therefore, wave-dominated estuaries comprise three main zones: (1) an outer zone dominated by marine processes; (2) a central zone where marine energy is dissipated by fluvial currents; and (3) an inner, river-dominated zone (Rahmani, 1988; Dalrymple *et al.*, 1992). As a result of energy distribution, these systems consist of: (1) a high-energy inner zone dominated by the discharge of fluvial tributaries (bay-head delta); (2) a low-energy middle zone, characterized by fine-grained deposition (central basin); and (3) a

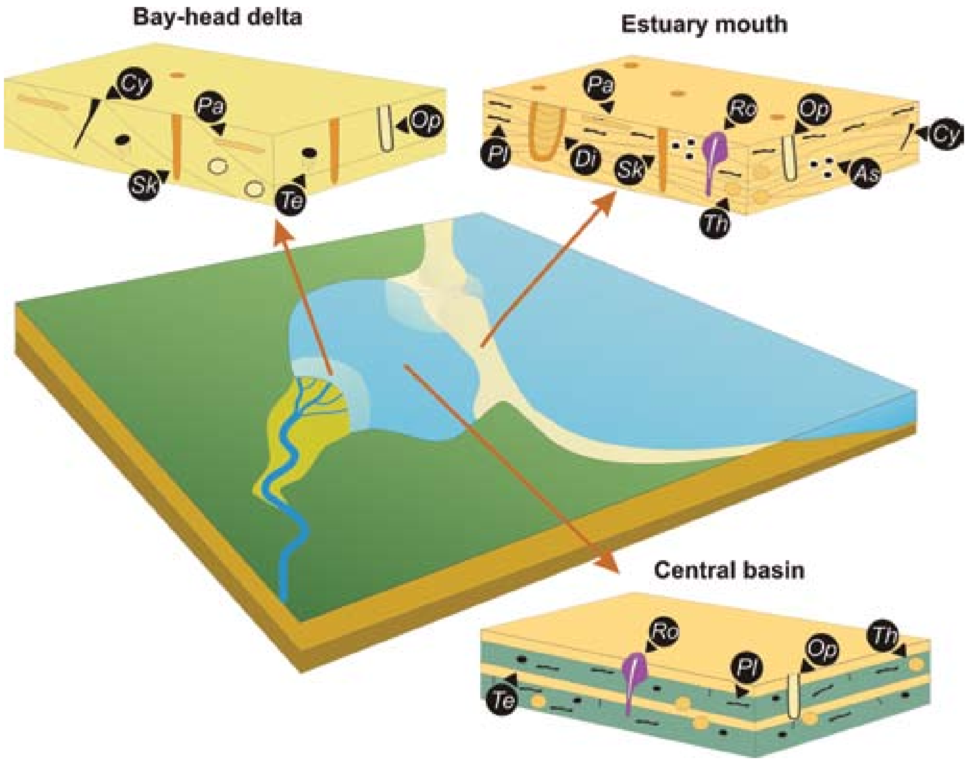

Figure 8.1 Schematic reconstruction of trace-fossil distribution in wave-dominated estuaries. Bay-head delta deposits are sparsely bioturbated and may contain a few ichnotaxa, typically *Cylindrichnus* (*Cy*), *Palaeophycus* (*Pa*), *Ophiomorpha* (*Op*), *Teichichnus* (*Te*), and *Skolithos* (*Sk*). Central-basin deposits also are sparsely bioturbated, and contain low-diversity suites, *Planolites* (*Pl*), *Teichichnus* (*Te*), and *Thalassinoides* (*Th*) being common components. *Ophiomorpha* (*OP*) *and Rosselia* (*Ro*) may be present. Estuary-mouth deposits tend to display more ichnodiversity and intensity of bioturbation, including *Cylindrichnus* (*Cy*), *Palaeophycus* (*Pa*), *Ophiomorpha* (*Op*), *Thalassinoides* (*Th*), *Diplocraterion* (*Di*), *Rosselia* (*Ro*), *Asterosoma* (*As*), *Planolites* (*Pl*), and *Skolithos* (*Sk*).

Box 8.1 Ichnology of a Lower Cretaceous wave-dominated estuary, the Viking Formation of subsurface Alberta, Canada

Recognition of estuarine deposits in the Lower Cretaceous Viking Formation of the Western Canada Sedimentary Basin had profound implications in petroleum exploration and reservoir characterization. The Viking has been previously interpreted as deposited in shoreface environments. However, the discovery of a number of fields (e.g. Crystal) running perpendicular to the paleoshoreline proved to be a challenge to the shoreface model. These fields were then interpreted as estuarine valley fills, and ichnology played a major role in the shaping of this new model. Detailed sedimentological and ichnological studies of cores from the Viking Formation indicated that these fields were actually wave-dominated estuaries. Deposits lateral and underlying Viking valley deposits are characterized by highly diverse ichnofaunas, which contrast with the more impoverished assemblage that typified the estuarine deposits. In addition, the estuarine ichnofauna is characterized by the dominance of opportunistic suites, and variable and sporadic distribution of bioturbation. The typical tripartite facies distribution of wave-dominated estuaries is well illustrated in these Viking fields. Bay-head delta deposits contain sporadic bioturbation as a result of extreme stress conditions. Central-basin deposits, although displaying sporadic bioturbation, reduced size and low ichnodiversities, may contain locally more elaborate and specialized feeding and grazing trace-fossils indicative of periods of less stressful salinity conditions. Estuarine-mouth deposits show a clear increase in ichnodiversity. Opportunistic strategies are dominant on the estuary side of the mouth, while climax ichnofaunas dominate on the seaward side of the estuary mouth. Reincision of channel facies at the top of the Viking valleys has been documented suggesting renewed sea-level fall. These deposits show an alternation of burrowed and unburrowed beds, most likely reflecting a combination of alternating freshwater and brackish-water conditions, and high energy due to dune migration. Studies in the Viking have been instrumental in the elaboration of the brackish-water model.

Reference: MacEachern and Pemberton (1994).

marine sand-plug formed at the seaward, high wave-energy end of the valley (estuary mouth) (Fig. 8.1) (Box 8.1).

Bay-head deltas are extremely stressful environments, being characterized by low salinity values and high sedimentation rates. These deposits are typically unbioturbated to sparsely bioturbated, with burrows displaying a tendency to concentrate on top of sandstone beds; ichnodiversity is very low (e.g. MacEachern and Pemberton, 1994; Buatois *et al.*, 1999, 2002b; MacEachern and Gingras, 2007). Trace-fossil assemblages tend to be dominated by dwelling structures of suspension feeders, such as *Palaeophycus* (Fig. 8.2a), *Ophiomorpha* (Fig. 8.2b), *Skolithos* (Fig. 8.2d), *Monocraterion*-like burrows (Fig. 8.2e),

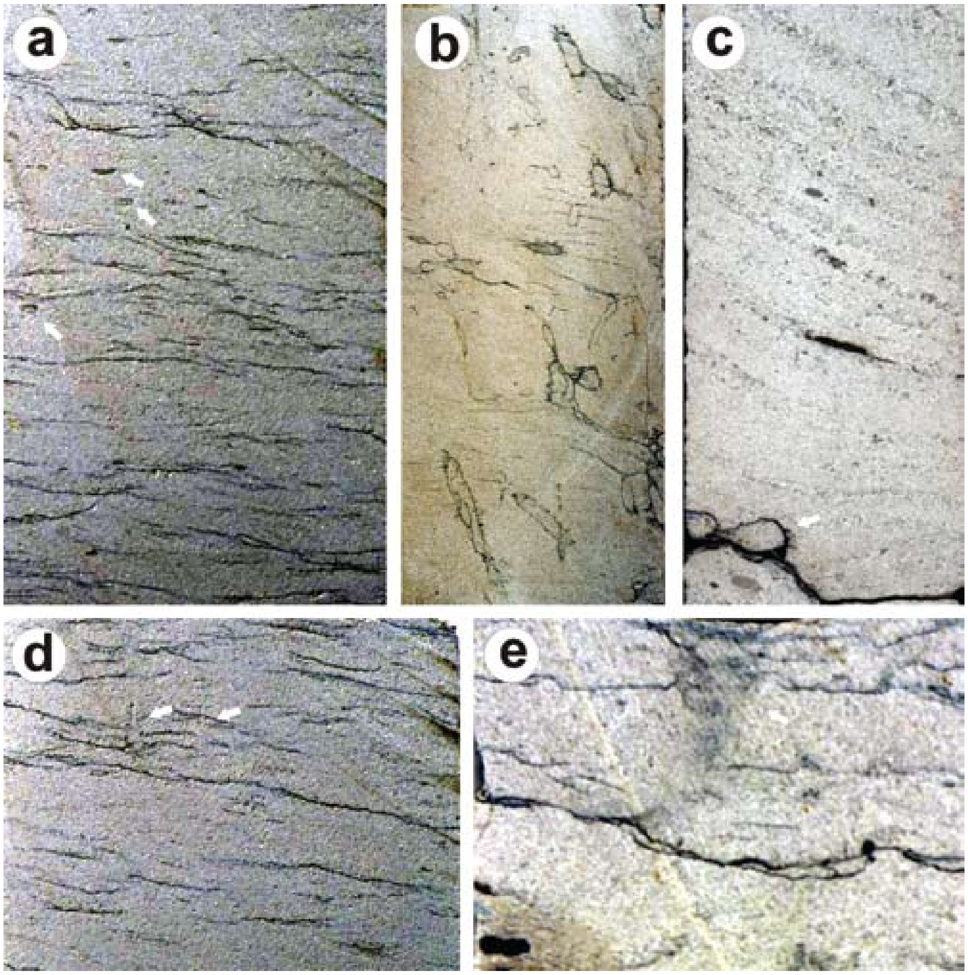

Figure 8.2 Ichnofaunas from bay-head delta deposits as expressed in core. Note tendency to form monospecific suites and small size. (a) Low density of small *Palaeophycus* (arrows) in sandstone with abundant mud drapes. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b). (b) *Ophiomorpha* forming a relatively high-density occurrence in a cross-bedded sandstone with mud drapes. Upper Oligocene–Lower Miocene, Naricual Formation, Pirital Field, Eastern Venezuela Basin. Core width 10 cm. (c) *Rhizocorallium* (arrow) along reactivation surface in a cross-bedded sandstone. Upper Cretaceous, Escandalosa Formation, Caipe Field, Barinas-Apure Basin, southwestern Venezuela. Core width is 10 cm. (d) Scattered tiny specimens of *Skolithos* (arrows) in sandstone with abundant mud drapes. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b). (e) Isolated occurrence of *Monocraterion*-like burrow (arrow) in a sandstone with stylolityzed mud drapes. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b).

and, more rarely, detritus feeders, such as *Cylindrichnus* of *Rhizocorallium* (Fig. 8.2c). These tend to occur in sandstone units commonly recording opportunistic colonization of subaqueous dunes and channels. Feeding trace fossils of deposit feeders are minor components, commonly present in mudstone interbeds associated with pauses in sedimentation (e.g. *Planolites*, *Teichichnus*). Individual beds rarely contain more than a few ichnogenera (MacEachern and Pemberton, 1994). In terms of archetypal ichnofacies, bay-head deltas predominantly contain the *Skolithos* ichnofacies with minor proportions of the impoverished *Cruziana* ichnofacies.

Central-basin settings are characterized by a combination of stress factors, such as brackish-water conditions, water turbidity and oxygen depletion. The degree of bioturbation is typically low, although some intervals may attain moderate to relatively intense bioturbation, reflecting slower depositional rates (e.g. MacEachern and Pemberton, 1994; MacEachern and Gingras, 2007). Ichnodiversity is low; moderate diversity levels most likely reveal less salinity stress. Trace fossils typically occur in heterolithic successions displaying wavy to lenticular bedding. The dominant components are non-specialized feeding traces of deposit feeders (e.g. *Planolites*, *Teichichnus*), although dwelling traces of deposit feeders (e.g. *Thalassinoides*) and detritus feeders (e.g. *Rosselia*), and, more rarely, suspension feeders (e.g. *Palaeophycus*, *Diplocraterion*) may occur. Burrow size reduction and synaeresis cracks are typical features in central-basin deposits (MacEachern and Gingras, 2007). Monospecific or low-diversity suites of *Planolites* (Fig. 8.3) and *Teichichnus* are common (e.g. Buatois *et al.*, 2002b). Storm sands in central-basin deposits commonly contain *Ophiomorpha*, which is thought to reveal transport of burrowing crustaceans rather than opportunistic colonization (Savrda and Nanson, 2003). These authors also noted that in proximal parts of the central bay, rapid event-related accumulation of suspended clays immediately followed sand emplacement, precluding the establishment of a fair-weather suite. Discrete layers with more specialized trace fossils (e.g. *Phycosiphon*, *Chondrites*) either reflect short-lived barrier breaching by storm washovers, incomplete barring of estuary mouths, or permanent barrier breaching during transgressions (MacEachern and Gingras, 2007). Central-basin deposits are characterized by the depauperate *Cruziana* ichnofacies with minor contributions from the *Skolithos* ichnofacies.

Estuary-mouth environments are highly variable in terms of ichnological content and sedimentary facies. The degree of

Figure 8.3 Typical core expression of ichnofaunas from central-basin deposits. Note small *Planolites*, synaeresis cracks, siderite layer (top), and sandstone lenses with very thin mud drapes. Lower Miocene, Oficina Formation, Oritupano Field, eastern Venezuela Basin. Core width is 10 cm.

bioturbation and ichnodiversity is moderate to relatively intense, reflecting near normal marine salinities (Fig. 8.4). Stress factors in this setting mostly consist of high depositional rates and high energy levels rather than reduced salinity (e.g. Savrda *et al.*, 1998). As a result, coarser grained deposits (e.g. conglomerate and very coarse-grained sandstone) are sparsely bioturbated in contrast to finer grained deposits that accumulate in more protected sites. Deposits of rapidly migrating large bedforms, such as those of dunes migrating along tidal inlets, are typically unburrowed or sparsely bioturbated (e.g. Savrda *et al.*, 1998). Behavioral categories and trophic types are much more varied than in inner- and central-estuarine areas, covering dwelling, feeding, and resting traces of suspension, deposit, and detritus feeders (e.g. MacEachern and Pemberton, 1994; Buatois *et al.*, 2002b; MacEachern and Gingras, 2007). *Ophiomorpha*, *Thalassinoides*, *Skolithos*, *Palaeophycus*, *Planolites*, *Cylindrichnus*, *Rosselia*, *Asterosoma*, *Teichichnus*, and *Diplocraterion* are common components, while *Bergaueria*, *Lockeia*, and *Siphonichnus* may be accessory elements.

Figure 8.4 Core expression of intensely bioturbated estuary-mouth coarse-grained deposits. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b).

Macaronichnus is commonly present in high-energy tidal-inlet and subtidal-bar sandstone (Savrda and Uddin, 2005), while large *Conichnus* occurs in the same deposits, reflecting equilibrium strategies (Savrda, 2002). *Ophiomorpha* is commonly present in dune deposits associated with slack-water mud drapes, reflecting relatively brief colonization windows (Savrda *et al.*, 1998). Deposits that occur on the estuarine side of the barrier are less bioturbated, and display less ichnodiversity than those that accumulate on the seaward side (MacEachern and Pemberton, 1994). On the seaward side, ichnotaxa that are less tolerant to salinity fluctuations may be rather common (e.g. *Chondrites*, *Helminthopsis*, and *Phycosiphon*). Estuarine-mouth deposits are characterized by the mixed depauperate *Cruziana* and *Skolithos* ichnofacies.

The overall distribution of biogenic structures along wave-dominated estuaries is likely controlled by the salinity gradient, displaying a transition from brackish water in the bay-head delta and central basin to near-normal salinity conditions at the seaward end of the valley. Other parameters, such as oxygenation, substrate consistency, and energy regime, play a significant role at a more local scale. For example, dwelling traces of suspension feeders are dominant in high-energy, oxygenated sandy channels and dunes of the bay-head delta, and feeding traces of deposit feeders are more typical of low-energy, poorly oxygenated, fine-grained sediments of the central basin. The importance of salinity becomes evident when facies formed under similar conditions of energy, substrate, and oxygenation are compared (Buatois *et al.*, 2002b). Organisms that inhabit bay-head deltas and upper-shoreface environments are adapted to a well-oxygenated sandy substrate under relatively high-energy conditions. However, while animals living in the bay-head delta experience stressful physiological conditions due to brackish water, those from the upper shoreface developed in normal salinity waters. The overall features of both ichnofaunas (e.g. lower ichnodiversity in the bay-head delta than in the shoreface) clearly support the importance of salinity as a limiting factor in trace-fossil distribution.

8.1.2 TIDE-DOMINATED ESTUARIES

The distribution of total energy that produces the tripartite style of sand-to-mud-to-sand fill is less pronounced in tide-dominated systems than in wave-dominated estuaries due to migrating tidal channels in the central zone of the estuary (Dalrymple *et al.*, 1992; Boyd *et al.*, 2006). Nevertheless, tide-dominated estuarine systems are characterized by: (1) an inner sandy zone representing a straight tidal-fluvial channel (upper estuary); (2) a middle muddy-sandy zone of a meandering to straight tidal channel and tidal flats, tidal creeks, and salt marshes along the sides of the estuary (middle estuary); and (3) an outer zone characterized by elongate tidal sand bars and tidal flats that flanked the estuary valley seaward (lower estuary) (Fig. 8.5).

In the fluvio-estuarine transition zone, tidal influence commonly extends further landward than the saltwater intrusion. This zone is therefore situated between the maximum landward limit of tidal currents and the salinity limit further towards the sea (Buatois *et al.*, 1997b). As noted by Allen (1991), upper-estuary channels are rarely affected by brackish water and no marine or brackish-water fauna is able to inhabit this portion of the estuary. The freshwater benthos inhabiting this inner zone does not have the special adaptations necessary to survive in the brackish environment, which results in the middle estuary being a border zone to their distribution area (Wolff, 1983). Tidal rhythmites formed in this innermost zone contain arthropod trackways (e.g. *Dendroidichnites*, *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Stiallia*, *Stiaria*) (Fig. 8.6a), insect resting traces (e.g. *Tonganoxichnus*) (Fig. 8.6a), grazing traces (e.g. *Gordia*, *Helminthoidichnites*, *Helminthopsis*) (Fig. 8.6b–d), subsurface feeding traces (e.g. *Treptichnus*) (Fig. 8.6e), fish locomotion traces (*Undichna*) (Fig. 8.6f), and reptile (e.g. *Notalacerta*, *Pseudobradypus*, *Attenosaurus*, *Alabamasauripus*, *Dimetropus*) and amphibian trackways (e.g. *Cincosaurus*) (Rindsberg, 1990b; Buatois *et al.*, 1997b, 1998a; Mángano and Buatois, 2004a; Hunt *et al.*, 2004a; Lucas *et al.*, 2004a; Lucas and Lerner 2005; Haubold *et al.*, 2005; Martin and Pyenson, 2005; Pashin, 2005; Minter and Braddy, 2009).

This ichnofauna reflects the activity of a mixed terrestrial and freshwater biota in low-energy tidal flats (Buatois *et al.*, 1997b, 1998a). Root trace fossils (Fig. 8.6g) and autochthonous upright plants are common, representing the only penetrative organic structures in an otherwise unbioturbated substrate characterized by thinly interbedded sandstone–mudstone couplets or siltstone–claystone couplets. Trails and trackways are preserved on mud drapes, and are commonly associated with a wide variety

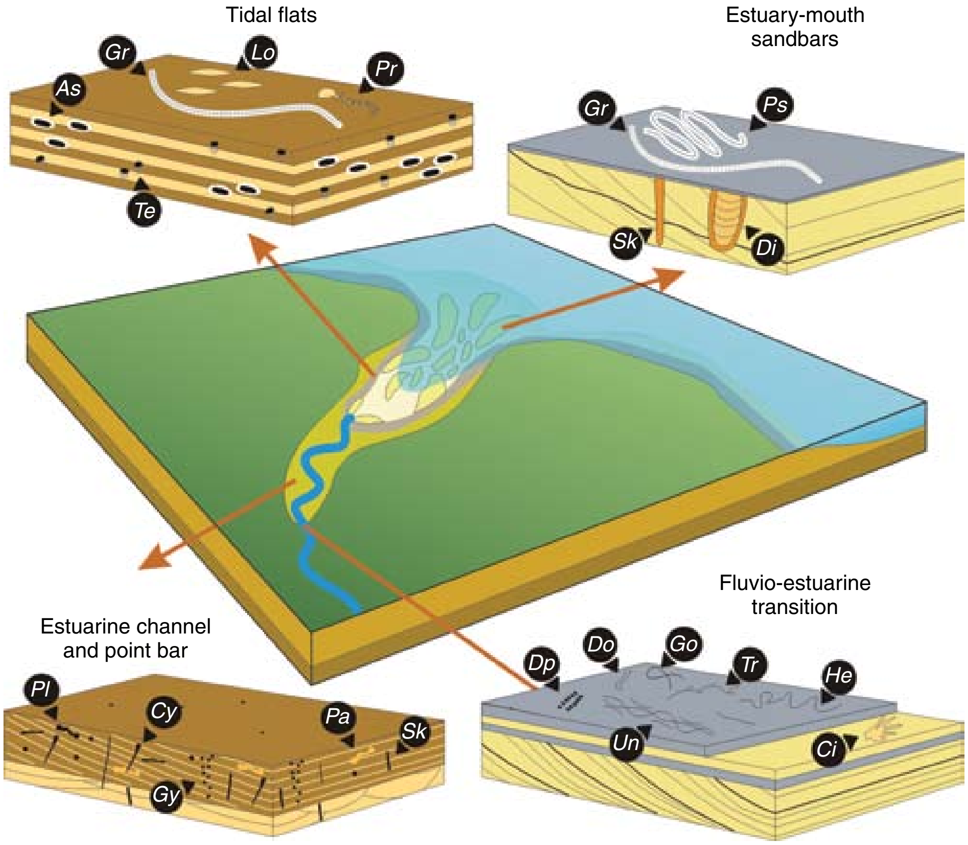

Figure 8.5 Schematic reconstruction of trace-fossil distribution in tide-dominated estuaries. The fluvio-estuarine transition displays relatively high-diversity suites, including *Diplichnites* (*Dp*), *Diplopodichnus* (*Do*), *Gordia* (*Go*), *Treptichnus* (*Tr*), *Helminthopsis* (*He*), *Undichna* (*Un*), and *Cincosaurus* (*Ci*). Estuarine-channel and point-bar deposits are sparsely bioturbated and contain a few ichnotaxa, such as *Gyrolithes* (*Gy*), *Cylindrichnus* (*Cy*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), and *Skolithos* (*Sk*). Associated tidal-flat deposits are slightly more bioturbated, but ichnodiversity remains low, with *Lockeia* (*Lo*), *Protovirgularia* (*Pr*), *Asterosoma* (*As*), *Gyrochorte* (*Gr*), and *Teichichnus* (*Te*) as common forms. Estuary-mouth sandbar deposits may contain *Diplocraterion* (*Di*), *Skolithos* (*Sk*), *Gyrochorte* (*Gr*), and *Psammichnites* (*Ps*).

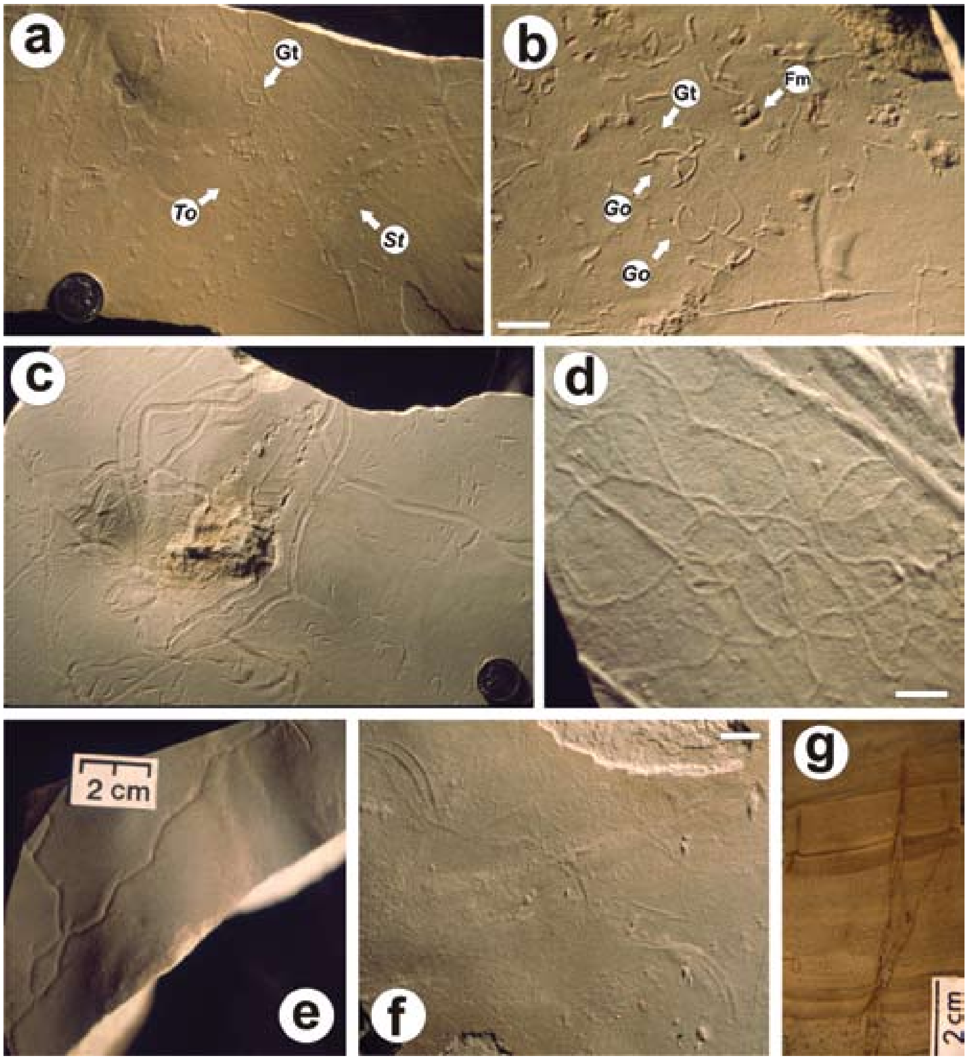

Figure 8.6 Ichnofaunas from fluvio-estuarine transition deposits. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, United States. (a) *Stiaria intermedia* (*St*), *Tonganoxichnus ottawensis* (*To*), and indeterminate grazing trails (Gt). Coin is 1.4 cm. (b) *Gordia indianaensis* (*Gi*) indeterminate grazing trails (Gt), and foam marks (Fm). Scale bar is 1 cm. (c) Grazing trails concentrated around a fossil leaf. Coin is 1.4 cm. (d) *Gordia indianaensis*. Scale bar is 1 cm. (e) *Treptichnus bifurcus*. (f) *Undichna britannica*. Scale bar is 1 cm. (g) Core view of a root trace fossil. See Buatois *et al*. (1997b, 1998a).

of bedding-surface structures, including tool marks, drainage or seepage rill marks, runnel marks, runoff washouts, foam marks, raindrop impressions, gas escape structures, falling-water marks, and wrinkle marks, the latter suggestive of microbial matgrounds (Buatois *et al*., 1997b, 1998a; Mángano and Buatois, 2004a; Rindsberg, 2005; Pashin, 2005). In terms of ichnofacies, the fluvial–estuarine transition is characterized by the mixed *Mermia–Scoyenia* ichnofacies, and by the *Serpentichnus* ichnocoenosis of the *Characichichnos* ichnofacies.

Further towards the sea, tidal channels display brackish-water conditions, allowing the establishment of the mixed depauperate *Cruziana* and *Skolithos* ichnofacies. Ichnodiversity reaches a minimum in these highly stressed settings, and bioturbation tends to be sparsely distributed (Ranger and Pemberton, 1992; Gingras *et al*., 1999b). Upper-estuarine channels encompass two main areas, the active portion of the channel and the point bar (MacEachern and Gingras, 2007). Active-channel deposits are typically unburrowed or contain a few trace fossils in mud interbeds or in the toesets of dune bedforms. As noted by MacEachern and Gingras (2007), the scarcity of bioturbation in active channels is for the most part due to the presence of rapidly migrating bedforms rather than brackish-water conditions per se. *Planolites*, *Cylindrichnus*, *Skolithos*, and *Palaeophycus* are among the ichnotaxa most commonly recorded. Logs with *Teredolites* may occur at the base of channels (Fig. 8.7).

The associated point bars, characterized by lateral accretion that produces inclined heterolithic stratification, generally display higher ichnodiversity and degree of bioturbation than the active channels (Box 8.2). Biogenic structures in inclined heterolithic stratification deposits display proximal–distal trends in response to a salinity gradient (Lettley *et al*., 2007b; MacEachern and Gingras, 2007). Landward expressions tend to be sandier, and are either unbioturbated or contain scarce *Planolites* (Fig. 8.8a). The degree of bioturbation and ichnodiversity tend to increase seaward with the progressive addition of *Skolithos*, *Gyrolithes* (Fig. 8.8c–d), and *Cylindrichnus* (Fig. 8.8b). However, mudstone-rich intervals sharply overlying point-bar deposits are commonly unbioturbated, and are thought to record deposition close to or at the turbidity-maximum zone, which promotes clay flocculation and rapid mud accumulation (Bechtel

Figure 8.7 Log with *Teredolites* at the base of an estuarine tidal channel sandstone. Upper Cretaceous, Desert Sandstone Member, Blackhawk Formation, Old Thompson Canyon, Book Cliffs, eastern Utah, United States. Scale bar is 5 cm.

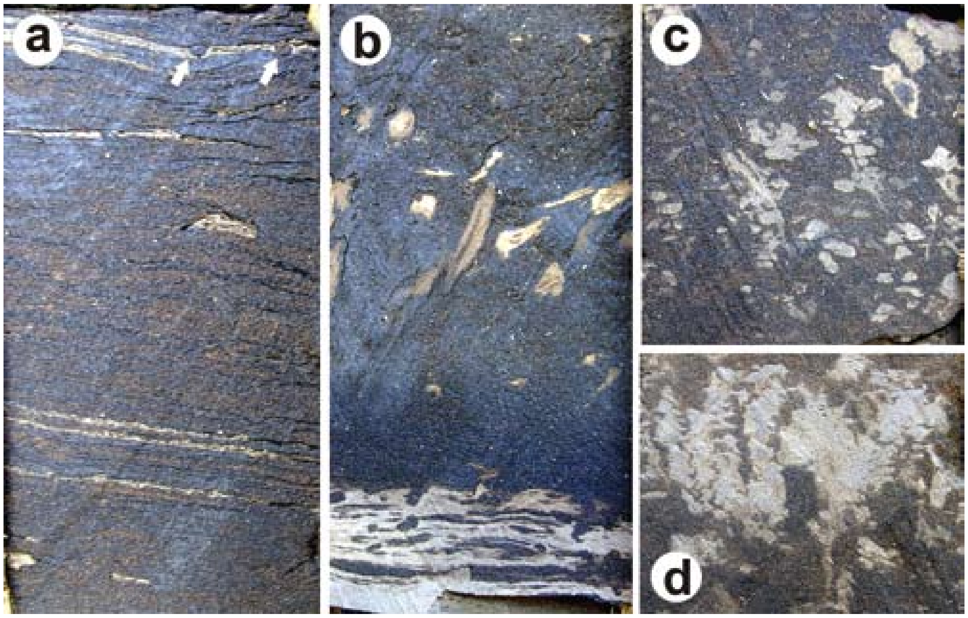

Figure 8.8 Core expression of ichnofaunas from estuarine-channel deposits with inclined heterolithic stratification. Sandstone is impregnated with hydrocarbon and is dark colored, while mudstone is light colored. Lower Cretaceous, McMurray Formation, northern Alberta, Canada. See Lettley *et al.* (2007b). (a) *Planolites* isp. (arrows) in mud drapes. (b) Concentrically laminated *Cylindrichnus* isp. (c) and (d) Vertical spiral burrow *Gyrolithes* isp. Core widths are 8 cm.

et al., 1994; MacEachern and Gingras, 2007; Lettley *et al.*, 2007b). Alternation of intensely bioturbated intervals and mostly unburrowed intervals are, therefore, interpreted as fluctuations in the position of the salt wedge within the turbidity-maximum zone. Notably, many ichnofabrics in estuarine point-bar deposits are composite, reflecting continental trace fossils overprinting brackish-water suites. Typical examples are represented by elements of the *Beaconites–Taenidium* ichnoguild cross-cutting trace-fossil suites with ichnogenera that indicate marine influence (e.g. *Teichichnus*) (Fig. 8.9a–e).

In modern macrotidal estuaries, zonations have been established to differentiate between upper subtidal–lower-intertidal, middle-intertidal, and upper-intertidal zones of muddy point bars and associated tidal flats (Pearson and Gingras, 2006). Upper-subtidal to lower-intertidal zones of the point bars contain incipient *Polykladichnus* and *Skolithos* produced by the capitellid polychaete *Heteromastus*. Middle-intertidal zones contain incipient *Arenicolites* and *Diplocraterion* produced by the amphipod *Corophium volutator*. In the upper-intertidal zone of the point bar and in the tidal flat, the nereid worms *Nereis virens* and *N. diversicolor* (producers of incipient *Polykladichnus*, *Palaeophycus*, and *Planolites*), and the bivalve *Macoma balthica* (producer of incipient *Siphonichnus*) are present. Similar zonations have been documented in sandy point bars of modern mesotidal estuaries (Gingras *et al.*, 1999b). However, *Callianassa* burrows (producers of incipient

Box 8.2 Ichnology of a Lower Cretaceous tide-dominated estuary, the McMurray Formation of Alberta

Understanding of the sedimentary architecture and depositional dynamics of the Lower Cretaceous McMurray Formation is essential because this unit is one of the most important producers of heavy oil in the world. Although the density of well cores is remarkably high, the complex distribution and architecture of these sandstone bodies complicate correlation of tide-dominated estuarine-channel units. Integration of ichnological and sedimentological datasets in the analysis of estuarine-channel deposits displaying inclined heterolithic stratification (IHS) has helped to address longitudinal variations in the character of estuarine point bars. Towards the fluvial end of the estuary, bioturbation is exceedingly rare in IHS deposits and restricted to sporadic occurrences of *Planolites* in interbedded sandstone and siltstone, while associated cross-bedded sandstone is unburrowed. The central zone of the estuary is characterized by fine- and very fine-grained sandstone associated with silt- and clay-rich deposits formed in the zone of turbidity maximum. Bioturbation is highly variable. Fine-grained deposits show little to moderate bioturbation and dominance of monospecific suites of *Planolites*. Sand-dominated deposits show more diversity particularly towards the seaward end of the turbidity maximum zone, where *Planolites* (Fig. 8.8a) and *Teichichnus* dominate, and *Cylindrichnus* (Fig. 8.8b), *Palaeophycus* and *Gyrolithes* (Fig. 8.8c–d) may occur also. The seaward end is characterized by well-sorted very fine- and fine-grained sandstone and minor amounts of mudstone and siltstone. Bioturbation is comparatively abundant and diverse, with *Cylindrichnus*, *Skolithos*, *Teichichnus*, *Palaeophycus*, *Planolites*, *Thalassinoides*, and escape trace fossils as relatively common elements. Seasonal variations in fluvial discharge, together with changes in water circulation and the position of the turbidity maximum played major roles in controlling trace-fossil distribution. This is one of the most detailed ichnological studies of tide-dominated (riverine) estuaries.

Reference: Lettley *et al*. (2007b).

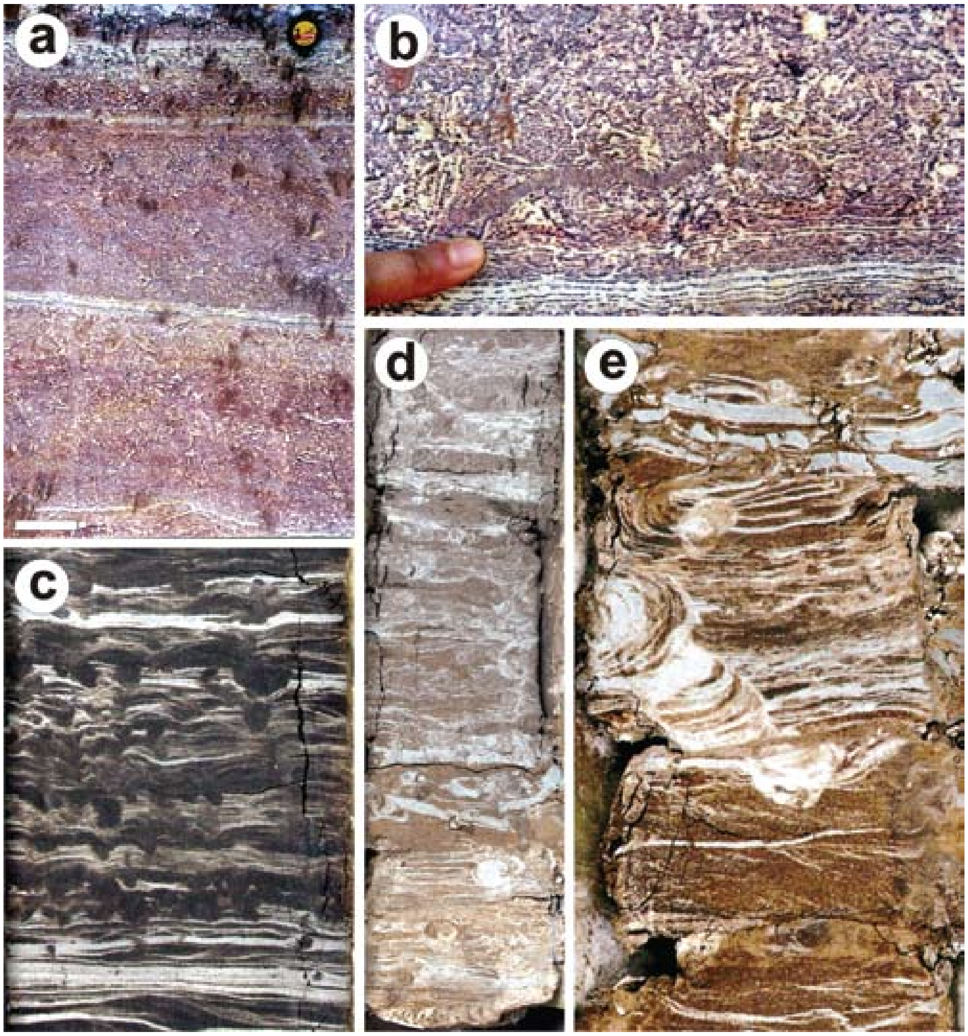

Figure 8.9 Composite ichnofabrics in estuarine-channel deposits with inclined heterolithic stratification. (a) Deposits with alternating intervals having well-preserved inclined heterolithic stratification and intensely bioturbated intervals as a result of the activity of a brackish-water infauna. Measuring tape is 5 cm wide. Lower Miocene Barreiras Formation, Peru Beach, Maranhão State, northern Brazil. See Netto and Rosetti (2003). (b) Close-up showing discrete continental *Taenidium* superimposed to a background brackish-water ichnofabric. Lower Miocene Barreiras Formation, Peru Beach, Maranhão State, northern Brazil. See Netto and Rosetti (2003). (c) *Teichichnus* ichnofabric in the lower interval of an estuarine point bar. Lower Miocene Oficina Formation of the Orinoco Belt, Venezuela. Core is 8 cm wide. (d) Intensely bioturbated upper interval of point-bar deposit shown in (c) The ichnofabric is dominated by continental *Taenidium* and *Beaconites* colonizing the abandoned point bar. Core width is 9.5 cm. (e) Close-up of *Beaconites* colonizing an abandoned point bar. Lower Miocene Oficina Formation of the Orinoco Belt, Venezuela. Core is 8 cm wide.

Thalassinoides and *Ophiomorpha*) tend to occur in these sandier substrates. Point-bar deposits are typically less bioturbated than the associated tidal flats (Gingras *et al*., 1999b). Some lateral-accretion surfaces identified in the fossil record contain sharp-walled, unlined and passively filled burrows (e.g. *Thalassinoides*, *Skolithos*) of the *Glossifungites* ichnofacies. This suite suggests rapid dewatering and formation of autogenic stiffgrounds (Gingras *et al*., 2000, 2001; Lettley *et al*., 2007a). Also, the *Glossifungites* ichnofacies may occur at the base of channels that erode into the underlying bedrock (e.g. Gingras *et al*., 1999b).

Salt marshes may form along the sides of the estuary. These marshes are dissected by a network of tidal creeks, and are commonly heavily vegetated by salinity tolerant plants (e.g. *Spartina*), resulting in intense bioturbation by root traces (e.g. Edwards and Frey, 1977; Basan and Frey, 1977). In modern salt marshes of macrotidal estuaries, *Corophium volutator* (producer of incipient *Arenicolites* and *Diplocraterion*) and *Mya arenaria* (producer of incipient *Siphonichnus* and *Lockeia*) are common (Dashtgard and Gingras, 2005). Tidal-creek migration may generate *Glossifungites*-demarcated surfaces. In tropical to subtropical estuaries, salt marshes are replaced by mangroves that form along sheltered shores, and consist mostly of trees and woody shrubs that have root adaptations to live in regularly submerged sediment (Cadée, 1998; Schaeffer-Novelli *et al*., 2002). Robust root traces (e.g. *Avicennia*, *Rhizophora*, and *Sonneratia*) are commonly pervasive. In addition, a number of invertebrates are active bioturbators in mangrove areas (Cadée, 1998). These include mostly crustaceans that construct U-shaped burrows connected to a horizontal segment (*Thalassina anomala*), vertical burrows (*Sesarma* sp. and *Uca* sp.), and U-shaped burrows (*Upogebia* sp.). Horizontal grazing traces by mollusks, although common, have low preservation potential.

Tidal flats also occur along the sides of tide-dominated estuaries. In contrast to tidal flats formed on open coasts, ichnofaunas from middle-estuarine tidal flats are not diverse, but contain ichnotaxa that clearly illustrate marine influence, thereby allowing distinction from intertidal areas at the fluvial–estuarine transition (Mángano and Buatois, 2004a). In strongly tidally dominated settings, tidal flats form under an upper-flow regime (Dalrymple and Choi, 2007), and may be sparsely bioturbated due to high-energy conditions. Common components in low-energy counterparts include resting traces (e.g. *Asteriacites* and *Lockeia*), locomotion traces (e.g. *Gyrochorte* and *Protovirgularia*), grazing traces (e.g. *Nereites* and *Psammichnites*), feeding traces (e.g. *Teichichnus*, *Asterosoma*, *Planolites*, and *Cylindrichnus*), and dwelling traces (e.g. *Diplocraterion*, *Lingulichnus*, and *Palaeophycus*). Although the degree of bioturbation is typically low, *Lingulichnus* and *Lockeia* may occur in profuse densities. Suites are commonly monospecific, but the association of bivalve (*Lockeia–Protovirgularia*) and ophiuroid (*Asteriacites*) trace fossils is quite common (Mángano and Buatois, 2004a).

Central-basin deposits, although widespread in wave-dominated estuaries, are rare in tide-dominated estuaries due to a large degree of tidal exchange and the absence of a mouth–barrier system (Dalrymple *et al*., 1992; Boyd *et al*., 2006; MacEachern and Gingras, 2007). These deposits typically consist of heterolithic facies that are more bioturbated and exhibit higher diversity levels than the associated point-bar deposits (MacEachern and Gingras, 2007). Some of the ichnotaxa recorded in central-basin deposits are *Teichichnus*, *Planolites*, *Cylindrichnus*, *Palaeophycus*, and *Skolithos*.

The outer region of tide-dominated estuaries is characterized by the establishment of elongate tidal bars that may be associated with upper-flow regime sand flats (Dalrymple *et al*., 1992; Boyd *et al*., 2006; Dalrymple and Choi, 2007). Although this region displays normal-marine salinities, high tidal velocities and high rates of sedimentation commonly preclude bioturbation (e.g. Buatois *et al*., 2006b). Locally, assemblages dominated by vertical burrows of suspension feeders, such as *Skolithos* (Fig. 8.10a–b), *Diplocraterion* (Fig. 8.10c) and *Ophiomorpha* (Fig. 8.10d), may occur in high densities reflecting colonization during short breaks in sedimentation or tidal-bar abandonment during transgression. Horizontal grazing and feeding traces, such as *Gyrochorte* (Fig. 8.10e) and *Psammichnites* (Fig. 8.10f), typically occur in mud drapes that result from longer breaks or in more protected sites showing interfingering with middle-estuarine deposits (Mángano and Buatois, 2004a). Vertical burrows of detritus or deposit feeders, such as *Asterosoma* (Fig. 8.10f), *Patagonichnus* (Fig. 8.10g), *Rosselia* (Fig. 8.11a), and *Teichichnus* (Fig. 8.11b) may occur also in this setting.

As in the case of wave-dominated estuaries, the salinity gradient plays a major role in distribution of biogenic sedimentary structures in tide-dominated estuaries. Ichnofaunas tend to display proximal–distal trends revealing the activity of freshwater and terrestrial biotas near or at the fluvial–estuarine transition, brackish-water faunas in the central zone of the estuary and fully marine biotas at the estuary mouth (Mángano and Buatois, 2004b). However, other factors may be equally important, albeit at a more local scale, including clay flocculation near the turbidity-maximum zone and high tidal energy at the elongate tidal-bar complex.

8.2 BAYS

In recent years, ichnologists have begun to recognize that some marginal-marine successions containing brackish-water assemblages do not strictly represent the infill of estuarine systems, but record deposition in embayments instead (e.g. MacEachern *et al*., 1998). The ichnology of these bay settings is less understood than that of other marginal marine environments. Comparatively little has been written on these environments and only a few case studies have been documented (e.g. MacEachern *et al*., 1998, 1999c; Pemberton *et al*., 2001; Spila *et al*., 2005; Buatois *et al*., 2007b; Desjardins *et al*., 2010b). MacEachern and Gingras (2007) suggested subdividing bay environments into restricted or barrier-barred bays and open or non-barred bays, a classification framework that is adopted here.

8.2.1 RESTRICTED BAYS

Restricted bays correspond to embayments that have limited or intermittent connection to the open sea (MacEachern and

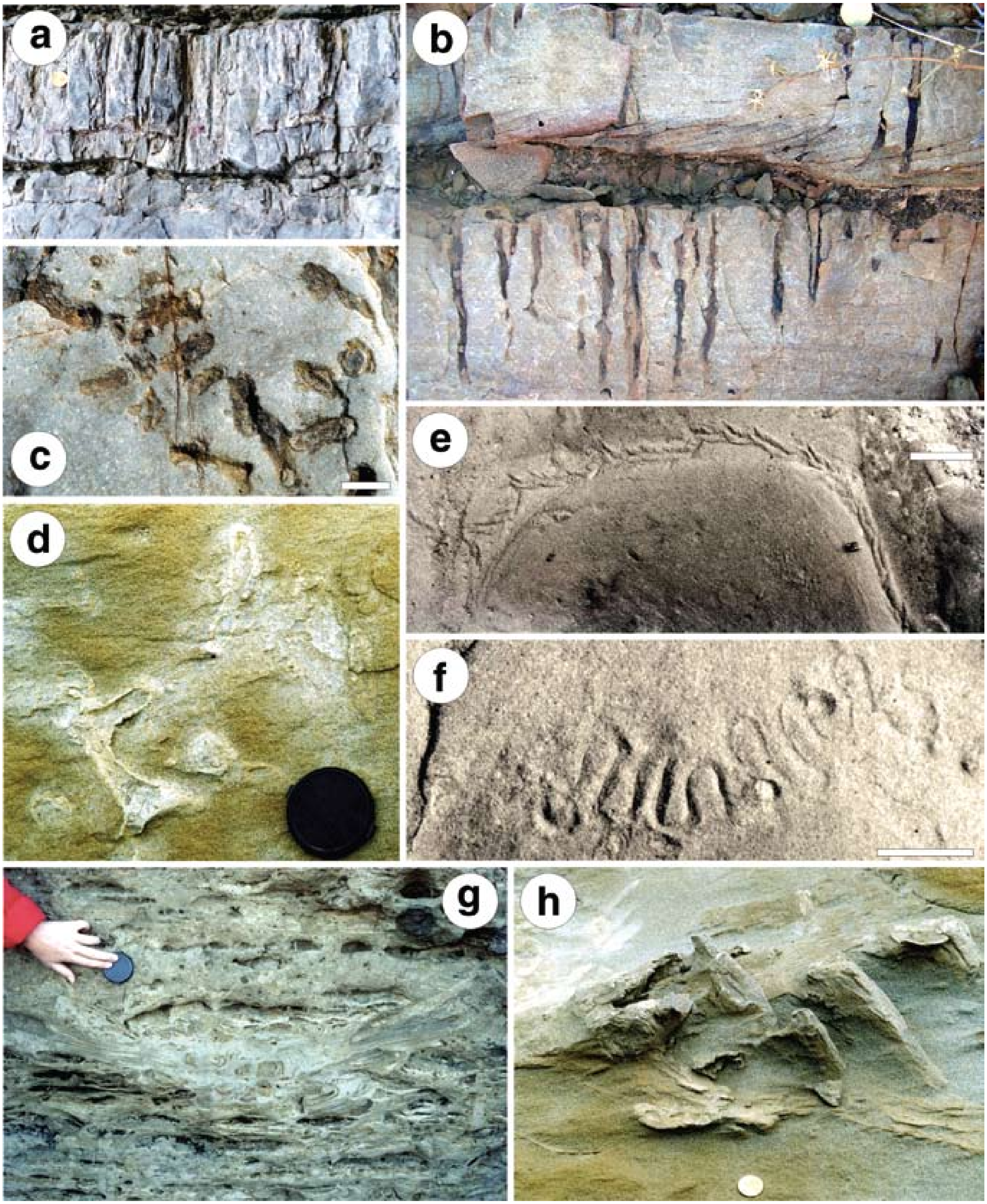

Figure 8.10 Ichnofaunas from deposits formed in the outer region of tide-dominated estuaries as expressed in outcrop. (a) *Skolithos linearis* forming a pipe rock. Upper Cambrian, Pico de Halcón Member, Quebrada del Salto Alto, Cordillera Oriental, northwest Argentina. Coin (upper left) is 1.8 cm. See Mángano and Buatois (2003a). (b) *Skolithos gyratus* in planar cross-bedded sandstone with abundant intraclasts and mud drapes. Upper Cambrian, Pico de Halcón Member, Quebrada del Abra Blanca, Cordillera Oriental, northwest Argentina. Coin (upper right) is 1.8 cm. (c) High density of *Diplocraterion parallelum* in bedding-plane view. Upper Cambrian, Pico de Halcón Member, Arroyo de Sapagua, Cordillera Oriental, northwest Argentina. Scale bar is 1 cm. (d) *Ophiomorpha nodosa*. Lower Miocene, Chenque Formation, roadcut near Comodoro Rivadavia, Patagonia, southern Argentina. Lens cap is 5.5 cm. (e) *Gyrochorte* isp. Upper Carboniferous, Bandera Shale, Bandera Sandstone Quarry, Bourbon County, eastern Kansas. Scale bar is 1 cm. See Mángano and Buatois (2004a). (f) *Psammichnites implexus*. Upper Carboniferous, Bandera Shale, Bandera Sandstone Quarry, Bourbon County, eastern Kansas. Scale bar is 1 cm. See Mángano and Buatois (2004a). (g) *Asterosoma radiciforme* displaying typical concentrically laminated ichnofabric. Lower Miocene, Patagonia Formation, cliff between Las Grutas and La Rinconada, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Olivero and López-Cabrera (2005). (h) *Patagonichnus stratiformis*. Note associated mud drapes. Lower Miocene, Chenque Formation, roadcut near Comodoro Rivadavia, Patagonia, southern Argentina. Coin is 1.8 cm.

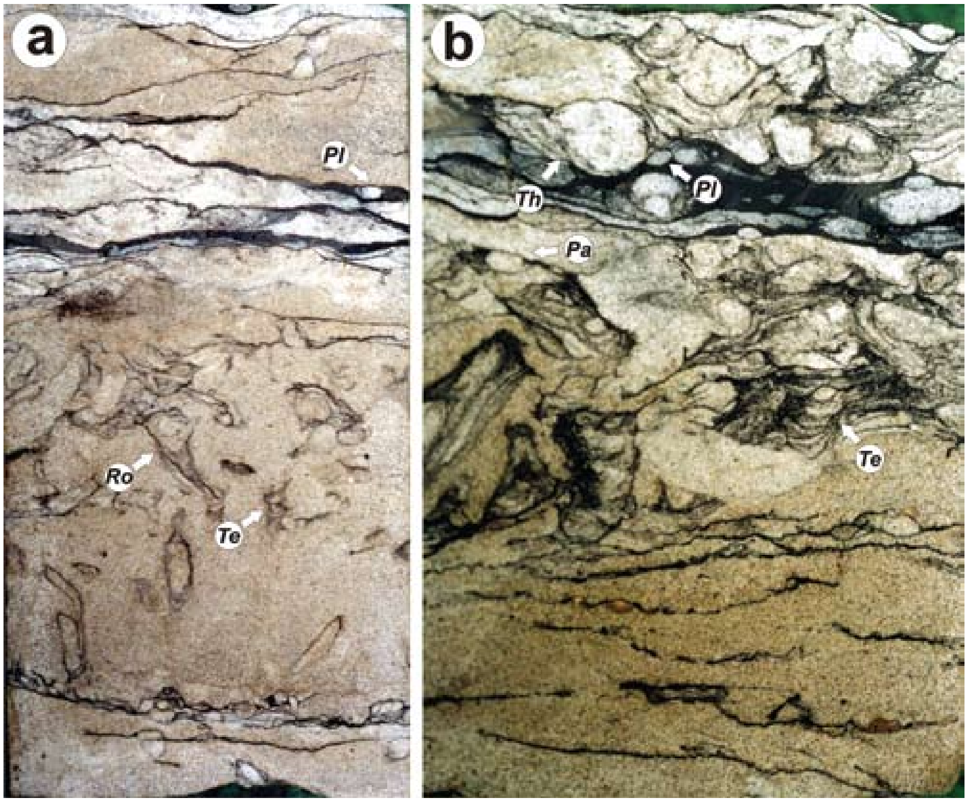

Figure 8.11 Core expression of ichnofaunas from the outer region of tide-dominated estuaries. (a) *Rosselia* isp. (*Ro*) and *Teichichnus rectus* (*Te*) in a sandstone bed. Note *Planolites* isp. (*Pl*) in mud drapes. Upper Cretaceous, Napo Formation, Auca Field, Oriente Basin, Ecuador. Core width is 10 cm. (a) *Thalassinoides* isp. (*Th*), *Teichichnus rectus* (*Te*), *Planolites* isp. (*Pl*) and *Palaeophycus* (*Pa*). Note abundant mud drapes and flaser bedding. Upper Cretaceous, Napo Formation, Shushufindi Field, Oriente Basin, Ecuador. Core width is 10 cm.

Gingras, 2007). Accordingly, they are typically characterized by brackish-water assemblages representing the mixed depauperate *Cruziana* and *Skolithos* ichnofacies (Fig. 8.12). Salinity fluctuations take place on a variety of temporal scales (e.g. daily, monthly and seasonally), imparting a stress signature to the associated biota (MacEachern and Gingras, 2007). This stress results in poorly diverse ichnofaunas and sparse bioturbation, *Teichichnus* (Fig. 8.13a–b) and *Planolites* (Fig. 8.13a–c), being some of the most common ichnogenera in severely restricted settings. Other common ichnogenera are *Rosselia* (Fig. 8.13a) and *Siphonichnus* (Fig. 8.13d). An increase in ichnodiversity, more intense bioturbation, and the presence of certain ichnogenera, such as *Asterosoma* and *Phycosiphon*, commonly suggest less restricted conditions or sporadic breaching of barriers as a result of storms (MacEachern and Gingras, 2007).

Bay-margin deposits consist of heterolithic facies with abundant synaeresis cracks and siderite nodules (MacEachern and Gingras, 2007). Trace fossils are sparsely distributed, with some intervals reaching relatively intense bioturbation. Ichnodiversity is low to rarely moderate. Monospecific suites are common. Typical ichnogenera are *Teichichnus*, *Planolites*, *Rosselia*, *Gyrolithes*, *Cylindrichnus*, *Palaeophycus*, and *Siphonichnus*. The *Glossifungites* ichnofacies is commonly associated with autogenic firmgrounds due to local erosion (MacEachern and Gingras, 2007).

The distal-bay deposits accumulate in the deepest parts of the bays or the most sheltered areas, and tend to be mud-dominated (MacEachern and Gingras, 2007). Thin tempestites layers may occur in strongly storm-affected bays, while dark parallel-laminated mudstones are typical of low-energy anoxic to dysaerobic embayments. Sandy tempestites may bear low-diversity assemblages consisting of *Palaeophycus*, *Planolites*, *Halopoa* (Fig. 8.13e), and *Rhizocorallium* (Fig. 8.13f) (Desjardins *et al.*, 2010b). Oxygen-depleted deposits are either unbioturbated, or contain sporadically distributed small *Planolites* (MacEachern and Gingras, 2007).

Bay-mouth deposits are sedimentologically and ichnologically more variable, and resemble wave-dominated estuary mouths (see Section 8.1.1). The salinity stress is not typically high because the outer region of the bay environment experiences slightly brackish to fully marine conditions. However, high-energy conditions predominate and, therefore, deposits are typically sparsely bioturbated (MacEachern and Gingras, 2007). Vertical burrows of suspension feeders are common in sandstone layers, including *Ophiomorpha*, *Skolithos*, and *Arenicolites*; horizontal traces of both deposit feeders (*Planolites*) and suspension feeders (*Palaeophycus*) occur in associated finer-grained intervals.

8.2.2 OPEN BAYS

Open bays have virtually unrestricted connection to the open sea (MacEachern and Gingras, 2007). As a result, the salinity stress is significantly lower than in restricted bays. However, these authors noted that salinity in the bay is in any case dependent of that of the adjacent seaway, which may be brackish. In addition, substrates are typically sandier than in restricted bays because of the deeper-water position of the wave base.

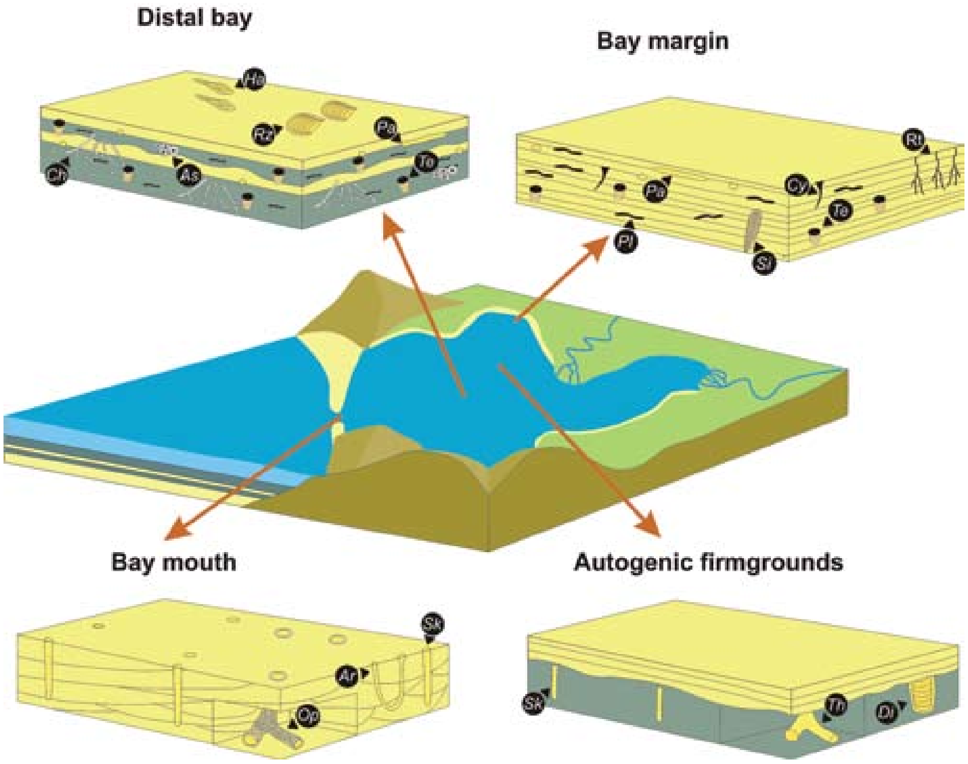

Figure 8.12 Schematic reconstruction of trace-fossil distribution in restricted bays. Bay-margin deposits commonly display low-diversity trace-fossil suites, including *Palaeophycus* (*Pa*), *Planolites* (*Pl*), *Siphonichnus* (*Si*), *Teichichnus* (*Te*), *Cylindrichnus* (*Cy*), and root trace fossils (Rt). Distal-bay deposits may contain more complex forms indicative of slightly less-stressful conditions. Typical ichnotaxa are *Rhizocorallium* (*Rz*), *Halopoa* (*Ha*), *Chondrites* (*Ch*), *Asterosoma* (*As*), *Palaeophycus* (*Pa*), and *Teichichnus* (*Te*). Bay-mouth deposits tend to contain ichnotaxa indicative of relatively high-energy conditions, such as *Ophiomorpha* (*Op*), *Arenicolites* (*Ar*), and *Skolithos* (*Sk*). Autogenic firmgrounds may contain *Skolithos* (*Sk*), *Diplocraterion* (*Di*), and *Thalassinoides* (*Th*).

As a result, open-bay deposits resemble shoreface successions (e.g. Pemberton *et al.*, 2001; MacEachern and Gingras, 2007). Depauperate expressions of the mixed *Cruziana* and *Skolithos* ichnofacies tend to alternate with more archetypal expressions of these ichnofacies (Fig. 8.14). A replacement of the *Skolithos* ichnofacies in bay-margin deposits by elements of the *Cruziana* ichnofacies in distal-bay deposits have been observed in some open bays (MacEachern *et al.*, 1998, 1999c).

Bay-margin deposits are very similar to shoreface successions both in physical and biogenic attributes (see Sections 7.1.3, 7.1.4, and 7.1.5), particularly in bays that are deep or not sheltered from wave approach (MacEachern and Gingras, 2007). Under strong tidal influence, heterolithic tidal-flat deposits become common. The degree of bioturbation is highly variable, with some deposits displaying intense bioturbation. Ichnodiversity is low to relatively high. Typical ichnotaxa include *Teichichnus*, *Thalassinoides*, *Planolites*, *Palaeophycus*, *Arenicolites*, *Cylindrichnus*, *Ophiomorpha*, and *Conichnus*, among many other forms. The presence, albeit restricted, of *Chondrites*, *Zoophycos*, and *Phycosiphon* suggests periods of fully marine conditions. *Teichichnus*, *Palaeophycus*, *Lingulichnus* (Fig. 8.15a), *Asteriacites* (Fig. 8.15b), *Protovirgularia* (Fig. 8.15b), and *Lockeia* (Fig. 8.15b) are common in tidal-flat areas; the latter three may display remarkable size reduction (Mángano *et al.*, 1999; Mángano and Buatois, 2004a).

Distal-bay deposits are mudstone-dominated, but contain a significant proportion of interbedded storm sandstones (MacEachern and Gingras, 2007). Sedimentologically and ichnologically these deposits closely resemble offshore and offshore-transition deposits. The degree of bioturbation is highly variable. Low to moderate bioturbation indexes tend to be common because of high rates of sedimentation in comparison with offshore deposits. However, intense bioturbation has been detected in some basins (Pemberton *et al.*, 2001; Spila *et al.*, 2005). Ichnodiversity varies from low to relatively high. Ichnotaxonomic composition is similar to that of proximal-bay deposits, but with a tendency to show lower proportions of elements of the *Skolithos* ichnofacies. As in the case of proximal-bay deposits, intervals containing less tolerant forms, such as *Chondrites*, *Zoophycos*, and *Phycosiphon*, are probably formed under fully marine conditions. Ichnodiversity levels commonly increase immediately above surfaces containing the *Glossifungites* ichnofacies, indicating transgressive events (MacEachern *et al.*, 1998, 1999c).

8.3 DELTAS

Deltas consist of discrete shoreline protuberances occurring where a river enters a standing body of water, supplying sediments more rapidly than they can be redistributed by basin processes, such as tides and waves (Bhattacharya, 2006). In this section, we will restrict our discussion to marine deltas. In recent years, deltaic systems have become the focus of increased scrutiny and a growing volume of new information is emerging (e.g. Sidi *et al.*, 2003; Giosan and Bhattacharya, 2005; Bhattacharya, 2006). As discussed above (see Section 8.1), ichnological information has been traditionally used to detect stresses associated with dilution of marine salinity in marginal-marine, brackish-water environments, most typically

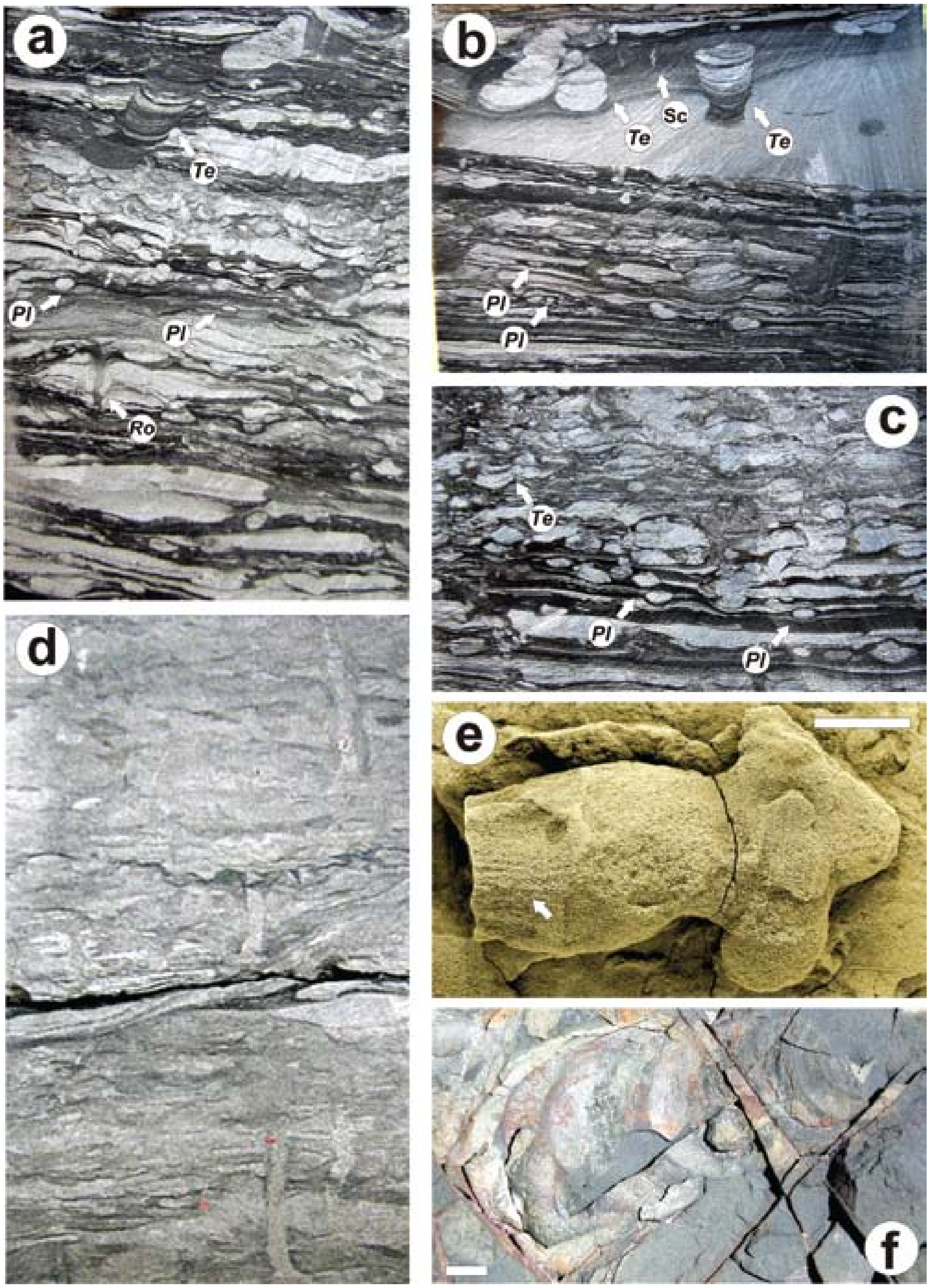

Figure 8.13 Outcrop and core expression of ichnofaunas from restricted bays. (a) Irregularly bioturbated heterolithic deposits containing *Teichichnus rectus* (*Te*), *Planolites montanus* (*Pl*), and small *Rosselia* isp. (*Ro*). Note abundant mud drapes. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (b) *Teichichnus rectus* (*Te*) at the top of a sharp-based tempestite. Note associated tiny *Planolites montanus* (*Pl*), synaeresis cracks (Sc), and mud drapes. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (c) Irregularly bioturbated heterolithic deposits containing *Teichichnus rectus* (*Te*) and *Planolites montanus* (*Pl*). Note well-developed wavy bedding and mud drapes. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (d) Deep-tier vertical *Siphonichnus eccacensis* overprinted to a background ichnofabric. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (e) *Halopoa* isp. with longitudinal striations (arrow). Upper Carboniferous, Tupe Formation, Cuesta de Huaco, Precordillera, Argentina. Scale bar is 1 cm. See Desjardins *et al.* (2010b). (f) *Rhizocorallium commune* with rod-like pellets organized in a spreiten structure. Upper Carboniferous, Tupe Formation, Cuesta de Huaco, Precordillera, Argentina. Scale bar is 1 cm. See Desjardins *et al.* (2010b).

estuarine deposits accumulated in incised valleys, resulting in the brackish-water model (Howard and Frey, 1975; Pemberton and Whightman, 1992; MacEachern and Pemberton, 1994; Buatois *et al.*, 2005) (see Section 6.1.4). However, there are relatively few studies that integrate ichnological information in the context of deltaic dynamics. Our understanding of the ichnology of deltas still suffers from several problems. One of these is the virtual absence of ichnological studies in modern deltas. In addition, some of these problems result from the incomplete picture available from sedimentological studies. In particular, while relatively detailed facies models are available for river- and wave-dominated deltas, the same is not true with respect to tide-dominated deltas (Willis, 2005). Unsurprisingly, tide-dominated deltas are also the least understood from an ichnological standpoint. Furthermore, while the brackish-water model is clearly of use in understanding ichnofaunas from embayment areas associated with the delta plain, its applicability in delta-front and prodelta settings is not straightforward (MacEachern *et al.*, 2005).

MacEachern *et al.* (2005) discussed the most important environmental controls and processes that represent stress factors in deltas. These factors result from the complex interplay of

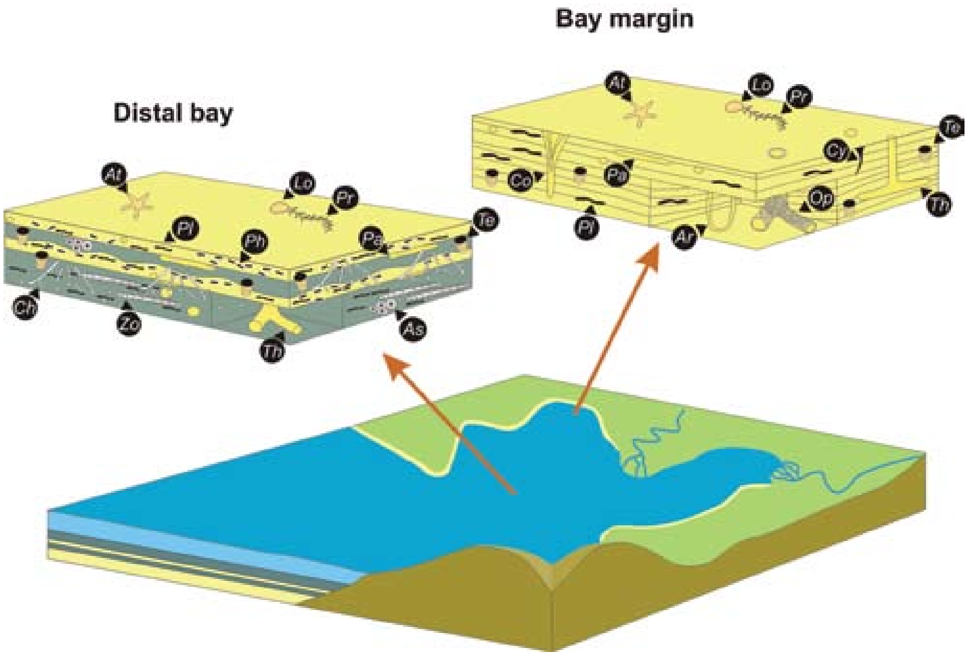

Figure 8.14 Schematic reconstruction of trace-fossil distribution in open bays. Ichnofaunas from open bays are more diverse than those in restricted bays. Bay-margin deposits may contain *Teichichnus* (*Te*), *Thalassinoides* (*Th*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Arenicolites* (*Ar*), *Cylindrichnus* (*Cy*), *Ophiomorpha* (*Op*), *Conichnus* (*Co*), *Asteriacites* (*At*), *Protovirgularia* (*Pr*), *Phycosiphon* (*Ph*), and *Lockeia* (*Lo*). Distal-bay deposits are ichnologically similar to proximal-bay deposits, but may also include ichnotaxa that are even less tolerant of brackish-water conditions, such as *Chondrites* (*Ch*), *Zoophycos* (*Zo*), and *Asterosoma* (*As*).

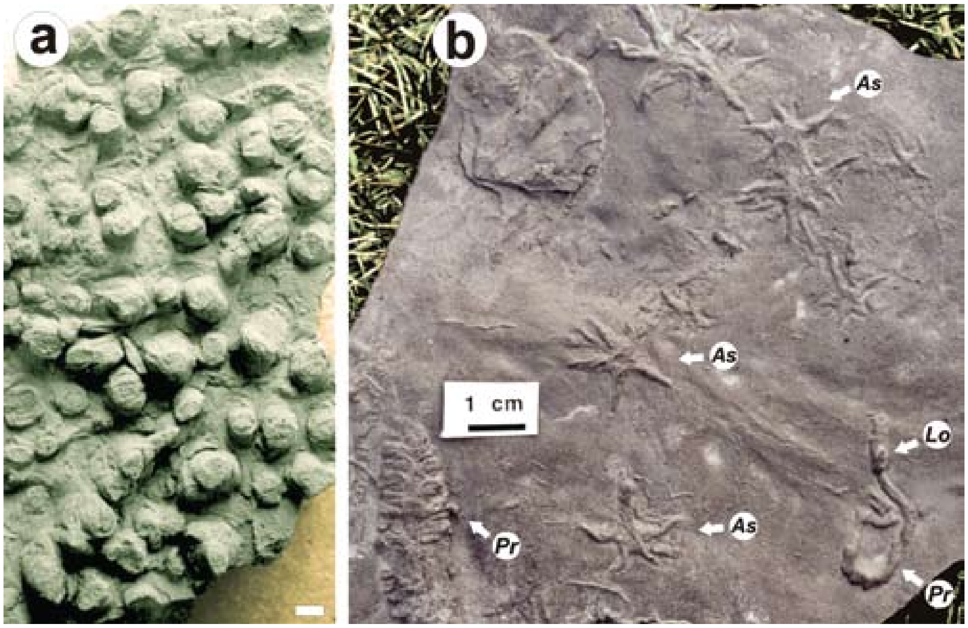

Figure 8.15 Ichnofaunas from open-bay deposits in outcrop. See Mángano and Buatois (2004b). (a) The lingulid dwelling trace *Lingulichnus* isp. on the base of a sandstone bed. Upper Carboniferous, Rock Lake Shale, Stanton Limestone, Lansing Group, quarry near Coleman Creek, southeast of Eudora, northeastern Kansas, United States. Scale bar is 1 cm. (b) The ophiuroid resting trace *Asteriacites lumbricalis* (*As*), and the bivalve traces *Lockeia siliquaria* (*Lo*) and *Protovigularia rugosa* (*Pr*) on the base of a sandstone bed. Note the small size of the compound bivalve trace fossil. Upper Carboniferous, Stull Shale, Kanwaka Shale Formation, Shawnee Group, roadcut along Country Road 6, south of Stull, northeastern Kansas, United States.

fluvial, wave, and tidal processes. River-induced stresses include heightened sedimentation rates, water turbidity, salinity changes (freshets), episodic sediment gravity deposition, hyperpycnal flows, and phytodetrital pulses. Wave-induced stresses include wave energy levels, repeated erosion, and longshore drift. Tidal-induced stresses comprise clay flocculation and fluid-mud deposition. Identification of these stress factors is essential to distinguish deltas from prograding strandplains. In this section, we address the ichnology of river-, wave- and tide-dominated deltas, following the genetic classification of Galloway (1975). However, this framework works at its best when combined with other classification schemes, which take into consideration other factors, such as sediment caliper (Orton and Reading, 1993) and site of emplacement (Porębski and Steel, 2006). In addition, most deltas are mixed, reflecting variable contributions of fluvial, wave, and tidal processes (e.g. Giosan *et al*., 2005).

8.3.1 RIVER-DOMINATED DELTAS

River-dominated deltas arguably rank among the most stressful of all deltas. This is mostly due to the overwhelming predominance of river-induced stresses. As a consequence, river-dominated

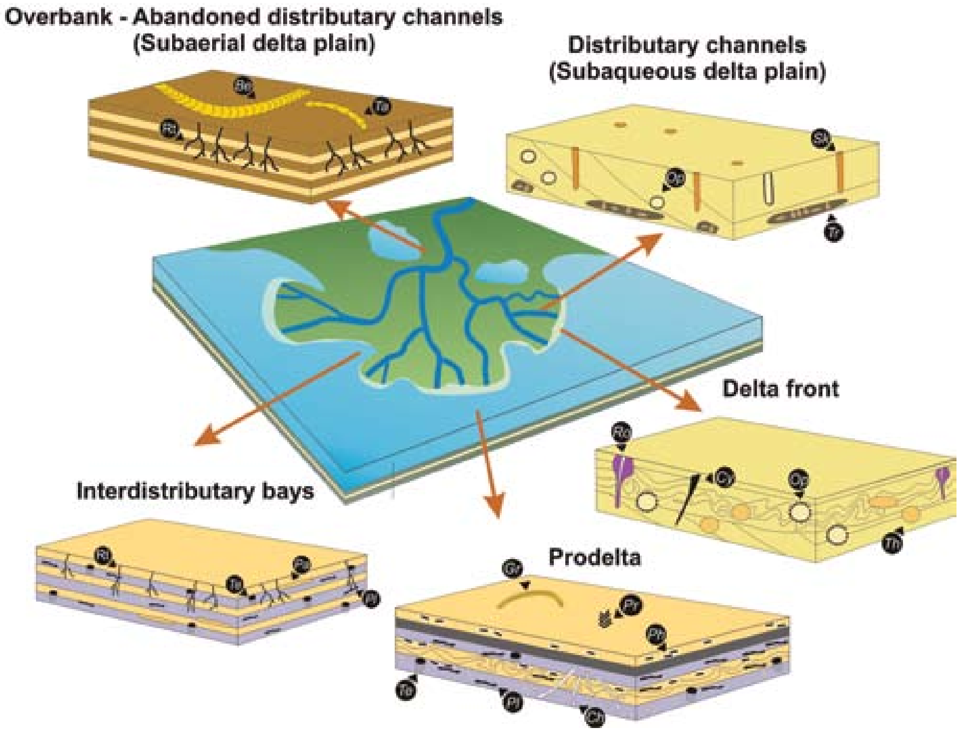

Figure 8.16 Schematic reconstruction of trace-fossil distribution in river-dominated deltas. Abandoned-channel and overbank deposits of the subaerial delta plain typically contain *Beaconites* (*Be*), *Taenidium* (*Ta*), and root traces (Rt). Distributary-channel deposits of the subaqueous delta plain may contain *Ophiomorpha* (*Op*) and *Skolithos* (*Sk*); *Teredolites* (*Tr*) may occur in wood logs at the base of the channel. Interdistributary-bay deposits typically host *Planolites* (*Pl*), *Teichichnus* (*Te*), *Palaeophycus* (*Pa*), and root traces (Rt). Delta-front deposits may contain *Rosselia* (*Ro*), *Ophiomorpha* (*Op*), *Cylindrichnus* (*Cy*), and *Thalassinoides* (*Th*). Prodelta deposits typically exhibit *Teichichnus* (*Te*), *Planolites* (*Pl*), *Phycosiphon* (*Ph*), *Chondrites* (*Ch*), *Protovirgularia* (*Pr*), and *Gyrochorte* (*Gr*).

Box 8.3 Ichnology of a late Quaternary fan-delta complex, South Island, New Zealand

Nearly continuous outcrops along the depositional strike of a late Quaternary fan delta in the South Island of New Zealand allows careful examination of its sedimentological and ichnological attributes. The complex consisted of a number of alluvial fans that prograded into the sea directly feeding small gravel and loess fan deltas separated by embayment areas. The embayment deposits consist of reworked loess, and sand and pebble forming bars. Trace fossils are remarkably well preserved, commonly showing full three-dimensional relief. No trace fossils occur in the subaerial fan delta-plain deposits, but marine biogenic structures are abundant in embayment, bar, and prodelta facies. Proximal deposits of the embayment contain abundant root trace fossils but not animal trace fossils, while distal loess deposits are characterized by the local presence of monospecific assemblages of *Phycosiphon incertum*, forming intensely bioturbated layers. Distal-embayment deposits also contain a trace-fossil association dominated by *Diplocraterion parallelum* with subordinate occurrences of other ichnotaxa, such as *Asterosoma* isp. and *Piscichnus* isp. The bar facies is also dominated by *Diplocraterion parallelum*; other trace fossils such as *Arenicolites* isp., *Cylindrichnus concentricus*, *Skolithos linearis*, and escape traces are locally abundant. Prodelta deposits are intensely bioturbated by poorly preserved specimens of *Planolites montanus*, with other ichnotaxa (e.g. *Diplocraterion parallelum*) locally present. A number of stress factors, such as salinity, interstitial oxygen, sediment composition and texture, hydrodynamic energy, and sedimentation rate, controlled the distribution of trace fossils in the fan-delta complex. Brackish water and reduced interstitial oxygen may have been limiting factors, particularly in the distal embayment, judging from the common occurrence of monospecific suites. This is consistent with limited circulation due to the presence of bars that partially isolated the embayment from the open sea. The presence of *Phycosiphon incertum* is restricted to fine-grained loess, indicating a strong substrate control. Loess cohesiveness may have allowed the *Phycosiphon* producer to keep its tunnel system open, allowing for respiration in poorly oxygenated substrate. High hydrodynamic energy in bar environments is suggested by the predominance of vertical burrows. In addition, high sedimentation rates in these settings are indicated by the presence of escape trace fossils.

Reference: Ekdale and Lewis (1991b), and Lewis and Ekdale (1991).

deltas tend to contain more depauperate ichnofaunas than wave- and tide-dominated deltas (Gingras *et al.*, 1998; MacEachern *et al.*, 2005) (Fig. 8.16) (Box 8.3). Ichnofaunas from the subaerial delta plain consist of a combination of terrestrial and freshwater trace fossils because they record conditions in the portion of the delta that is located above the high tide. Therefore, distributary channel and overbank ichnofaunas closely resemble those of fluvial channels and overbanks of alluvial plains (see Section

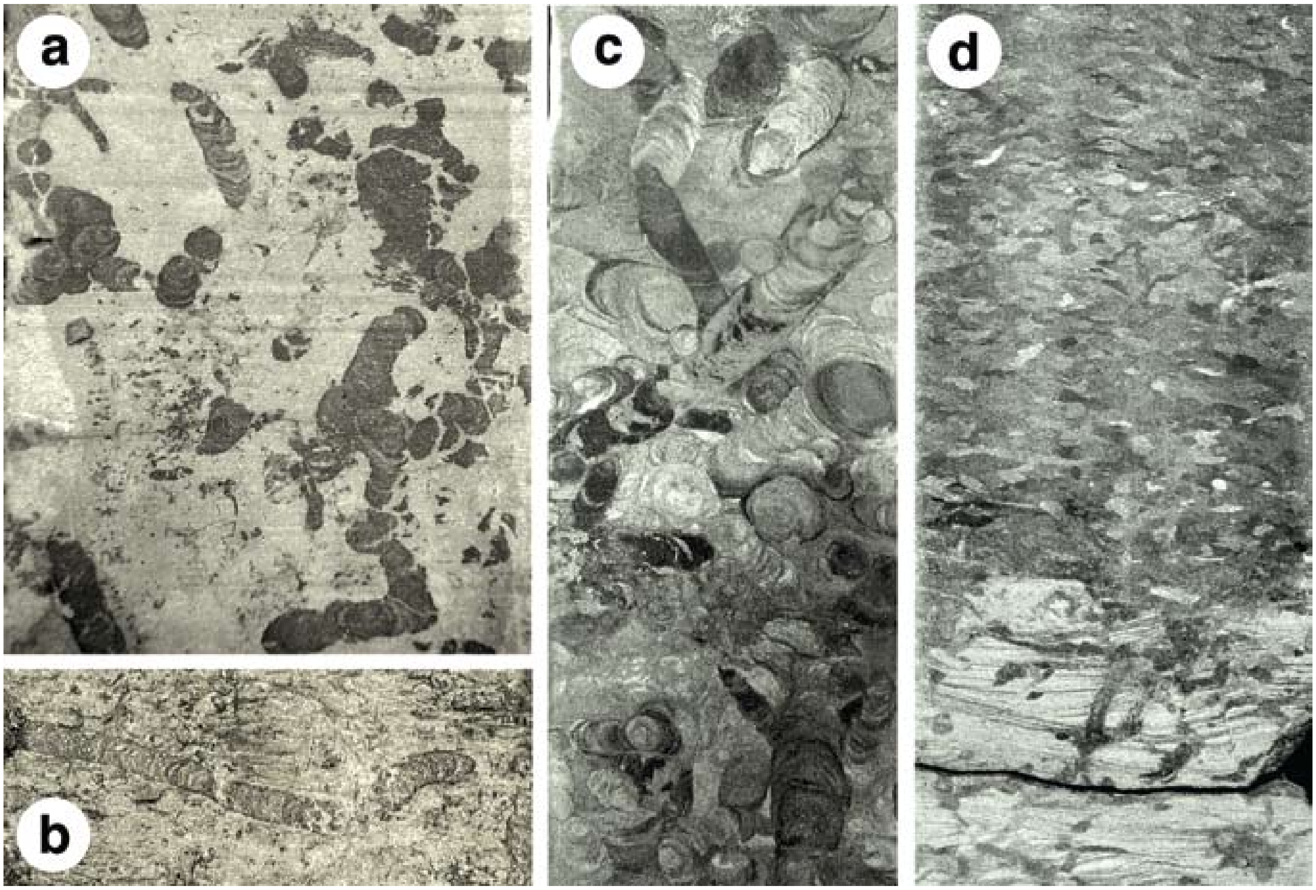

Figure 8.17 Core expression of ichnofaunas from subaerial delta-plain deposits. Oligocene–Middle Miocene, Guafita Formation, Guafita Field, Apure, Venezuela. (a) The meniscate trace fossil *Taenidium* in red siltstone. Core width is 10 cm. (b) Close-up of *Taenidium*. Core width is 10 cm. (c) High-density of meniscate trace fossils in red siltstone. Core width is 10 cm. (d) Crevasse-splay sandstone (lower interval) and floodplain siltstone (upper interval). Note colonization by *Taenidium* and high intensity of bioturbation in the siltstone. Core width is 9 cm.

10.2). *Taenidium* and *Beaconites* are typical components of the *Scoyenia* ichnofacies in these settings (Fig. 8.17a–d). Because of the high frequency of crevassing and overbank events, the *Scoyenia* ichnofacies tends to be common in the subaerial delta plain of river-dominated systems (e.g. Pollard, 1988). Bivalve (*Lockeia*) and xiphosurid (*Kouphichnium* and *Selenichnites*) trace fossils may occur also (Eagar *et al*., 1985). However, during times of reduced or no discharge, the salt wedge may extend upstream, generating brackish-water conditions across the delta plain and colonization by elements of the mixed depauperate *Cruziana* and *Skolithos* ichnofacies (e.g. Corbeanu *et al*., 2004; Garrison and van der Berg, 2004).

Brackish-water conditions are persistent in the proximal regions of deltas, particularly the subaqueous delta plain, interdistributary bays, and the distributary mouth bars at the proximal delta front (MacEachern *et al*., 2005). Ichnofaunas in these subenvironments basically display the diagnostic features outlined by the brackish-water model (see Section 6.1.4). Bioturbation is remarkably sparse and ichnodiversity levels are very low. *Ophiomorpha* and *Diplocraterion* occur locally in abandoned delta-plain distributary-channel, abandoned terminal distributary-channel and mouth-bar sandstone (e.g. Hobday and Tavener-Smith, 1975). Retrusive forms of *Diplocraterion* may be common, indicating high sedimentation rates (e.g. Turner *et al*., 1981). Logs with *Teredolites* are common on channel floors (e.g. MacEachern *et al*., 2005). Escape trace fossils may occur locally reflecting rapid sedimentation within the channels. Interdistributary-bay mudstone commonly contains *Planolites* and *Teichichnus* as dominant components, typically associated with synaeresis cracks. Root traces record the presence of waterlogged paleosols in swamp areas.

Periodic salinity fluctuations due to freshwater input from rivers (freshets of MacEachern *et al*., 2005) may take place in more distal areas, and, in fact, play a major role in delta-front and prodelta environments. As a result, even in these distal settings, ichnofaunas from river-dominated deltas are impoverished. Freshets are typically revealed by the association of synaeresis cracks, siderite bands and nodules, and depauperate occurrences of the *Cruziana* ichnofacies (MacEachern *et al*., 2005). Low ichnodiversity of individual suites (Fig. 8.18a–b) reveals a stress factor due to reduced salinity, and allows distinction from non-deltaic strandplain–shoreface successions. However, the local occurrence

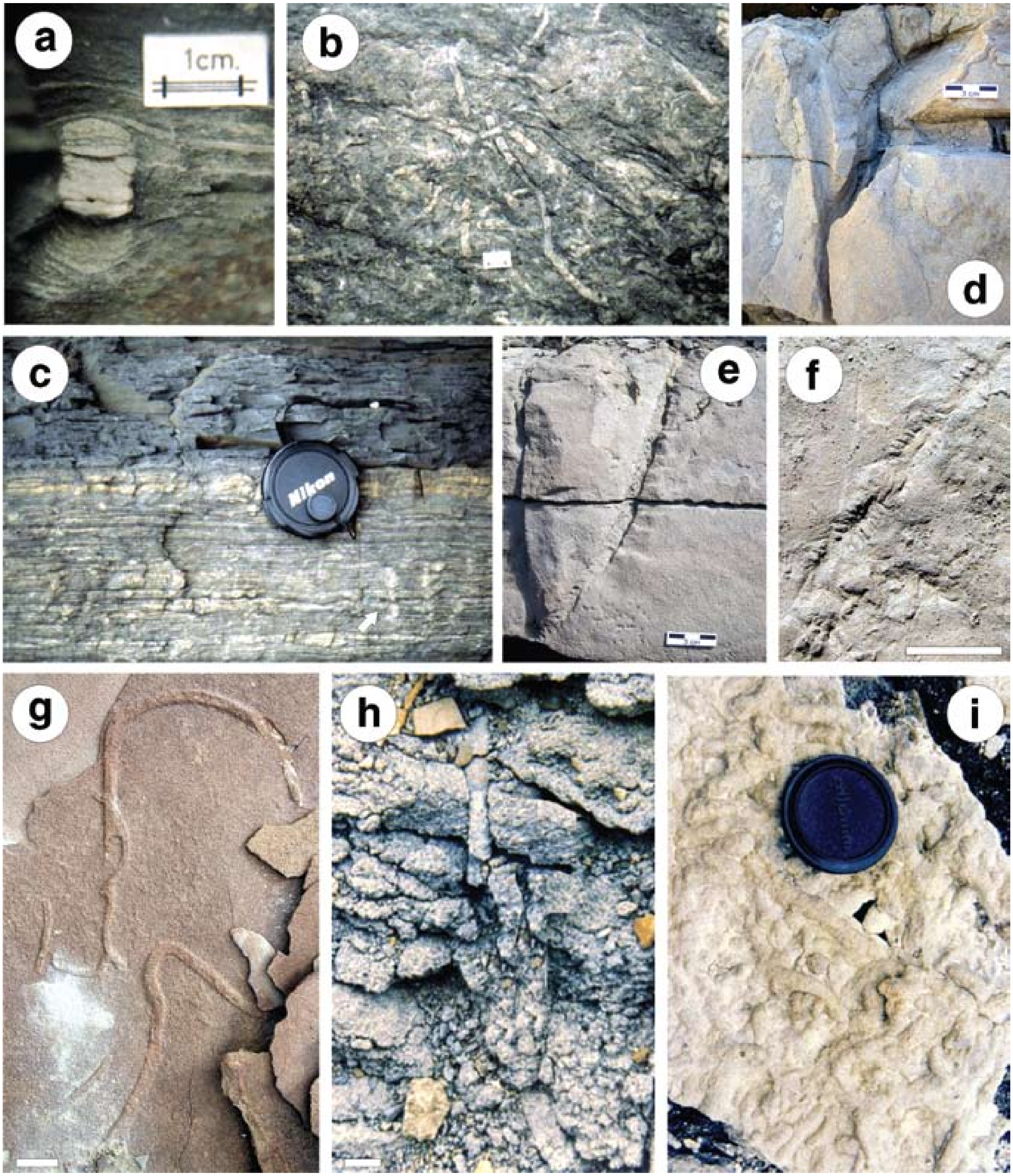

Figure 8.18 Outcrop expression of ichnofaunas from river-dominated delta-front and prodelta deposits. (a) *Teichichnus rectus* with well-defined causative burrow in prodelta siltstone-rich deposits. Upper Carboniferous, Westward Ho! Formation, Bideford Group, north Devon coast, southwestern England. (b) Bedding-plane view of a monospecific suite of *Teichichnus rectus* in prodelta siltstone-rich deposits. Upper Carboniferous, Westward Ho! Formation, Bideford Group, north Devon coast, southwestern England. Scale bar is 1 cm. (c) Escape trace fossils (arrow) in prodelta siltstone-rich deposits. Note overlying unburrowed fluid mudstone. Upper Carboniferous, Westward Ho! Formation, Bideford Group, north Devon coast, southwestern England. Lens cover is 5 cm. (d) *Rosselia chonoides* in delta-front turbidites. Upper Cretaceous, Panther Tongue, Star Point Formation, Gentile Wash, near Price, Book Cliffs, eastern Utah, United States. See Bhattacharya *et al*. (2007). (e) Vertical *Ophiomorpha nodosa* in delta-front turbidites. Upper Cretaceous, Panther Tongue, Star Point Formation, Gentile Wash, near Price, Book Cliffs, eastern Utah, United States. See Bhattacharya *et al*. (2007). (f) *Protovirgularia* isp. in prodelta-lobe deposits. Upper Cretaceous, Kennilworth Member, Blackhawk Formation, Hatch Mesa, Book Cliffs, eastern Utah, United States. Scale bar is 1 cm. (g) *Gyrochorte* isp. in prodelta-lobe deposits. Upper Cretaceous, Kennilworth Member, Blackhawk Formation, south entrance to Tusher Canyon, Book Cliffs, eastern Utah, United States. Scale bar is 1 cm. (h) *Skolithos* isp. in coarse-grained fan-delta front deposits. Upper Cretaceous, Hidden Lake Formation, Bajo de la Angustia, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois and López Angriman (1992a). (i) *Palaeophycus tubularis* in coarse-grained fan-delta front deposits. Upper Cretaceous, Hidden Lake Formation, Bajo de la Angustia, James Ross Island, Antarctica. Lens cover is 5 cm. See Buatois and López Angriman (1992a).

of ichnotaxa more typical of open-marine environments (e.g. *Phycosiphon*, *Chondrites*) suggests periods of normal-marine salinity that alternated with dilution due to fluvial discharge.

In addition to freshwater discharge, water turbidity represents another stress factor in river-dominated deltas (see Section 6.1.8). Deltas that developed under hypopycnal conditions are commonly characterized by buoyant plumes leading to rapid flocculation of clays (Bates, 1953; Wright, 1977; Kineke *et al.*, 1996). High suspended loads of fine-grained material related to river influx clog the filter-feeding apparatus of suspension feeders, therefore resulting in an impoverishment or direct suppression of the *Skolithos* ichnofacies (Gingras *et al.* 1998; MacEachern *et al.* 2005). In addition, accumulation of fluid muds in distal delta fronts and prodeltas imparts a substrate stress by reducing boundary shear stress, preventing benthic organisms from constructing permanent structures or actively backfill tunnels (see Section 6.1.2). Sediment swimming is the only possible strategy in these soupy substrates (Schieber, 2003). Even in the case that benthic organisms are able to burrow into these substrates, preservation of these structures is unlikely (Ekdale, 1985). As a result, fluid mud is typically unbioturbated or, more rarely, contains “mantle and swirl” biogenic structures (Schieber, 2003; Bhattacharya and MacEachern, 2009).

The delta front and prodelta of river-dominated deltas is also influenced by rapid rates of sedimentation. Under hyperpycnal conditions, underflow currents move off river mouths along the sea floor. Underflow triggering is particularly common at the mouth of small- to medium-sized rivers (Mulder and Syvitski, 1995). Hyperpycnal flows are commonly conducive to rapid deposition. Also, rapid rates of sedimentation are associated with sediment gravity flows produced by delta-front bar failure. In both situations, colonization of the substrate by benthic organisms is inhibited or reduced due to a combination of rapid deposition and high frequency of sedimentation events (MacEachern *et al.*, 2005). As a consequence, these rapidly emplaced layers tend to be sparsely bioturbated, may contain escape trace fossils (Figs. 8.18c and 8.19e), and commonly display a colonization surface at the top of the event bed (Fig. 8.18d–e). The low degree of bioturbation of these event beds may contrast with the more intense bioturbation of associated finer-grained deposits if background sedimentation rate is not high (Fig. 8.19a). Under more continuous deposition from river-fed density underflows, ichnological evidence indicates animal activity contemporaneous with sedimentation instead of colonization after a major break in deposition. Highly compressed specimens of *Thalassinoides* filled with parallel-laminated sand may occur in sandy hyperpycnites, suggesting high rates of sedimentation and emplacement of water-saturated sand (Buatois *et al.*, 2011) (Fig. 8.19b). Associated trace fossils are *Teichichnus* (Fig. 8.19c) and *Diplocraterion* (Fig. 8.19d). In some case, lobes may consist of a complex facies mosaic of classic turbidites, sandy hyperpycnites, wave-modified turbidites, and storm-generated beds (Pattison, 2005; Pattison *et al.*, 2007). Common ichnogenera in these deposits are *Protovirgularia* (Fig. 8.18f), *Palaeophycus*, *Skolithos*, *Gyrochorte* (Fig. 8.18g), *Phycosiphon*, and *Rosselia* (Buatois *et al.*, 2010b). MacEachern *et al.* (2005) noted that hyperpycnal events are commonly linked to freshets and increased phytodetrital influx (Fig. 8.19e) creating a whole set of stress factors to benthic life. In turn, phytodetrital pulses are linked to oxidation of organic carbon and oxygen depletion. It is therefore unsurprising that *Chondrites* is one of the dominant forms in many river-dominated prodelta mudstones (MacEachern *et al.*, 2005). Freshwater discharge may be extreme in glaciated basins significantly affecting coastal ecosystems (see Section 8.4).

The importance of sediment caliper in deltaic depositional systems has long been recognized (Orton and Reading, 1993). In the case of coarse-grained systems, such as fan deltas, high-energy conditions, high rates of sedimentation and dominance of coarse grain size are major factors leading to reduced diversity and bioturbation restricted to localized levels (e.g. Ekdale and Lewis, 1991b; Buatois and López Angriman, 1992a) (Fig. 8.18h–i). However, Ekdale and Lewis (1991b) noted relatively high diversity levels in bar deposits of a gravel and loess fan-delta complex (Box 8.3). Robust dwelling structures (e.g. *Thalassinoides*, *Ophiomorpha*) seem to be the dominant components of fan-delta ichnofaunas (e.g. Buatois and López Angriman, 1992a; Siggerud and Steel, 1999). Fan-delta plain deposits are typically unbioturbated (Ekdale and Lewis, 1991b).

8.3.2 WAVE-DOMINATED DELTAS

In terms of the importance of stress factors, wave-dominated deltas rank among the least stressful of all deltaic systems (Fig. 8.20) (Box 8.4). In fact, distinction of wave-dominated delta front and prodelta from wave-dominated strandplain deposits is exceedingly difficult and the precise depositional setting of many successions remains controversial (e.g. Howell and Flint, 2003; Bhattacharya and Giosan, 2003; Bhattacharya, 2006). Ichnofaunas from the subaerial delta plain are identical to those from river-dominated deltas (see Section 8.3.1), although frequency of crevassing and overbank events is lower and, therefore, the *Scoyenia* ichnofacies is not as widespread.

The subaqueous delta plain is by far the most stressful setting in wave-dominated deltas. Distributary-channel and interdistributary-bay deposits are sparsely bioturbated and contain typical brackish-water assemblages. In fact, distributary-channel deposits are commonly unbioturbated; *Ophiomorpha* (Fig. 8.21a) and *Skolithos* may locally occur at colonization surfaces typically reflecting pauses in sedimentation or channel abandonment. Escape trace fossils may occur also. Interdistributary-bay deposits contain suites that reflect lower-energy conditions. *Planolites* (Fig. 8.21b), *Palaeophycus*, *Teichichnus* (Fig. 8.21b), and root trace fossils (Fig. 8.21c) are the dominant components in protected bay areas. *Rosselia* (Fig. 8.21d) and *Cylindrichnus* may be present locally. Subaqueous delta-plain assemblages display all the characteristics of brackish-water ichnofaunas, namely low ichnodiversity, forms typically found in marine environments, dominance of infaunal traces rather than epifaunal trails, simple structures produced by trophic generalists, mixture of vertical and horizontal traces from the *Skolithos*

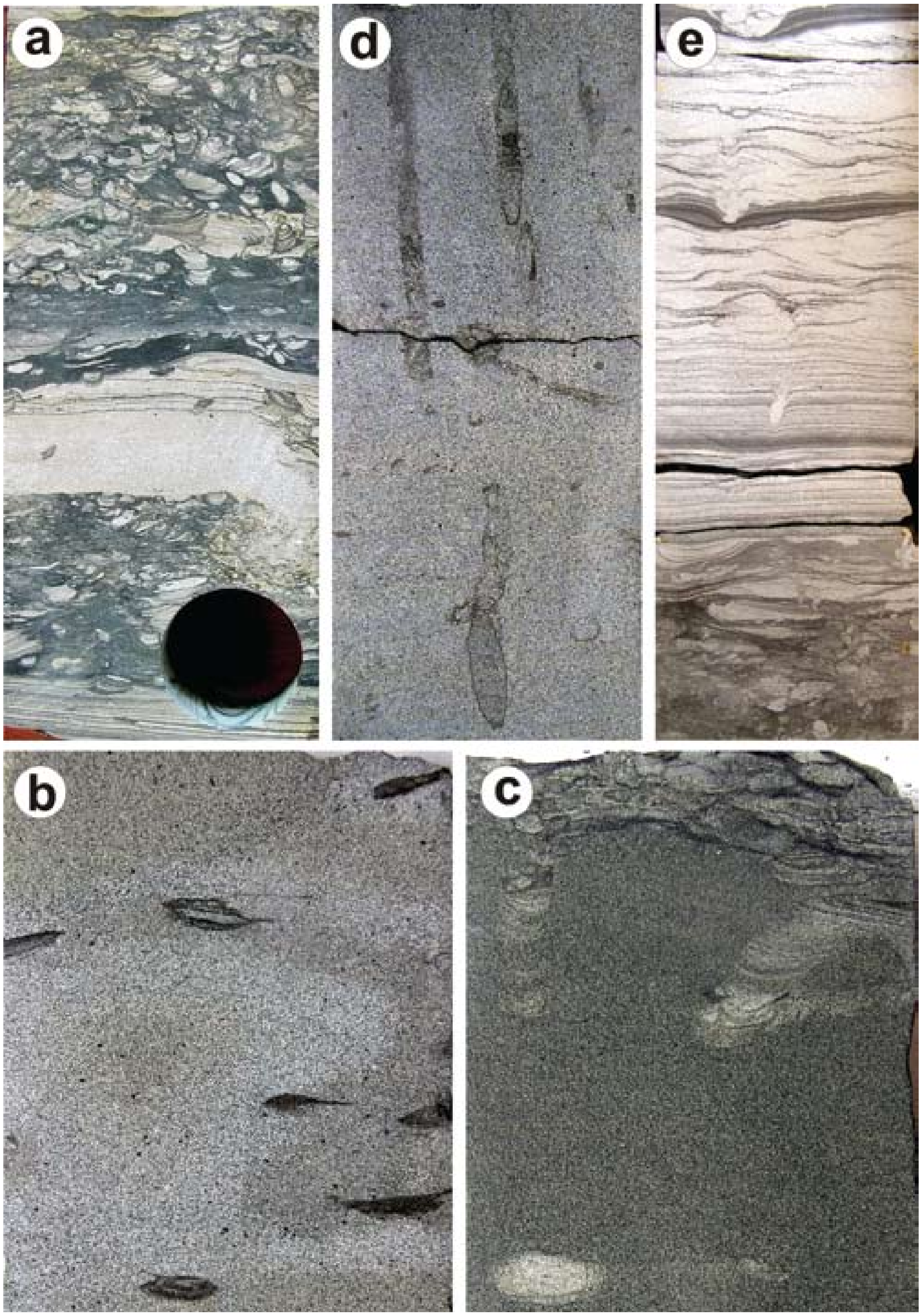

Figure 8.19 Core expression of ichnofaunas from river-dominated delta-front and prodelta deposits. (a) Proximal-prodelta sharp-based sparsely bioturbated event sandstone layer interbedded with intensely bioturbated finer-grained deposits containing a trace-fossil suite dominated by *Teichichnus rectus*. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (b) Highly compressed, mud-lined *Thalassinoides* isp. showing infill with passive parallel lamination in sandy hyperpycnal-lobe deposits. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (c) Retrusive *Teichichnus* isp. in sandy hyperpycnal-lobe deposits. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (d) Long U-shaped *Diplocraterion* isp. burrows in sandy hyperpycnal-lobe deposits. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (e) Escape trace fossils in distal delta-front deposits. Note more intense bioturbation in underlying mudstone. Thin dark lamina of carbonaceous detritus record phytodetrital pulses. Upper Cretaceous, Ferron Sandstone, Ivie Creek #3, Ivie Creek area, eastern Utah, United States. Core width is 9 cm. See MacEachern *et al.* (2007b).

and *Cruziana* ichnofacies, abundance of some ichnotaxa, and presence of monospecific suites (see Section 6.1.4).

Proximal to distal delta-front deposits of wave-dominated deltas are commonly characterized by a combination of the *Skolithos* and *Cruziana* ichnofacies (MacEachern *et al.*, 2005). As in the case of river-dominated deltas, *Ophiomorpha* is common in terminal distributary-channel deposits (Fig. 8.21e). Some detritus-feeding traces (e.g. *Cylindrichnus*) are components of the *Skolithos* ichnofacies in proximal delta-front deposits. Impoverishment of the *Skolithos* ichnofacies rather than suppression seems to be the norm in wave-dominated deltas in contrast to more stressful river-dominated ones. In storm-dominated settings, periodic fluvial discharges alternate with storm events and suspension fallout, leaving diagnostic ichnological signatures in the deposits. Repeated storm events rank among the most important controlling factors in these deltas. Storm-influenced clastic deposits comprise two contrasting trace-fossil assemblages that reflect the behavioral response of the benthic fauna that developed under two successive and contrasting environmental conditions (see Section 7.1). The

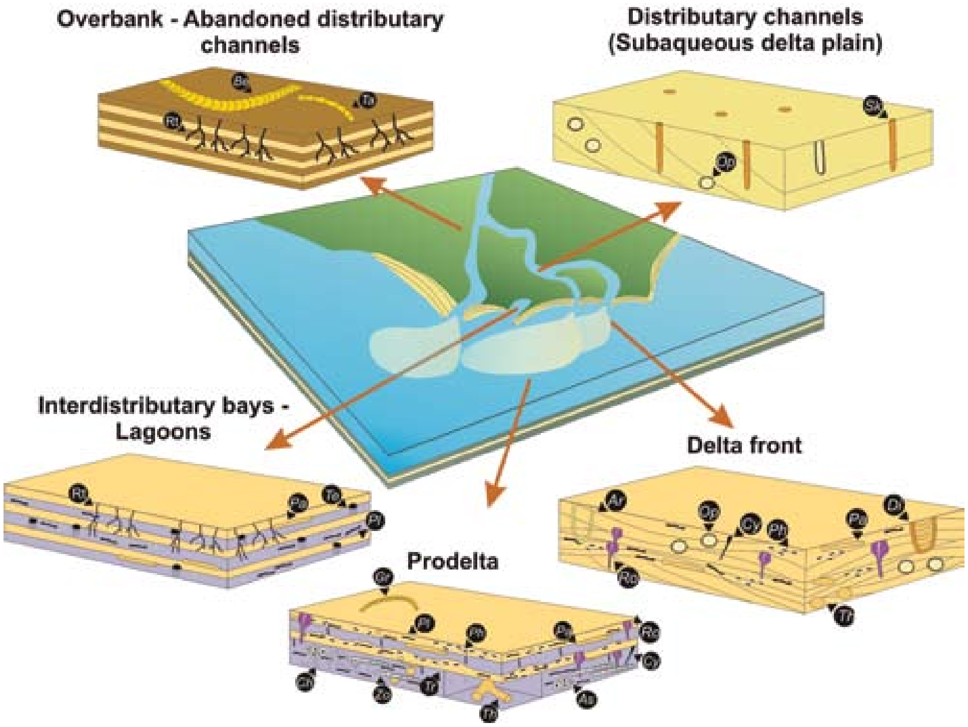

Figure 8.20 Schematic reconstruction of trace-fossil distribution in wave-dominated deltas. As in the case of river-dominated deltas, abandoned-channel and overbank deposits of the subaerial delta plain typically contain *Beaconites* (*Be*), *Taenidium* (*Ta*), and root traces (Rt). Distributary-channel deposits of the subaqueous delta plain may contain *Ophiomorpha* (*Op*) and *Skolithos* (*Sk*). Interdistributary-bay and lagoonal deposits typically display *Planolites* (*Pl*), *Teichichnus* (*Te*), *Palaeophycus* (*Pa*), and root traces (Rt). Delta-front deposits may contain *Rosselia* (*Ro*), *Ophiomorpha* (*Op*), *Cylindrichnus* (*Cy*), *Thalassinoides* (*Th*), *Palaeophycus* (*Pa*), *Diplocraterion* (*Di*), *Phycosiphon* (*Ph*), and *Arenicolites* (*Ar*). Prodelta deposits exhibit various ichnotaxa, such as *Teichichnus* (*Te*), *Planolites* (*Pl*), *Phycosiphon* (*Ph*), *Chondrites* (*Ch*), *Protovirgularia* (*Pr*), *Zoophycos* (*Zo*), *Trichichnus* (*Tr*), *Asterosoma* (*As*), *Thalassinoides* (*Th*), *Palaeophycus* (*Pa*), and *Gyrochorte* (*Gr*).

Box 8.4 Ichnology of a Lower Miocene wave-dominated delta in the subsurface of the Eastern Venezuela Basin

The Eastern Venezuela Basin hosts a number of deltaic sandstones that have been intensely explored petroleum targets. Detailed ichnological and sedimentological observations in cores allow the interpretation of Lower Miocene deposits in the Tácata field as the result of progradation of a wave-dominated delta complex. Repeated storms were one the most important controlling factors on the front of the Tácata deltas and on the lower/middle shoreface of associated strandplains. Amalgamated, thick-bedded storm deposits are typically unburrowed or contain deep vertical *Ophiomorpha* (Fig. 8.22a). Delta-front and prodelta deposits, although being characterized by sparse bioturbation and depauperate trace-fossil suites (Fig. 8.22b–c), contain some ichnotaxa that typically do not occur in brackish-water settings, such as *Chondrites* and *Phycosiphon* (Fig. 8.22d). Preservation of very thin storm layers was regarded as more common of wave-dominated deltas than of strandplain systems because deltaic stresses preclude the establishment of an abundant infauna that otherwise would have completely reworked such thin sandstone layers. Tidal influence was subordinate and restricted to distributary-channel and, particularly, interdistributary-bay deposits. Interdistributary-bay deposits are sparsely bioturbated and their ichnofaunas, typically dominated by *Teichichnus* (Fig. 8.21b) and *Planolites*, tend to display all the characteristics expected from brackish-water settings. Distributary-channel deposits are sparsely bioturbated, but the presence of certain ichnotaxa (e.g. *Ophiomorpha*; Fig. 8.21e) allows distinction from freshwater fluvial channels. Ichnological evidence has been essential to differentiate between deltaic and associated along-strike strandplain–shoreface successions, and to detect possible delta asymmetry. In particular, *Scolicia* ichnofabrics (Fig. 8.22e–f) are restricted to fully marine offshore deposits that accumulated on the updrift side of the river mouths. Associated fully marine deposits are also characterized by an overall increase in ichnodiversity and degree of bioturbation (Fig. 8.22g). This study illustrates how ichnological data used in conjunction with sedimentological evidence helps to identify deltaic signatures that otherwise may remain undetected.

Reference: Buatois *et al*. (2008).

resident, fair-weather trace-fossil assemblage records the establishment of a benthic community developed under stable and rather predictable conditions, and commonly belongs to the *Cruziana* ichnofacies. The storm-related trace-fossil assemblage reflects colonization after storm deposition and records the establishment of an opportunistic community, commonly represented by the *Skolithos* ichnofacies (Fig. 8.23a–b). Deep, vertical *Ophiomorpha*, *Cylindrichnus*, *Rosselia*, *Palaeophycus*, *Arenicolites*, *Diplocraterion*, *Skolithos*, robust *Thalassinoides*, and escape trace fossils are common components in delta fronts of wave-dominated deltas characterized by frequent and intense storm events. In these settings the fair-weather suite is poorly

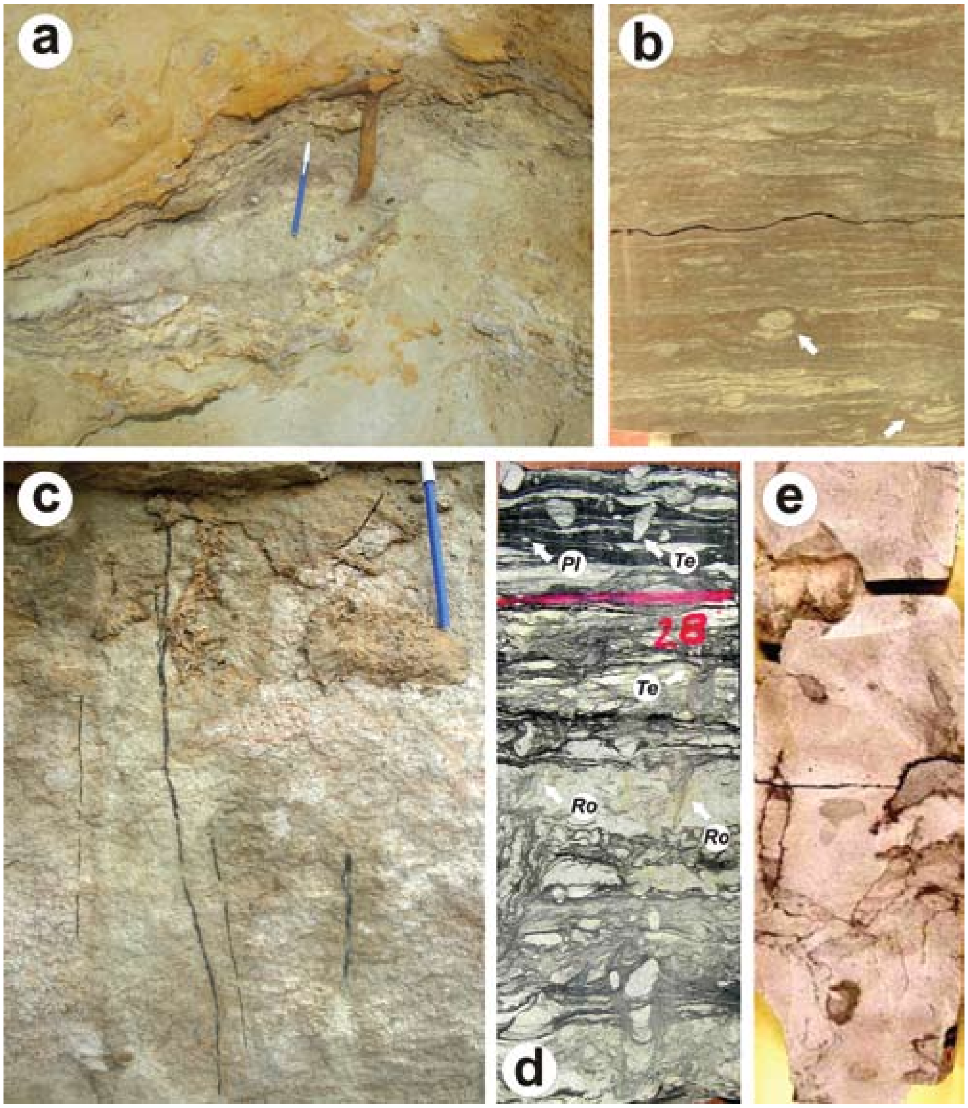

Figure 8.21 Outcrop and core expression of ichnofaunas from subaqueous delta-plain and terminal distributary-channel deposits in wave-dominated deltas. (a) *Ophiomorpha* isp. at the top of a distributary-channel deposit. Upper Miocene, Urumaco Formation, Urumaco River, northwest Venezuela. Pen is 15 cm. (b) Sparsely bioturbated interdistributary bay/lagoonal deposits containing a low-diversity trace-fossil suite dominated by *Teichichnus rectus* (arrows). Lower Miocene, Tácata Field, Eastern Venezuela Basin. Core width is 7 cm. See Buatois *et al*., (2008). (c) Root trace fossils in crevasse-splay deposits in an interdistributary bay. Upper Miocene, Urumaco Formation, Urumaco River, northwest Venezuela. Pen is 15 cm. (d) Interdistributary-bay deposits containing a low-diversity suite dominated by *Rosselia* isp. (*Ro*). *Teichichnus rectus* (*Te*) and *Planolites montanus* (*Pl*) are also abundant. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (e) *Ophiomorpha nodosa* in terminal distributary-channel deposits. Lower Miocene, Tácata Field, Eastern Venezuela Basin. Core width is 7 cm. See Buatois *et al*., (2008).

developed or directly absent and the storm-related suite dominates. Storm-dominated delta-front deposits formed under less frequent and intense events display a laminated to burrowed pattern (lam-scram), and are characterized by the alternation of the storm-related and fair-weather assemblages (Fig. 8.23c–f). The storm-related suite is similar to that of strongly storm-dominated types. *Rosselia*, *Planolites*, *Palaeophycus*, *Teichichnus*, *Phycosiphon*, *Chondrites*, “Terebellina”, *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Rhizocorallium*, *Gyrochorte*, and *Thalassinoides* are common components of the fair-weather suite. Some ichnogenera, such as *Chondrites*, *Phycosiphon* (Fig. 8.24a) and *Thalassinoides* (Fig. 8.24b) can penetrate relatively deep into storm sandstone beds. This suite becomes more diverse in the distal delta front (Fig. 8.24c–d). Overall, ichnofaunas from wave-dominated delta fronts are relatively diverse and very similar to those from shoreface settings (see Section 7.1).

The prodelta of wave-dominated deltas is commonly characterized by the alternation of suspension fall-out silt and clay during fair-weather times and sand emplacement during storms. In general, prodelta deposits contain diverse trace-fossil assemblages of the *Cruziana* ichnofacies, including *Rosselia* (Fig. 8.24e), *Asterosoma*, *Cylindrichnus, Planolites*, *Palaeophycus*, *Teichichnus*, *Helminthopsis*, *Chondrites*, *Phycosiphon* (Fig. 8.24f), “Terebellina”, *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Rhizocorallium*, *Phycodes*, *Gyrochorte*, *Zoophycos*, *Taenidium*, and *Thalassinoides* (Fig. 8.23g) as common elements. Escape trace fossils may occur in distal storm beds (Fig. 8.24g).

In any case, the sporadic occurrence of other stress factors related with fluvial discharge (e.g. freshets, high sedimentation rates), although not as significant as in river-dominated deltas, still imparts a signature in the ichnological record. As noted by MacEachern *et al.* (2005), the juxtaposition of “open marine ichnogenera” (e.g. *Zoophycos*, *Phycosiphon*, “Terebellina”, *Chondrites*) and stressed suites (e.g. dominated by *Teichichnus* or *Planolites*) seems to be particularly typical of distal delta-front and proximal prodelta settings. In addition to ichnodiversity, the

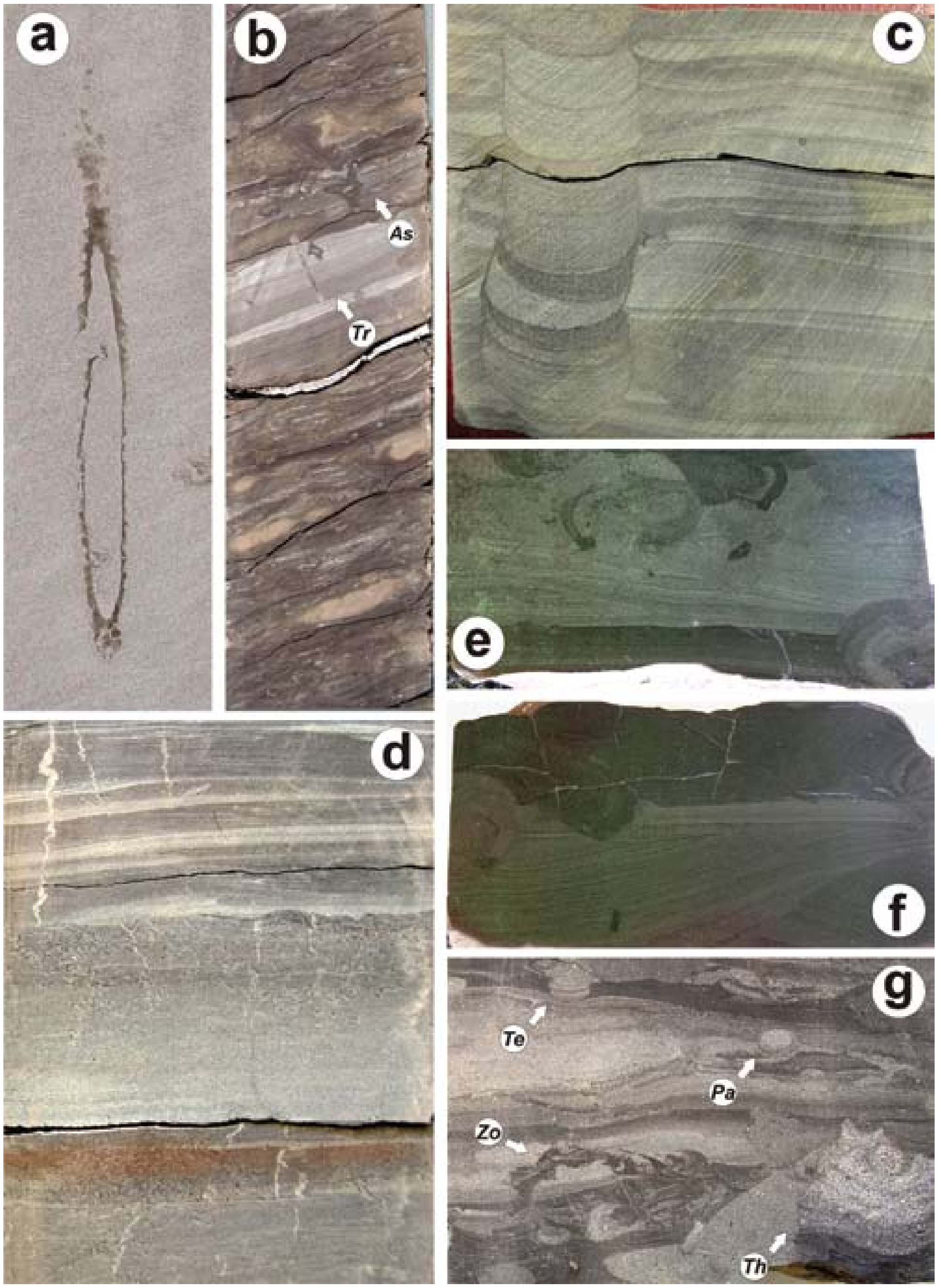

Figure 8.22 Contrasting trace-fossil assemblages in deltaic and strandplain shorelines. (a) *Ophiomorpha* representing the storm-related suite of proximal delta-front deposits. Lower Miocene, Tácata Field, Eastern Venezuela Basin. See Buatois *et al.* (2008). (b) *Trichichnus* isp. (*Tr*) colonizing a distal-prodelta tempestite. *Asterosoma* isp. (*As*) represents the re-establishment of the background suite. (c) *Diplocraterion* isp. colonizing hummocky bed in distal delta-front deposits. (d) Proximal-prodelta deposits displaying unburrowed to sparsely bioturbated hummocky cross-stratified very fine-grained sandstone with synaeresis cracks and high-density suite of *Phycosiphon incertum* in fair-weather mudstone. (e) *Scolicia* isp. displaying characteristic backfill in fully marine offshore deposits. Note trace-fossil emplacement within the storm sandstone and at the sandstone–mudstone interface. (f) *Scolicia* isp. concentrated at the top of the offshore storm sandstone layer. (g) Intensely bioturbated lower-offshore deposits displaying *Thalassinoides* isp. (*Th*), *Zoophycos* isp. (*Zo*), *Teichichnus* isp. (*Te*), and *Palaeophycus* isp. (*Pa*). Core widths are 7 cm.

degree of bioturbation shows some departures from that typical of non-deltaic fully marine settings. Intensity of bioturbation in prodelta and delta-front deposits may range from low to moderate. This results in the common preservation of very thin tempestites that otherwise would have been totally destroyed by the infauna under fully marine conditions. The links between bioturbation and event-bed preservation have been analyzed by Wheatcroft (1990), who noted that if the transient time (i.e. time required to advect the signal through the biologically active zone) is less than the dissipation time (i.e. time required to destroy the event bed), then some evidence of the event layer should be preserved in the stratigraphic record (see Section 7.1). Locally, higher degrees of bioturbation are attained in discrete layers dominated by fully marine ichnotaxa, indicating times of little deltaic influence. Wave-dominated settings do not seem to be conducive to emplacement of fluid muds. However, distal delta-front and proximal prodelta deposits may locally display unbioturbated, dark gray mudstone layers that may reflect fluid-mud sedimentation, and the influence of deltaic-related buoyant plumes.

Integration of ichnological and sedimentological data may help to detect asymmetry in wave-dominated deltas. Bhattacharya and Giosan (2003) noted that in wave-dominated settings with strong longshore drift currents, an asymmetric delta may result due to preferential sediment movement

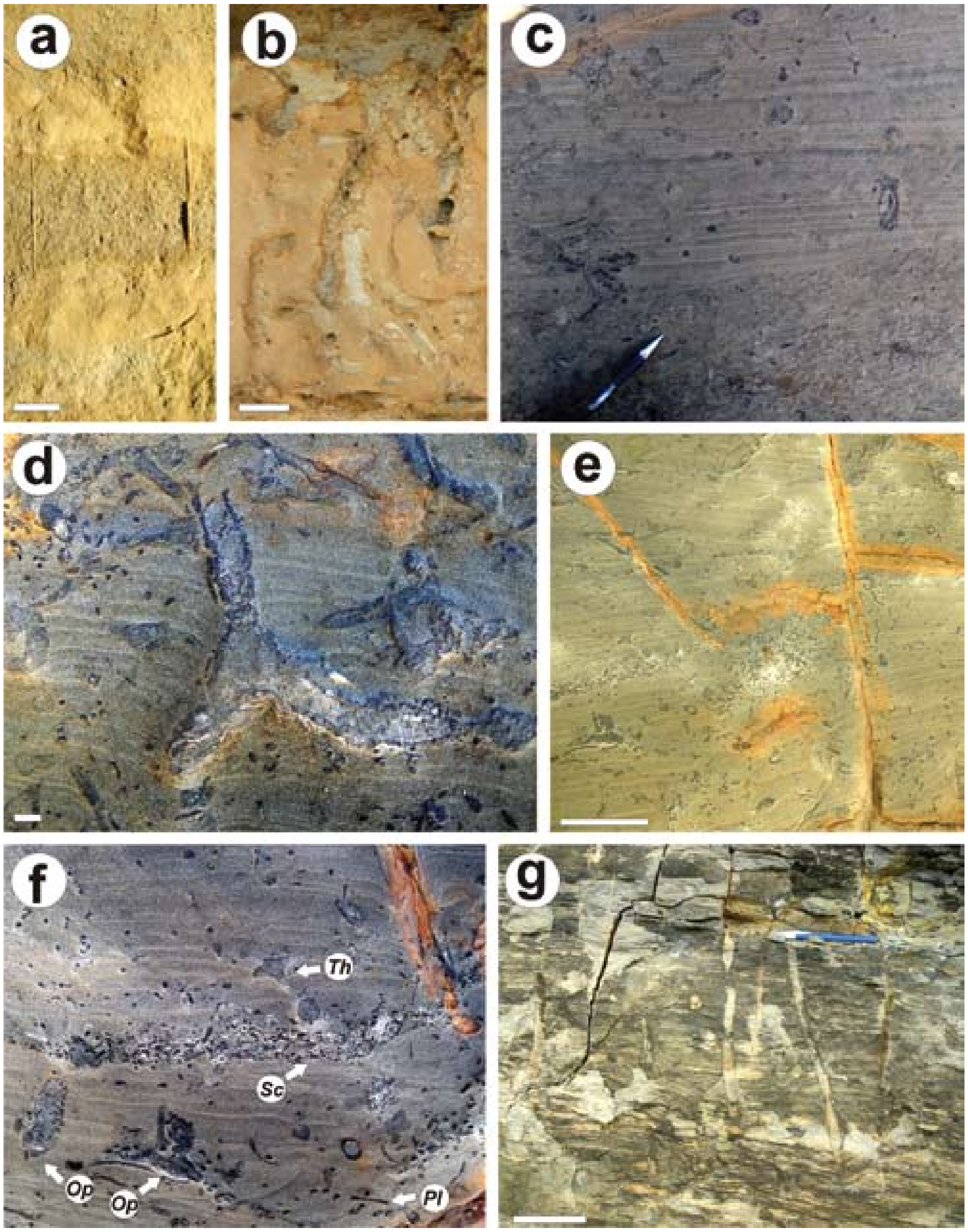

Figure 8.23 Ichnofaunas in outcrops of wave-dominated delta-front and prodelta deposits. (a) Deep *Skolithos* in distal delta-front tempestite. Upper Cretaceous, Ferron Sandstone, Ivie Creek, eastern Utah, United States. Scale bar is 10 cm. See Bhattacharya *et al.* (2007). (b) Vertical *Ophiomorpha* in distal delta-front tempestite. Upper Miocene, Urumaco Formation, Quebrada Bejucal, northwest Venezuela. Scale bar is 5 cm. (c) Intensely burrowed fair-weather deposit overlain by a sharp-based sparsely bioturbated hummocky cross-stratified sandstone emplaced in a proximal delta front. Pliocene, Caleta Godoy Formation, Mar Brava, near Carelmapu, southern Chile. Pencil is 15 cm. (d) Close-up of a specimen of *Ophiomorpha nodosa* penetrating deep into a proximal delta-front hummocky layer. Pliocene, Caleta Godoy Formation, Mar Brava, near Carelmapu, southern Chile. Scale bar is 1 cm. (e) General view of sparsely bioturbated thick hummocky cross-stratified sandstone formed in a proximal delta front. Pliocene, Caleta Godoy Formation, Mar Brava, near Carelmapu, southern Chile. Scale bar is 10 cm. (f) Close-up of (e) showing *Ophomorpha nodosa* (*Op*), patches of *Schaubcylindrichnus coronus* (*Sc*), *Thalassinoides suevicus* (*Th*), and *Planolites beverleyensis* (*Pl*) commonly reworking crustacean burrows. (g) Deep vertical *Thalassinoides* penetrating into proximal-prodelta deposits. Upper Miocene, Urumaco Formation, Urumaco River, northwest Venezuela. Scale bar is 10 cm.

downdrift of the distributary mouth. Delta asymmetry is commonly reflected by trace-fossil distribution with suites displaying a strong deltaic signature downdrift, but with establishment of strandplain shoreface complexes having more marine, less stressed suites in an updrift direction (MacEachern *et al.*, 2005; Hansen and MacEachern, 2007; Buatois *et al.*, 2008).

8.3.3 TIDE-DOMINATED DELTAS

In comparison with river- and wave-dominated deltas, tide-dominated deltas are less understood from both sedimentological and ichnological viewpoints (Fig. 8.25). The subaerial delta plain is similar in terms of ichnological content to that of river- and wave-dominated settings and is dominated by structures produced by freshwater and terrestrial elements. The subaqueous delta plain combines a set of stress factors, mostly consisting of clay flocculation and fluid-mud deposition (MacEachern *et al.*, 2005). Distributary-channel deposits are sparsely bioturbated, and trace fossils commonly occur along surfaces that reflect colonization windows during slack-water periods. *Diplocraterion*, *Ophiomorpha*, and *Planolites* are common components, the latter typically present along mud drapes (e.g. Martinius *et al.*, 2001). Retrusive forms of *Diplocraterion* tend to be dominant, reflecting equilibrium behaviors under relatively high rates of sedimentation (e.g. Martinius *et al.*, 2001; MacEachern *et al.*, 2005). Some tide-dominated distributary channels, however, are the site of fluid-mud emplacement and are, therefore, unbioturbated (e.g. Dalrymple *et al.*, 2003). Interdistributary-bay deposits are dominated by *Teichichnus* and *Planolites*, commonly associated with synaeresis cracks.

Box 8.5 Ichnology of Lower Miocene delta-front and prodelta deposits of a tide-dominated delta of Patagonia, Argentina

Excellent deltaic outcrops of the Lower Miocene Chenque Formation are exposed along cliff areas near Caleta Olivia, Patagonia, Argentina. Their ichnological and sedimentological study allows recognition of clear tidal signatures in prodelta and delta-front deposits, which are stacked forming a progradational coarsening-upward succession. Heterolithic prodelta deposits with lenticular and wavy bedding are sparsely bioturbated and display sporadic distribution of trace fossils. Deposit-feeder structures, such as *Planolites montanus* (Fig. 8.26a), *Protovirgularia* isp. (Fig. 8.26b), and *Teichichnus rectus*, are dominant, representing an impoverished expression of the *Cruziana* ichnofacies. Flaser-bedded sandstone characterizes the prodelta-delta front transition. These deposits are almost completely obliterated by equilibrium/adjustment trace fossils of large bivalves (*Atrina*) (Fig. 8.26c and d). Associated trace fossils are *Nereites missouriensis*, *Teichichnus rectus* (Fig. 8.26e), *Phycosiphon incertum* (Fig. 8.26f), *Thalassinoides* isp. (Fig. 8.26f), and *Schaubcylindrichnus freyi*. Trough and planar cross-stratified distal delta-front sandstone is dominated by large *Rosselia socialis* and *Macaronichnus segregatis* (Fig. 8.26g). The associated mud drapes blanketing the sandstone foresets commonly contain *Nereites missouriensis* and *Protovirgularia* isp. Proximal delta-front deposits are characterized by sigmoidal cross-stratification and very sparse bioturbation, represented by *Macaronichnus segregatis* and isolated specimens of *Rosselia socialis*. Changes in salinity, water turbidity, fluid mud substrates, and fluctuations in energy and in sedimentation rates are among the most important stress factors that affected these deltaic infaunal communities. Overall, this ichnofauna is characterized by shallow-tiered communities, impoverished trace-fossil assemblages, dominance of deposit-feeder structures, and inhibition of suspension-feeder elements. This study helps to explain how tide-influenced deltaic ichnofaunas are shaped by the relative influence of the different stress factors.

References: Carmona *et al*. (2009).

Root traces occur in interdistributary-bay deposits and at the top of channel-abandonment successions. In general, ichnofaunas from the subaqueous delta plain of tide-dominated deltas follow the tenets of the brackish-water model (see Section 6.1.4).

Delta-front and prodelta environments contain representatives of the *Cruziana* ichnofacies, including *Gyrochorte*, *Thalassinoides*, *Phycosiphon*, *Chondrites*, *Siphonichnus*, *Diplocraterion*, *Teichichnus*, *Palaeophycus*, *Planolites*, and *Rhizocorallium*, among other ichnotaxa (McIlroy, 2004b, 2007b; MacEachern *et al*., 2005; Carmona *et al*., 2008, 2009) (Box 8.5). Equilibrium structures (*Rosselia*, bivalve adjustment structures) are rather common (Carmona *et al*., 2008, 2009). High-energy subtidal sandbars and dunes are either unbioturbated or contain elements of the *Skolithos* ichnofacies, such as *Skolithos* and *Diplocraterion*, reflecting short-term colonization windows during breaks in sedimentation. Mud drapes along foresets are sparsely bioturbated, and typically contain *Planolites*. Synaeresis cracks occur locally probably in relation with salinity fluctuations (MacEachern *et al*., 2005). Ichnodiversity levels in tide-dominated delta-front and prodelta environments are poorly understood. MacEachern *et al*. (2005) summarized known occurrences and noted size reduction, sparse bioturbation, and low diversity levels, with trace fossils concentrated along pause planes. In contrast, McIlroy (2004b) documented relatively diverse ichnofaunas in a case study of deltaic ichnology. Nevertheless, there is general agreement that tide-dominated delta fronts and prodeltas are less diverse than their wave-dominated counterparts (McIlroy, 2004b; MacEachern *et al*., 2005). However, ichnodiversity levels seem to be higher than in river-dominated deltas (McIlroy, 2007b).

8.4 FJORDS

Fjords are deep, high-latitude estuaries that have been excavated or modified by land-based ice (Syvitski *et al*., 1987). The ichnology of fjords remains poorly explored, with only a few papers dealing with modern (e.g. Aitken *et al*., 1988), Cenozoic (e.g. Eyles *et al*., 1992; Corner and Fjalstad, 1993), and late Paleozoic (e.g. Nogueira and Netto, 2001; Buatois and Mángano, 2003b; Balistieri *et al*., 2002, 2003; Gandini *et al*., 2007; Buatois *et al*., 2006a, 2010a; Schatz *et al*., 2011) examples (Fig. 8.27). However, ichnological evidence is essential to resolve paleoenvironmental interpretations in fjord successions, commonly representing the only available biological data because of the low preservation potential of shelly faunas in marine environments adjacent to glaciated margins (Aitken, 1990).

Fjords include a wide variety of environmental stresses that affect benthic colonization, including extreme salinity dilution, high rates of sedimentation, variable degree of substrate consolidation, oxygen-depleted conditions, high water turbidity, and intense storm activity. In polar areas, seasonal light restriction and floating ice masses contributing to ice-rafted debris rainfall may be important stress factors.

Salinity dilution is undoubtedly one of the most significant stress factors because fjords are characterized by strong meltwater discharge issuing from seasonal glacial melting. Increased precipitation and runoff during summer lead to reduced salinity (e.g. Feder and Keiser, 1980). As a result, most Cenozoic and Holocene fjords are dominated by brackish-water ichnofaunas (Eyles *et al*., 1992; Corner and Fjalstad, 1993). High freshwater discharges due to glacier melting and associated catastrophic outburst floods are known for a number of glaciated margins, such as the Baltic

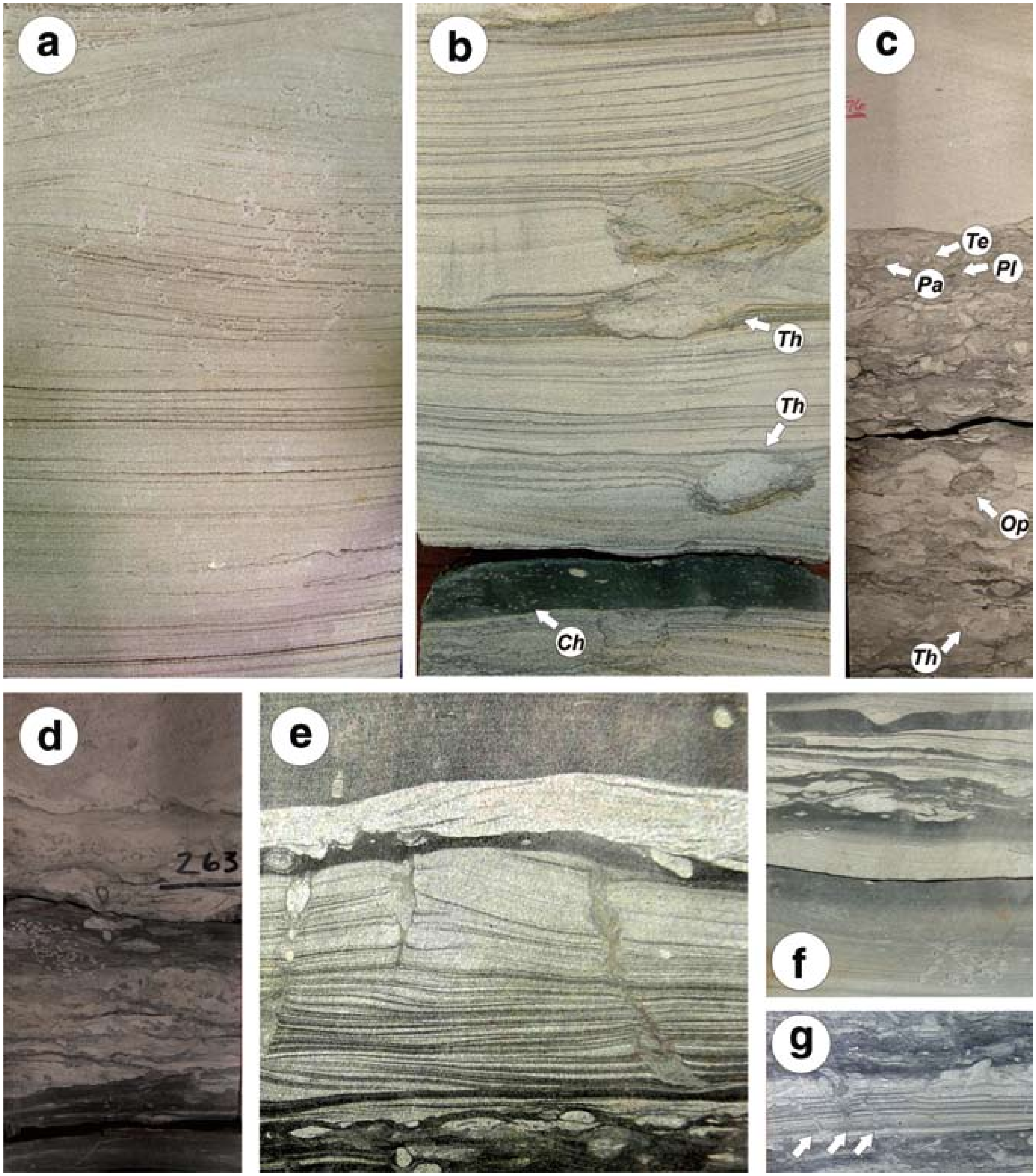

Figure 8.24 Core expression of ichnofaunas from wave-dominated delta-front and prodelta deposits. (a) *Phycosiphon* penetrating into a hummocky cross-stratified sandstone emplaced in the proximal delta front. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (b) Distal delta-front sandstone tempestite containing deeply emplaced *Thalassinoides* isp. (*Th*). *Chondrites* isp. (*Ch*) occurs in associated fair-weather deposits. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (c) Distal delta-front heterolithic deposits containing a diverse fair-weather trace-fossil suite consisting of *Teichichnus rectus* (*Te*), *Ophiomorpha nodosa* (*Op*), *Palaeophycus* isp. (*Pa*), *Thalassinoides* isp. (*Th*), and *Planolites* isp. (*Pl*). Note the presence of an overlying sharp-based storm sandstone bed. Upper Cretaceous, Ferron Sandstone, Ivie Creek #11, Ivie Creek area, eastern Utah, United States. Core width is 9 cm. See MacEachern *et al*. (2007b). (d) Sparsely bioturbated to locally moderately bioturbated distal delta-front deposits containing well-defined *Chondrites*. Upper Cretaceous, Ferron Sandstone, Muddy Creek #11, Muddy Creek area, eastern Utah, United States. Core width is 9 cm. See Pemberton *et al*. (2007). (e) *Rosselia* isp. in thin storm sandstone layers emplaced in a proximal prodelta. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (f) *Phycosiphon* penetrating into a distal sandstone tempestite emplaced in a proximal prodelta. Note associated mud drapes indicative of tidal influence, load cast at the base of an overlying tempestite, and unbioturbated mudstone units interpreted as fluid muds. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (g) Escape trace fossils (arrows) in proximal-prodelta sandstone tempestites. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm.

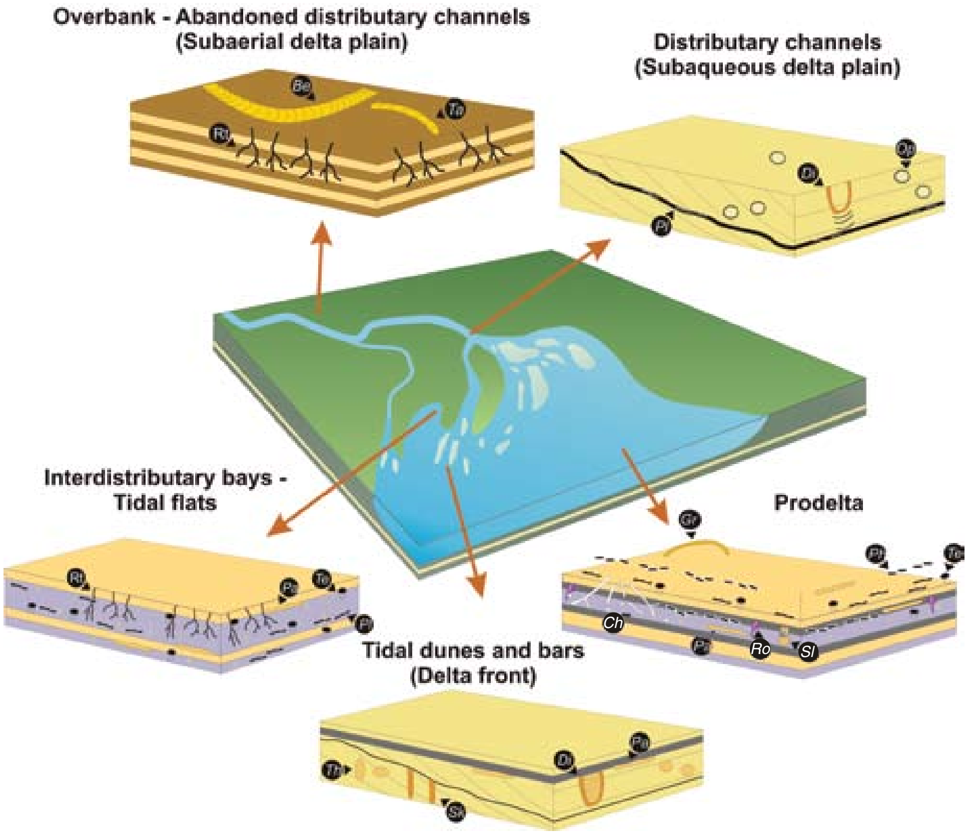

Figure 8.25 Schematic reconstruction of trace-fossil distribution in tide-dominated deltas. Abandoned-channel and overbank deposits of the subaerial delta plain may contain *Beaconites* (*Be*), *Taenidium* (*Ta*), and root traces (Rt). Distributary-channel deposits of the subaqueous delta plain may contain *Ophiomorpha* (*Op*) and *Diplocraterion* (*Di*); *Planolites* (*Pl*) may occur on mud drapes along foresets. Interdistributary-bay and tidal-flat deposits typically exhibit *Planolites* (*Pl*), *Teichichnus* (*Te*), *Palaeophycus* (*Pa*), and root traces (Rt). Tidal-dune and bar deposits of the delta-front may host *Thalassinoides* (*Th*), *Palaeophycus* (*Pa*), *Diplocraterion* (*Di*), and *Skolithos* (*Sk*). Prodelta deposits exhibit various ichnotaxa, such as *Teichichnus* (*Te*), *Phycosiphon* (*Ph*), *Chondrites* (*Ch*), *Rosselia* (*Ro*), *Palaeophycus* (*Pa*), *Scalichnus* (*Sl*), and *Gyrochorte* (*Gr*).

and Labrador Seas (Lord, 1990; Shaw and Lesemann, 2003). Some of the most extreme cases of freshwater discharges occur during deglaciation times. In fact, glacial melting may lead to the formation of extensive freshwater bodies that are physically connected with the open sea. For example, the Holocene Yoldia Sea was freshwater in the northern Baltic Sea Basin due to high input meltwater during deglaciation during most of its history (Virtasalo *et al.*, 2006). Times of elevated concentration of suspended sediment promote formation of hyperpycnal flows in fjord environments (Syvitski *et al.*, 1987). Only exceptional discharges overcome the buoyancy effect of seawater in modern examples, but high-discharge hyperpycnal flows may have been the norm during deglaciation. In addition, because large discharges reduce the salinity of the fjord, the likelihood of hyperpicnal flows is increased providing a positive feedback. In these situations marine benthic fauna are inhibited due to reduced salinity, allowing colonization by a freshwater biota. This situation seems to have been quite common in late Paleozoic glaciated margins of Gondwana, which display ichnological signatures of extreme freshwater release during deglaciation (Buatois *et al.*, 2006a, 2010a). In fact, some Gondwana fjord ichnofaunas are virtually identical to those from Pleistocene glacial lakes (e.g. Gibbard and Stuart, 1974; Gibbard, 1977; Gibbard and Dreimanis, 1978; Walter and Suhr, 1998; Gaigalas and Uchman, 2004; Uchman *et al.*, 2009; Benner *et al.*, 2009; Knecht *et al.*, 2009) (see Section 10.3.2) (Fig. 8.28a–c). Although some of these settings have been referred to as "brackish seas", in fact they may be more appropriately called "freshwater seas" because of the dominance of freshwater conditions due to extensive melting during postglacial times (Buatois *et al.*, 2006a, 2010a; Buatois and Mángano, 2007). In many cases, however, brackish-water ichnofaunas also occur in these late Paleozoic successions, reflecting increased marine influence.

High rates of sedimentation are persistent in the fjord environment as a result of high fluvial input. In addition, mass-sediment transport, eolian transport, and input from wave and tidal erosion also play a role (Syvitski *et al.*, 1987). In particular, high sedimentation rate affects the epifauna by subjection to floc and agglomerate rain, microturbidity flows due to biological resuspension of unstable slope sediment, and disturbances due to major slides (Farrow *et al.*, 1983). Bioturbation is commonly inhibited close to the bay-head delta due to rapid sediment accumulation. Abundance of escape trace fossils and dwelling structures, such as *Conichnus* and *Diplocraterion*, has been linked to rapid sedimentation (e.g. Eyles *et al.*, 1992). Rapid sedimentation is also a limiting factor for larval settlement (Farrow *et al.*, 1983). As a result of high sedimentation rates and steep margins, fjords are strongly affected by sediment gravity flows, most commonly turbidity currents and debris flows. High frequency of sediment gravity flows carrying significant amounts of food seems to have prevented establishment of the *Nereites* ichnofacies, allowing extension of the *Cruziana* ichnofacies into deeper water (Eyles

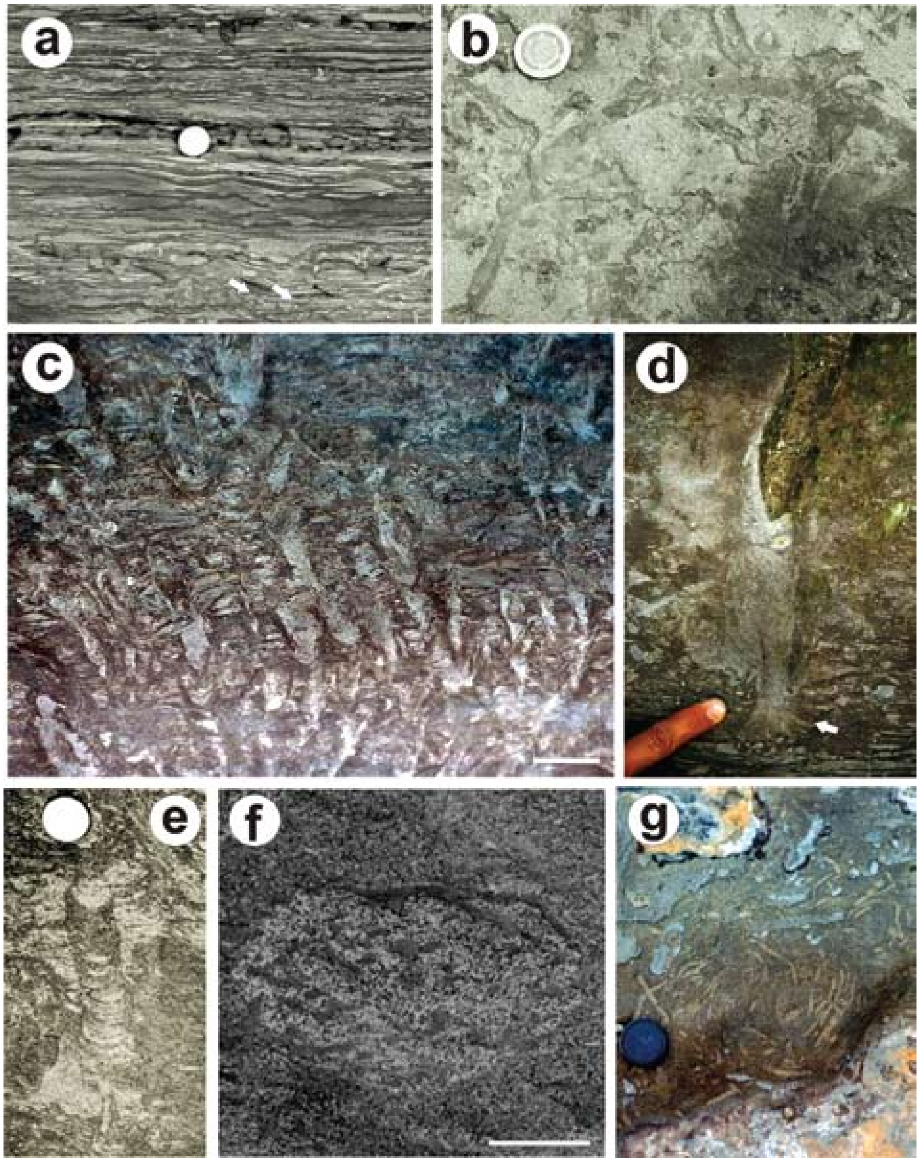

Figure 8.26 Ichnofaunas from delta-front and prodelta deposits of a Lower Miocene tide-dominated delta, Chenque Formation, Caleta Olivia, Patagonia, Argentina. See Carmona *et al.* (2008, 2009). (a) Heterolithic proximal-prodelta deposits containing a monospecific suite of small *Planolites montanus* (arrows). Note abundance of synaeresis cracks. Coin is 2.4 cm. (b) *Protovirgularia* isp. in proximal-prodelta deposits. Coin is 2.4 cm. (c) High density of equilibrium/adjustment trace fossils produced by the bivalve *Atrina* in deposits emplaced at the transition between the delta front and the prodelta. Scale bar is 10 cm. (d) Close-up of equilibrium/adjustment trace fossil showing structures left by the byssal threads (arrow) and the body fossils of their tracemakers at the end of the trace fossil. (e) Transitional prodelta-delta front deposits containing *Teichichnus rectus*. Coin is 1.8 cm. (f) *Thalassinoides* isp. reworked by *Phycosiphon incertum* in transitional deposits. Scale bar is 1 cm. (g) *Macaronichnus segregatis* in distal delta-front deposits. Lens cover is 5.5 cm.

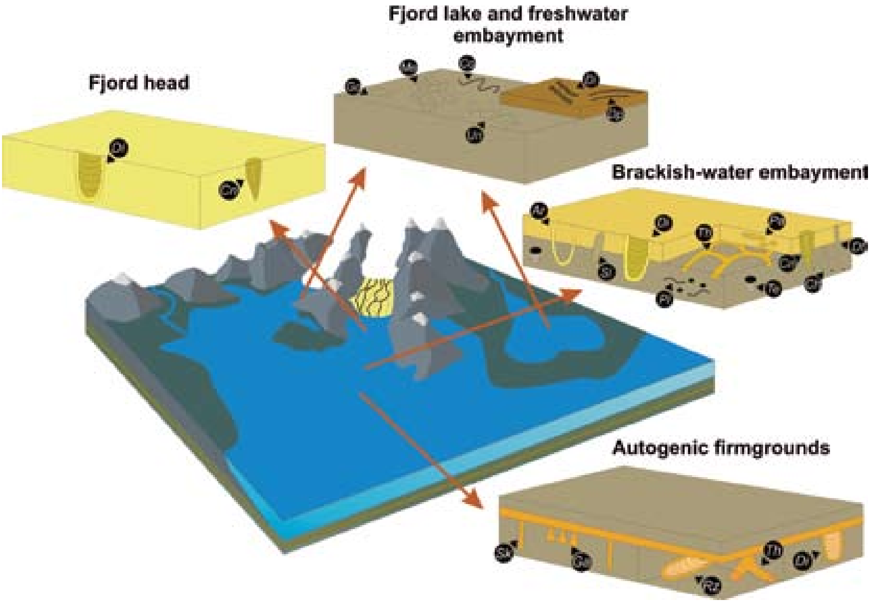

Figure 8.27 Schematic reconstruction of trace-fossil distribution in fjords. Fjord-head-deposits are sparsely bioturbated, and contain a few forms, such as robust *Diplocraterion* (*Di*) and *Conichnus* (*Cn*). An increase in degree of bioturbation and trace-fossil diversity characterizes brackish-embayment deposits, which may contain *Arenicolites* (*Ar*), *Diplocraterion* (*Di*), *Siphonichnus* (*Si*), *Teichichnus* (*Te*), *Thalassinoides* (*Th*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Conichnus* (*Cn*), *Chondrites* (*Ch*), and *Diopatrichnus* (*Dt*). Fjord-lake and freshwater-embayment deposits are characterized by *Undichna* (*Un*), *Mermia* (*Me*), *Cochlichnus* (*Co*), *Gordia* (*Go*), *Diplopodichnus* (*Dp*), and *Diplichnites* (*Di*). Associated firmground surfaces contain *Skolithos* (*Sk*), *Gastrochaenolites* (*Ga*), *Rhizocorallium* (*Rz*), *Diplocraterion* (*Di*), and *Thalassinoides* (*Th*).

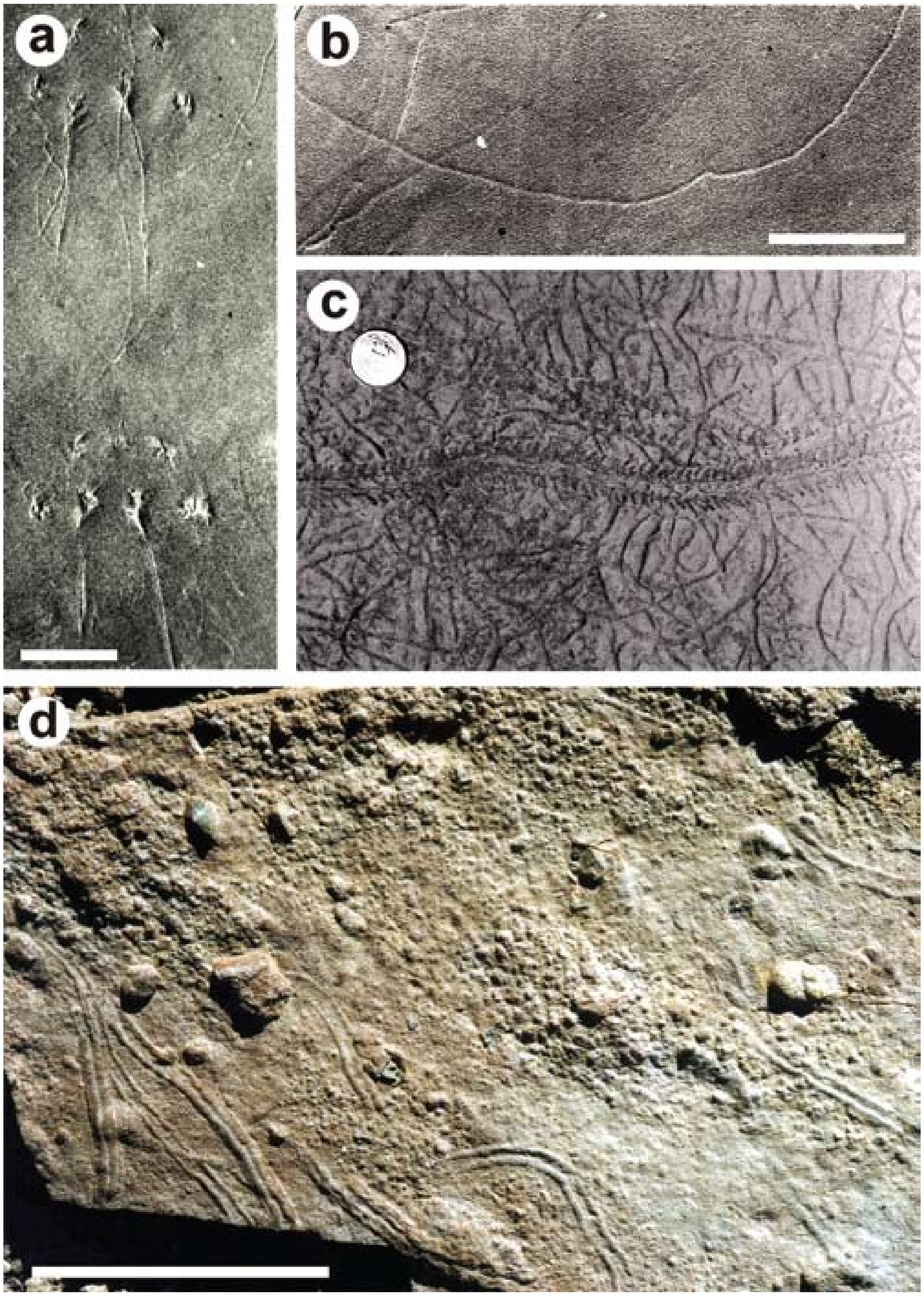

Figure 8.28 Ichnofaunas from late Paleozoic fjord deposits of Gondwana. (a) *Orchesteropus atavus*. Upper Carboniferous, Guandacol Formation, Huerta de Huachi, Paganzo Basin, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003b). (b) *Helminthoidichnites tenuis*. Upper Carboniferous, Guandacol Formation, Huerta de Huachi, Paganzo Basin, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003b). (c) *Diplichnites* isp. cross-cutting a high-density suite consisting of *Helminthoidichnites tenuis*. Upper Carboniferous–Lower Permian, Rio do Sul Formation, Trombudo Central, Santa Catarina State, Paraná Basin, southern Brazil. Coin is 2 cm. See Nogueira and Netto (2001). (d) *Diplopodichnus biformis* and *Cruziana* isp. with associated dropstones. Upper Carboniferous, Guandacol Formation, Cuesta de Huaco, Paganzo Basin, western Argentina. Scale bar is 10 cm. See Schatz *et al*. (2011).

et al., 1992). Ice-rafted debris rainfall also represents a stress factor on the benthic biota, and the presence of trace fossils in direct association with dropstones is not uncommon in late Paleozoic fjord deposits (e.g. Schatz *et al*., 2011) (Fig. 8.28d).

A number of papers have documented the role of water turbidity in modern fjords (e.g. Feder and Matheke, 1980; Farrow *et al*., 1983). Modern fjord waters contain high concentrations of fine-grained particles that commonly preclude the establishment of suspension-feeder organisms (see Section 6.1.8). The dominance of horizontal feeding traces of deposit and detritus feeders, and the absence of vertical burrows of suspension feeders in ancient fjord deposits is also suggestive of high amounts of suspended fine-grained material (Buatois *et al*., 2006a). The abundance of deeply plowing deposit feeders may also have contributed to the exclusion of suspension feeders (Feder and Matheke, 1980; Eyles *et al*., 1992) (see Section 6.7).

The degree of substrate consolidation is extremely variable in fjord environments. Muddy soupgrounds seem to be rather common close to the glacier margin, imparting a strong stress to epifaunal communities (see Section 6.1.2). Eyles *et al*. (1992)

noted that polychaetes and deposit-feeding bivalves are the dominant components in these soupy substrates. Suspension feeders are typically absent. Softground communities containing more varied epifauna and infauna tend to occur towards more distal positions. Fluid muds are typically unbioturbated. In addition, current-winnowed substrates commonly contain firmgrounds with associated suites of the *Glossifungites* ichnofacies characterized by deep gravel-filled *Skolithos* and *Gastrochaenolites* (Dale *et al*., 1989; Eyles *et al*., 1992).

Dissolved oxygen concentration in fjord bottom waters is extremely variable (Syvitski *et al*., 1987). The bottom of some fjords may be characterized by oxygen depletion, particularly in enclosed basins with a high concentration of organic matter. In these settings, the redox discontinuity surface is very close to the sediment–water interface, restricting the activity of infaunal organisms (Syvitski *et al*., 1987). As a result, shallow-tier structures of small deposit feeders tend to be the dominant components (Pearson, 1980). Anoxic to dysaerobic conditions are particularly common at times. However, the activity of bottom currents may supply oxygen to the fjord floor in some basins (e.g. Eyles *et al*., 1992).

Some fjords are subjected to intense wave action due both to wind funneled from the interior to the sea and to large shoreward-traveling swells (Syvitski *et al*., 1987). This results in the deep emplacement of the storm wave base in some Arctic and Antarctic fjords. For example, the storm wave base is deeper than 200 m in the Gulf of Alaska, influencing the entire shelf bottom (O'Clair and Zimmerman, 1987). Therefore, repeated storms impart a strong stress in benthic communities and affect populations established in relatively deep water (see Section 7.1). This stress is expressed by deep erosion and strong resuspension of sediment that remains close to the sediment–water interface.

As a consequence of these series of commonly interconnected stress factors, the taxonomic composition of fjord ichnofaunas is highly variable. Late Paleozoic fjord ichnofaunas typically contain representatives of the *Mermia* and *Scoyenia* ichnofacies as a result of the predominance of freshwater conditions (e.g. Buatois and Mángano, 2003b). Simple grazing trails (e.g. *Cochlichnus*, *Gordia*, *Helminthoidichnites, Helminthopsis, Mermia*), feeding traces (e.g. *Circulichnis*, *Treptichnus*), resting traces (e.g. *Rusophycus*), arthropod trackways (e.g. *Diplichnites, Maculichna*, *Umfolozia*, *Orchesteropus*), and fish trails (e.g. *Undichna*) are common ichnotaxa. Because these structures are preserved along bedding planes, recording emplacement in very shallow tiers, the degree of bioturbation is typically zero. Associated brackish-water intervals are slightly more bioturbated, and contain the depauperate *Cruziana* ichnofacies (Buatois *et al*., 2010a). Most Cenozoic and modern fjords contain ichnofaunas that record the activity of organisms adapted to brackish water (e.g. Aitken *et al*., 1988; Eyles *et al*., 1992). Common components include bivalve vertical burrows (*Siphonichnus*), U-shaped vertical burrows (e.g. *Arenicolites*, *Diplocraterion*), gravel-lined polychaete burrows (*Diopatrichnus*), and crustacean galleries (*Thalassinoides*), among other forms. The degree of bioturbation is typically low to moderate.

9 Ichnology of deep-marine clastic environments

> Y cuando me hundo en el mar
> de la fertilidad,
> un silencio visual:
> es la fauna abisal
> reflejando el color del sol
> Gustavo Cerati
> *Lisa* (1993)

Deep-marine trace fossils have long fascinated ichnologists with their amazing variety of shapes and sizes, arranged in regular and recurrent patterns (Fuchs, 1895). Graphoglyptids preserved at the base of sandy turbidites have represented a challenging puzzle. Trace fossils preserved in turbidites exposed mostly in European Mountain Chains (Fuchs, 1895; Azpeitia-Moros, 1933; Seilacher, 1962, 1977a; Książkiewicz, 1970, 1977; Crimes, 1977; Crimes *et al.*, 1981), but also in South (Macsotay, 1967) and North (Chamberlain, 1971) America rapidly captured the attention of ichnologists. These structures were originally interpreted as post-turbidite (Seilacher, 1960), but after further research Seilacher (1962) was able to demonstrate that graphoglyptids were in fact pre-turbidite trace fossils formed as shallow-tier open burrow systems in the hemipelagic mud and preserved due to uniform stripping of the uppermost muddy layer by the incoming turbidity current and subsequent casting with sand. In another seminal paper, Seilacher (1977a) introduced a morphological classification of these structures, including continuous meanders (e.g. *Helminthorhaphe* and *Cosmorhaphe*), uniramous meanders (e.g. *Belorhaphe*, *Helicolithus*, and *Urohelminthoida*), biramous meanders (e.g. *Desmograpton* and *Paleomeandron*), radial structures (e.g. *Glockerichnus* and *Lorenzinia*), irregular networks (e.g. *Megagrapton* and *Acanthorhaphe*), and regular networks (e.g. *Paleodictyon*). The fact that these structures were originally described and interpreted from the fossil record, and only later recorded in the modern deep sea has been regarded as an example of reverse uniformitarianism, in which the past is the key to the present (Frey and Seilacher, 1980). Recent years have witnessed extraordinary progress in our understanding of the ichnotaxonomy of deep-marine trace fossils. Following a long tradition started by Polish ichnologist Marian Książkiewicz, a number of monographs have been published during the last 15 years or so (Uchman, 1995, 1998, 1999, 2001), allowing the establishment of a systematic framework to classify deep-marine trace fossils. Parallel to this, significant progress was attained in our knowledge of biogenic structures formed in the modern deep sea (e.g. Werner and Wetzel, 1982; Wetzel, 1981, 1984, 1991, 2002, 2008). Integration of modern observations and detailed systematic work are now resulting in more finely tuned ichnological and sedimentological models of turbidite systems (e.g. Wetzel and Uchman, 2001; Ponce *et al.*, 2007; Olivero *et al.*, 2010; Wetzel, 2010; Carmona and Ponce, 2011), including studies in based on cores (Knaust, 2009). In all probability, future work will emphasize the search for comparative ichnological signatures of various deep-sea processes, such as episodic turbidity currents, hyperpycnal flows, and bottom currents (e.g. Wetzel *et al.*, 2008). In this chapter, we will review the ichnology of deep-marine environments, covering both slopes and base-of-slope turbidity systems. In order to do so, we will subdivide slopes in topographically simple and topographically complex, and turbidite systems into fine-grained and coarse-grained.

9.1 SLOPES

The continental slope extends from the slope break at the shelf edge to the basin plain (Stow, 1985; Pickering *et al.*, 1989; Flint and Hodgson, 2005). Slopes are topographically variable ranging from relatively simple to complex, including depressions and highs that result from faulting, folding, salt tectonics, and mud diapirism (Smith, 2004). Because most ichnological studies of deep-marine deposits have focused on the diverse suites present in thin-bedded sandstone turbidites that typically accumulate in base of slope–basin–plain submarine fans, those ichnofaunas present on the slope itself have received comparatively little attention. However, examination of a number of studies (e.g. Werner and Wetzel, 1982; Wetzel, 1981, 1983; Buatois and Mángano, 1992; Fu and Werner, 1994; Savrda *et al.*, 2001; Löwemark *et al.*, 2004; Shultz and Hubbard, 2005; Encinas *et al.*, 2008) allows some generalizations to be established. Slope systems are herein classified in topographically simple and topographically complex, which should be regarded as end members (see also Smith, 2004). Oxygen content is a first-order limiting factor on slope benthic faunas, and is in turn a reflection of topographic confinement which controls water circulation (Pickering *et al.*, 1989).

9.1.1 TOPOGRAPHICALLY SIMPLE SLOPES

Topographically simple slopes are characterized by open unconfined areas separated by confined incised canyons

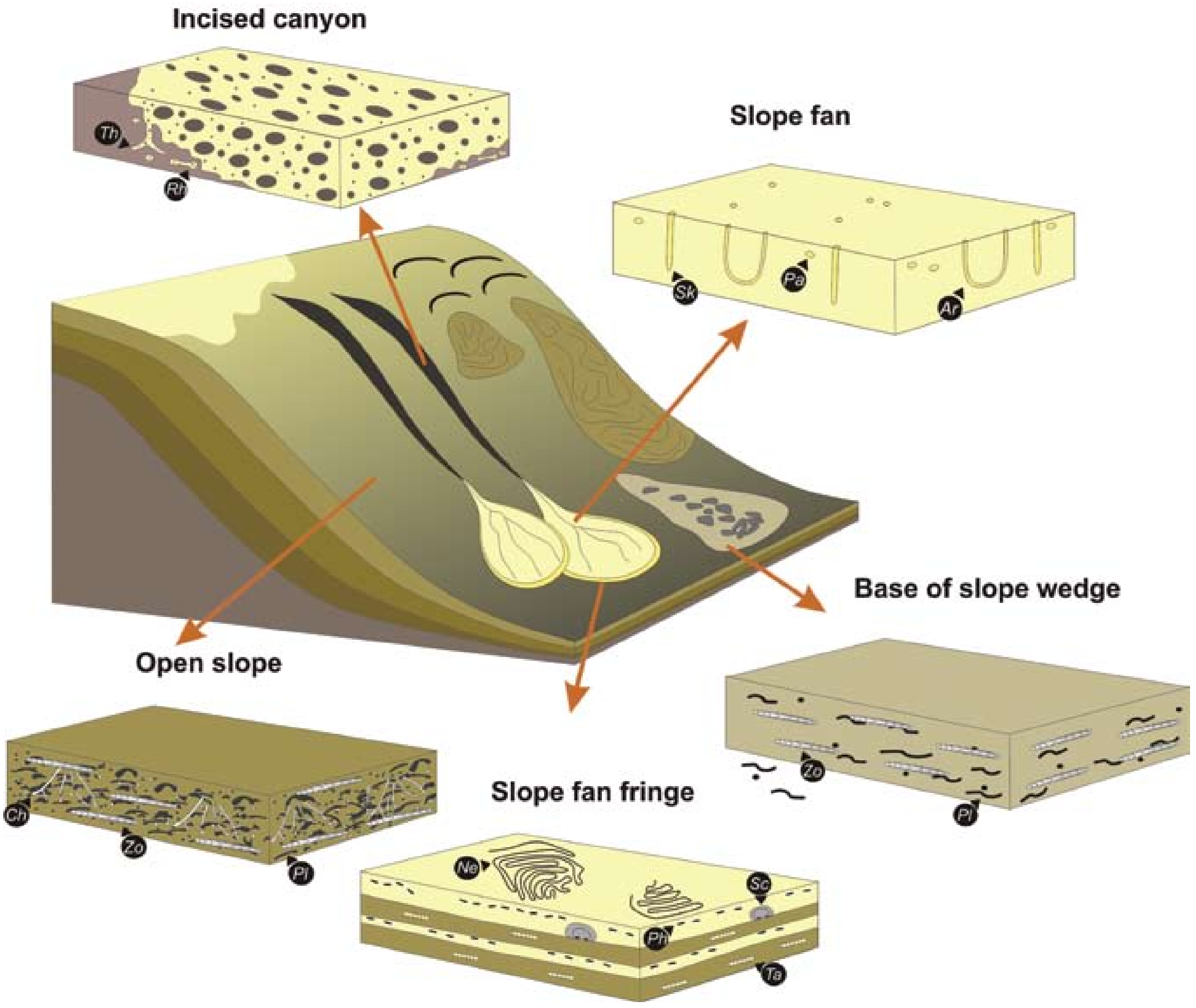

Figure 9.1 Schematic reconstruction of trace-fossil distribution in topographically simple slopes. Trace-fossil associations may be relatively diverse. Firmground *Thalassinoides* (*Th*) and *Rhizocorallium* (*Rh*) are relatively common at the base of incised canyon surfaces. Slope-fan deposits are characterized by dwelling traces of suspension feeders, such as *Skolithos* (*Sk*), *Arenicolites* (*Ar*), and *Palaeophycus* (*Pa*). Slope-fan fringe deposits tend to display feeding and grazing traces of deposit feeders, such as *Nereites* (*Ne*), *Scolicia* (*Sc*), *Phycosiphon* (*Ph*), and *Taenidium* (*Ta*). Base-of-slope-wedge deposits are sparsely bioturbated, and may contain *Zoophycos* (*Zo*) and *Planolites* (*Pl*). Open-slope deposits are intensely bioturbated, and typically display *Zoophycos* (*Zo*), *Chondrites* (*Ch*), and *Planolites* (*Pl*).

(Fig. 9.1). Levee channels may be locally present (Posamentier and Walker, 2006). Slope fans flanked by fringe areas occur on the open unconfined areas. The base of the slope is commonly characterized by a wedge of coarse-grained sediment. Examples include both passive margins, such as the continental slope off northwest Africa (Wetzel, 1981) and active margins, such as the Sulu Sea (Wetzel, 1983). In these settings, ponded intra-slope minibasins are relatively rare. Topographically simple slopes display less stressful conditions and tend to have higher oxygen content than in ponded systems as a result of water circulation. The base of the incised canyons may be delineated by elements of the *Glossifungites* ichnofacies (see Section 12.2.2). Bioturbation is commonly inhibited within the canyon due to high frequency of sediment gravity flows, but open unconfined areas of the slope are typically completely bioturbated (Wetzel, 1981, 1983; Uchman, 1995) (Box 9.1).

Topographically simple slope systems contain a much wider diversity of oxygen-related suites, reflecting more variable conditions of water circulation (Wetzel, 1983; Buatois and Mángano, 1992; Löwemark *et al.*, 2004) (Fig. 9.1). Ichnofaunas are dominated by feeding traces of deposit feeders, particularly in the unconfined open-slope and slope-fan fringe deposits. *Zoophycos*, *Chondrites* (Fig. 9.2a), *Trichichnus*, *Teichichnus* (Fig. 9.2a), and *Planolites* are typically abundant in both modern and ancient examples, and *Scolicia* and *Taenidium* may be

Box 9.1 Ichnology of modern slope to deep-sea sediments in the Sulu Sea Basin of the Philippines

Studies of cores from modern slope to deep-sea deposits of the Sulu Sea Basin provide valuable information to understand environmental distribution of biogenic structures, as well as controls on the benthic fauna and preservation potential of animal traces. Three main ichnocoenoses have been identified. The slope and rise ichnocoenose occurs in sediments down to water depths of 3800 m. Slope and rise muds and oozes are thoroughly bioturbated, and the ichnocoenose is dominated by incipient *Helminthopsis*, *Planolites*, and *Thalassinoides*, with the subordinate presence of *Chondrites*, *Scolicia*, *Trichichnus*, *Skolithos*, and *Zoophycos*. Biodeformational structures are also common. This ichnocoenose essentially represents the *Zoophycos* ichnofacies. The transitional slope to abyssal-plain ichnocoenose occurs between 3800 and 4400 m deep. The degree of bioturbation is lower than in adjacent slope and abyssal-plain environments, and biogenic structures tend to be rather small. *Planolites* is the dominant discrete trace. The abyssal-plain ichnocoenose is present below water depths of 4400 m, in areas with abundant intercalation of turbidites. Although the degree of bioturbation is only 20%, the diversity of biogenic structures is the highest, with 15 ichnotaxa recognized. *Taenidium* and *Phycosiphon* are dominant. Graphoglyptids are absent, most likely reflecting a combination of erosion by turbidity currents, high rates of sedimentation, high nutrient availability, and destruction by deep-tier burrows. Biogenic structures are of small size and maintain a connection with the sea bottom to allow circulation of oxygenated waters essential for animal respiration. Overall, the Sulu Sea ichnofauna is clearly limited by oxygen content; high sedimentation rates and abundant food supply also play a role.

Reference: Wetzel (1983).

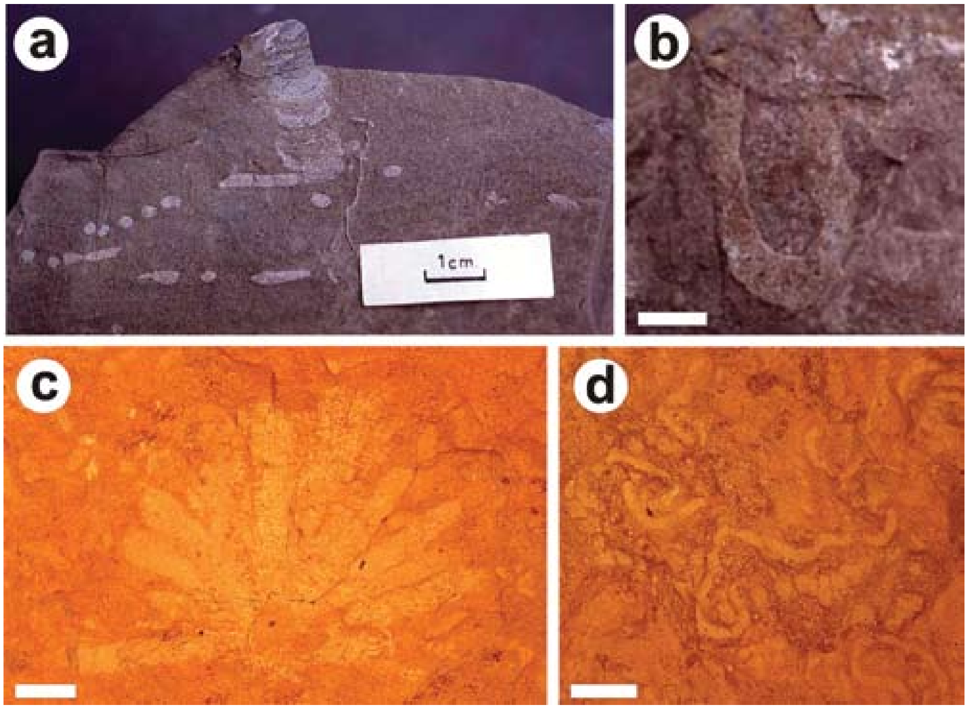

Figure 9.2 Characteristic trace fossils of slope deposits from the Lower Cretaceous Kotick Point Formation, Kotick Point, James Ross Island, Antarctica. (a) *Chondrites* isp. and *Teichichnus rectus*. (b) *Arenicolites* isp. (c) *Cladichnus fischeri* reworked by *Phycosiphon incertum*. (d) *Nereites missouriensis*. All scale bars are 1 cm. See Buatois and Mángano (1992).

also present. Dwelling structures of suspension feeders, such as *Palaeophycus*, *Skolithos*, and *Arenicolites* (Fig. 9.2b) and burrow systems (*Thalassinoides*) occur locally, mostly in slope-fan deposits. The radial trace fossil *Cladichnus* (Fig. 9.2c), the spreite structure *Phycosiphon* (Fig. 9.2c), and grazing trails of deposit feeders, such as *Nereites missouriensis* (Fig. 9.2d) occur in sandy turbidite layers (Buatois and Mángano, 1992). Base-of-slope-wedge deposits are typically sparsely bioturbated, and only locally may contain *Zoophycos* (*Zo*) and *Planolites* (*Pl*). Ichnofabrics tend to show more complex tiering structures than in topographically complex slopes (Buatois and Mángano, 1992). Moderately diverse ichnofaunas are also present in partially ponded slope minibasins, which tend to contain abundant sand-rich turbidites (Shultz and Hubbard, 2005). Although ichnodiversity levels are higher than in the *Zoophycos* ichnofacies of topographically complex slopes, these are remarkably lower than those in the *Nereites* ichnofacies. Substrates are nutrient rich, and therefore highly complex systems, such as those

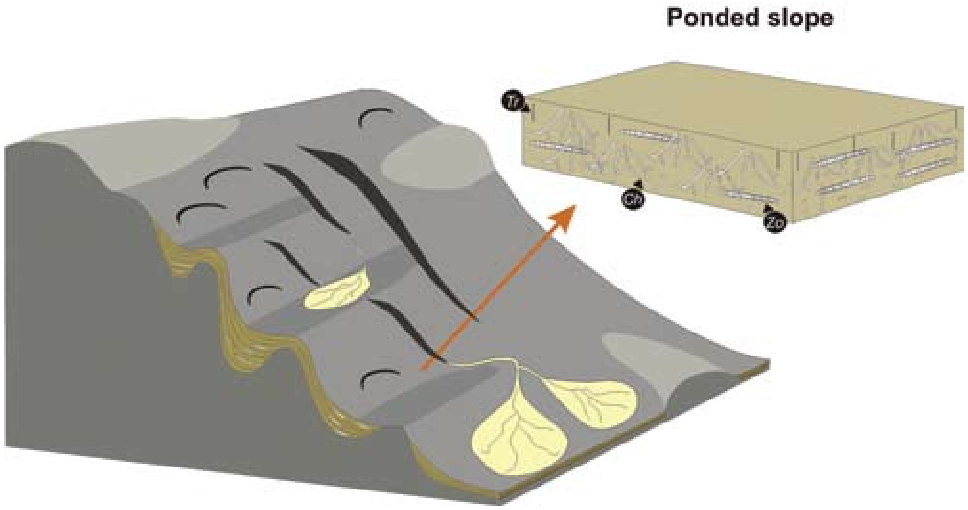

Figure 9.3 Schematic reconstruction of trace-fossil distribution in topographically complex slopes. These deposits are only locally bioturbated, and may contain *Zoophycos* (*Zo*), *Chondrites* (*Ch*), and *Trichichnus* (*Tr*).

illustrated by graphoglyptids, are not present (Wetzel, 1983). Overall, ichnofaunas from topographically simple slopes illustrate the *Zoophycos* ichnofacies with the addition of elements more typical of a distal *Cruziana* ichnofacies.

9.1.2 TOPOGRAPHICALLY COMPLEX SLOPES

Topographically complex slopes exhibit local topographic depressions and highs induced by deformation in the substrate (Smith, 2004) (Fig. 9.3). The classic example of topographically complex slopes is the Gulf of Mexico (Prather *et al*., 1998; Pirmez *et al*., 2000), but silled basins also occur in active-plate margins, such as the southern California borderland (Ingle, 1980). Available information indicates that these slopes are characterized by the formation of fault-controlled, silled, intra-slope minibasins, display limited deep-water circulation, and are commonly anoxic or dysaerobic. Turbidite systems tend to show various degrees of confinement, from cascades of silled sub-basins to connected tortuous corridors (Smith, 2004). Low current velocities and enhanced deposition of particulate organic matter in ponded areas lead to low pore-water oxygen levels (Löwemark *et al*., 2004). Ingle (1980) noted that if the depth of the sill is within the oxygen-minimum layer, all of the water below sill depth will be anoxic regardless of the maximum depth of the basin floor. Therefore, silled intra-slope minibasins are commonly non-bioturbated due to anoxic conditions or, more rarely, may contain very low-diversity ichnofaunas due to dysaerobia (Fig. 9.3). Monospecific assemblages of *Chondrites* are the most abundant suites in ponded slopes (Fu and Werner, 1994; Encinas *et al*., 2008). *Zoophycos* and *Trichichnus* may also be present. In any case, bioturbation is restricted to discrete intervals, which alternate with non-bioturbated units. Increased intensity of bioturbation and ichnodiversity may in some cases reflect shallowing (Conybeare *et al*., 2004). If bioturbated at all, topographically complex slope systems are characterized by the *Zoophycos* ichnofacies.

9.2 DEEP-MARINE TURBIDITE SYSTEMS

Deep-marine turbidite systems or submarine fans are formed by deposition of sediment gravity flows. Turbidite systems are remarkably complex and a wide variety of classification schemes and facies models have been proposed over the years (e.g. Mutti and Ricci Lucchi, 1972; Walker, 1978; Mutti, 1979, 1985, 1992; Mutti and Normark, 1991; Reading and Richards, 1994). A useful subdivision that helps to frame observations on deep-marine ichnofaunas is that of fine-grained and coarse-grained turbidite systems (Bouma, 2000a, b, 2004).

9.2.1 FINE-GRAINED TURBIDITE SYSTEMS

Fine-grained turbidite systems are characterized by (1) high sandstone/shale ratio at the base-of-slope and outer fan, but low ratio in the mid fan; (2) fine- and very fine-grained sand with abundant silt and clay particles; and (3) interfingering with basin deposits (Bouma, 2000a, b, 2004). Because of the abundance of very fine-grained sediment, fine-grained turbidite systems are efficient systems (Mutti, 1979). These systems are more typical of passive margins (although examples are known from foreland basins), and tend to occur in basins with wide shelves and coastal plains. A channel complex is formed at the base of the slope, consisting of channels flanked by levees and overbanks, and separated by interchannel areas. The breaching of levees results in the formation of crevasse-splay deposits (Posamentier and Kolla, 2003). Channels bifurcate, forming distributary channels in the mid fan, which feed sheet-sand depositional lobes in the outer fan, also known as frontal-splay complexes (Bouma, 2000a, b, 2004; Posamentier and Kolla, 2003).

Fine-grained turbidite systems commonly contain some of the most spectacular ichnofaunas described from the fossil record with respect to diversity, abundance, and complexity (e.g. Książkiewicz, 1970, 1977; Seilacher, 1977a; Crimes, 1977; Crimes *et al*., 1981; Leszczyński, 1992a; Uchman, 1995, 1998, 1999,

Box 9.2 Ichnology of Eocene fine-grained turbidite systems of the Hecho Group in the Ainsa–Jaca Basin of the Spanish Pyrenees

The Eocene Hecho Group is well known among turbidite sedimentologists because many deep-marine depositional models have resulted from its study. However, its ichnological content remained poorly documented until very recently when a monographic work and an integrated ichnological–sedimentological study were performed. More confined channelized environments are recorded in the more proximal Ainsa sub-basin, while more distal and unconfined deposits are present in the Jaca sub-basin. Ninety five ichnospecies and 49 ichnogenera have been recorded. In the Ainsa sub-basin there is an increase in ichnodiversity and intensity of bioturbation from channel to inter-channel deposits. Channel deposits are dominated by crustacean burrows, such as *Ophiomorpha rudis*, *O. annulata*, *Ophiomorpha* isp., and *Thalassinoides suevicus*. *Scolicia prisca* and *Arenicolites* isp. occur in some sandstone beds. The assemblage illustrates the *Ophiomorpha rudis* ichnosubfacies. Low ichnodiversity and sparse bioturbation are typical of channelized facies elsewhere. Interchannel deposits, both channel-margin and levee facies, contain a high diversity of trace fossils, including graphoglyptids, such as *Megagrapton irregulare* and *Paleodictyon minimum*, together with dwelling structures (e.g. *Ophiomorpha rudis* and *Thalassinoides suevicus*), feeding structures (e.g. *Phycosiphon incertum*) and grazing trails (e.g. *Gordia arcuata* and *Gordia marina*). This assemblage illustrates a mixed *Ophiomorpha rudis* and *Paleodictyon* ichnosubfacies. In the Jaca sub-basin, there is an increase in ichnodiversity and intensity of bioturbation from the channel-lobe transition to the lobe fringe. The channel-lobe transition is characterized by moderate ichnodiversity and sparse bioturbation. Deposits display a dominance of dwelling burrows (e.g. *Ophiomorpha annulata, Thalassinoides suevicus*, and *Palaeophycus tubularis*), but grazing trace fossils (*Nereites irregularis*), feeding trace fossils (*Halopoa imbricata*), and graphoglyptids (*Paleodictyon maximum*) are present locally. In the depositional lobe (frontal splay), a wide variety of trace fossils is preserved, including feeding structures (e.g. *Halopoa storeana*, *Halopoa imbricata*, and *Chondrites intricatus*), dwelling structures (*Ophiomorpha annulata*, *O. rudis*, and *Thalassinoides* isp.), grazing trace fossils (*Nereites irregularis*, *Scolicia prisca*, and *Scolicia strozzi*), and graphoglyptids (*Helminthorhaphe flexuosa*, *Spiroraphe involuta*, *Cosmorhaphe lobata*, and *Paleodictyon strozzi*). Lobe-fringe deposits display the highest trace-fossil diversity and intensity of bioturbation, representing a typical *Paleodictyon* ichnosubfacies of the *Nereites* ichnofacies. Although feeding, dwelling, and grazing trace fossils are present, suites tend to be dominated by graphoglyptids, including *Paleomeandron robustum*, *Desmograpton dertonensis*, *Helmithorhaphe flexuosa*, *Protopaleodictyon spinata*, and various ichnospecies of *Paleodictyon*. A decrease in trace-fossil diversity and degree of bioturbation is detected from the lobe fringe to the basin plain. Basin-plain deposits are characterized by a sharp increase in the proportion of feeding structures (e.g. *Phycosiphon incertum*, *Zoophycos* isp.), a high proportion of graphoglyptids (e.g. *Megagrapton submontanum* and "*Rotundusichnium*" *zumayense*), and a decrease in dwelling structures (e.g. *Ophiomorpha rudis*). The overall high trace-fossil diversity is typical of deep-marine deposits of similar age, and has been attributed to moderate oligotrophy as a result of large-scale oceanographic and climatic changes. The Hecho Group illustrates the most diagnostic ichnological features of a fine-grained turbidite system.

References: Uchman (2001); Heard and Pickering (2008).

2007; Wetzel and Uchman, 1997; Kozur *et al.*, 1996; Buatois *et al.*, 2001; Wetzel *et al.*, 2007; Rodríguez-Tovar *et al.*, 2010a) (Box 9.2) (Fig. 9.4). In deep-marine environments, low-energy conditions and temporal stability promote the establishment of a wide variety of graphoglyptids and grazing trails, representing the *Nereites* ichnofacies. The overall abundance of graphoglyptids is indicative of reduced food supply and appropriate bottom energy conditions allowing their preservation. This is consistent with the site of emplacement of fine-grained turbidite systems, typically far away from the source area, and separated from the nearshore zone by a wide continental shelf. Interestingly, although delta-fed turbidite systems represent a departure to this standard scenario, graphoglyptids are also present in these organic-rich turbidites and related deposits (Olivero *et al.*, 2010).

Graphoglyptid ichnofaunas, illustrating the *Paleodictyon* ichnosubfacies of the *Nereites* ichnofacies, occur in thin-bedded sandy turbidites, and are mostly present in the outer fan, more precisely in frontal splays (e.g. Crimes, 1977; Crimes *et al.*, 1981; McCann, 1993; Uchman, 1995, 2001; Uchman and Demircan, 1999; Wetzel and Uchman, 2001; Demircan and Toker, 2003; Uchman *et al.*, 2004a; López-Cabrera *et al.*, 2008; Heard and Pickering, 2008; Rodríguez-Tovar *et al.*, 2010a). Together with a large number of graphoglyptids, such as *Paleodictyon* (Fig. 9.5a–b), *Desmograpton* (Fig. 9.5c), *Protopaleodictyon*, *Megagrapton*, *Helicolithus* (Fig. 9.5d), *Spirorhaphe* (Fig. 9.5e), *Helminthorhaphe* (Fig. 9.5f), *Lorenzinia* (Fig. 9.5g–h), *Cosmorhaphe*, and *Urohelminthoida*, there are other basic morphological types. These include the circular burrow *Circulichnis* (Fig. 9.5i), sinuous trails, such as *Helminthopsis*, *Nereites*, and *Scolicia* (Fig. 9.5j), various feeding burrows, including *Zoophycos*, *Lophoctenium*, and *Phycosiphon* (Fig. 9.6a), and the chevronate trail *Protovirgularia* (Fig. 9.5k)

In more proximal positions, graphoglyptid-dominated ichnofaunas also occur in levee and crevasse-splay deposits of the channel complex (e.g. McCann and Pickerill, 1988; McCann, 1993; Uchman, 1995; Wetzel and Uchman, 1997; Buatois *et al.*, 2001; Heard and Pickering, 2008; Olivero *et al.*, 2010). In addition to a wide variety of graphoglyptids (Fig. 9.7a–g)

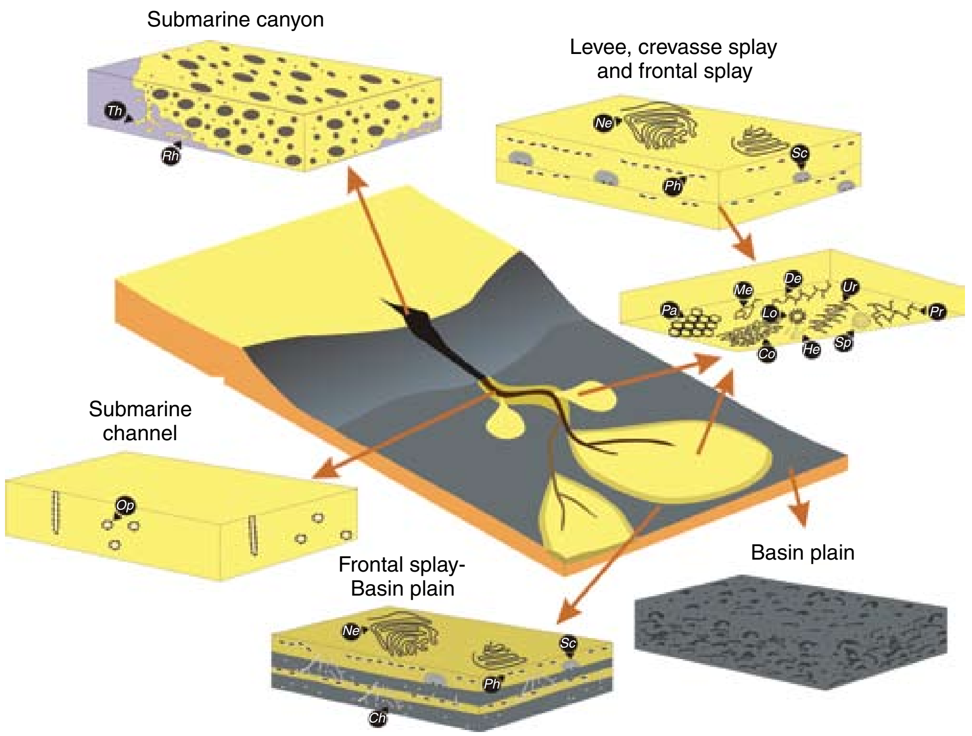

Figure 9.4 Schematic reconstruction of trace-fossil distribution in fine-grained turbidite systems. The base of the incised canyon is characterized by a firmground suite that may contain *Thalassinoides* (*Th*) and *Rhizocorallium* (*Rh*) illustrating the *Glossifungites* ichnofacies. Submarine-channel deposits typically contain *Ophiomorpha* (*Op*). Thin-bedded sandy turbidites in levee, crevasse-splay, and frontal-splay areas contain *Nereites* (*Ne*), *Scolicia* (*Sc*), and *Phycosiphon* (*Ph*) as post-depositional elements, and a wide variety of pre-depositional components, such as *Paleodictyon* (*Pa*), *Megagrapton* (*Me*), *Desmograpton* (*De*), *Lorenzinia* (*Lo*), *Cosmorhaphe* (*Co*), *Helicolithus* (*He*), *Spirorhaphe* (*Sp*), and *Protopaleodictyon* (*Pr*). Distal muddy turbidites of the transitional zone between the frontal splay and the basin plain may contain *Nereites* (*Ne*), *Scolicia* (*Sc*), *Phycosiphon* (*Ph*), and *Chondrites* (*Ch*). Basin-plain deposits are characterized by an indistinct bioturbated mottling.

such as those mentioned for the frontal-splay deposits, levee and crevasse-splay deposits also contain abundant dwelling structures (e.g. *Palaeophycus* and *Ophiomorpha*), sinuous grazing trails, such as *Gordia*, *Helminthopsis*, *Nereites*, and *Scolicia* (Fig. 9.7h), the robust spiral trace *Spirophycus* (Fig. 9.7i), the branched system *Chondrites* (Fig. 9.7j), and various spreite feeding structures, including *Zoophycos*, *Polykampton*, and *Phycosiphon* (Fig. 9.6b).

The *Nereites* ichnosubfacies tends to occur in more distal muddy turbidites, which are more typical of the distal overbank and the transition between the frontal splays and the basin plain. In these settings, various ichnospecies of *Nereites*, most commonly *N. irregularis* (Fig. 9.8a–b), and *Scolicia*, together with *Chondrites* (Fig. 9.8c–d), *Phycosiphon*, *Dictyodora* (in Paleozoic rocks), *Zoophycos*, and *Helicodromites* (Fig. 9.8c) are dominant. Formation of graphoglyptids is commonly inhibited under oxygen-deficient conditions (Leszczyński, 1991a) or high frequency of turbidity currents (D'Alessandro *et al.*, 1986). For example, Uchman (1991b, 1992) documented Cretaceous and Cenozoic turbidites emplaced in oxygen-depleted settings, having very few to almost no agrichnial structures. These ichnofaunas are also characterized by unusually low ichnodiversity and dominance of opportunistic post-turbidite trace fossils. In these distal settings, deposits showing characteristics intermediate between mud turbidites and pelagites are common. These deposits, referred to as hemiturbidites (Stow and Wetzel, 1990; Wetzel and Balson, 1992), are intensely bioturbated and accumulate slowly from a dilute suspension cloud formed beyond and above a large low-concentration turbidity current. In these outer regions of deep-sea fans, sedimentation and bioturbation are in equilibrium and, as a result, hemiturbidite mudstones are completely burrowed.

In the channels and in the most proximal areas of the sheet-sand depositional lobes, continuous erosion and high rates of sedimentation prevent development or preservation of graphoglyptid ichnofaunas and, in fact, most channelized deposits are unburrowed. However, these high-energy settings locally may host ichnofaunas that contain elements typical of shallow water (e.g. *Skolithos*, *Diplocraterion*, and *Ophiomorpha*), representing a deep-marine example of the *Skolithos* ichnofacies (Crimes, 1977; Crimes *et al.*, 1981; McCann and Pickerill, 1988). Uchman (2001, 2007, 2009) noted that some of these thick-bedded sandy turbidites are dominated by horizontal components, typically crustacean galleries (Fig. 9.9a–d), rather than vertical burrows and ascribed this association to the *Ophiomorpha rudis* ichnosubfacies. *Ophiomorpha rudis* and *O. annulata* (Fig. 9.9a–c) are typical in these deposits. Channelized areas and inner zones of depositional lobes, characterized by sandy substrates, organic particles in the water column, and good oxygenation, allow the establishment of a benthic fauna that produce trace fossils that commonly typify nearshore areas. However, shallow-water elements are not restricted to these high-energy regions of submarine fans, occurring in more distal, thin-bedded turbidites also (Uchman, 1991a; Uchman and Demircan, 1999). The crustacean producer of *Ophiomorpha rudis* may have been transported from shallower water by turbidity currents or may represent a resident fauna adapted to deep-water environments (Uchman and Demircan, 1999). These crustaceans may have penetrated into the sandy substrate in search for nutrient-rich deeply buried plant detritus (Uchman *et al.*, 2004a; López-Cabrera *et al.*, 2008).

Therefore, sandy turbidites may contain two different suites, pre- and post-turbidite, recording different times of emplacement and contrasting environmental conditions (Seilacher, 1962;

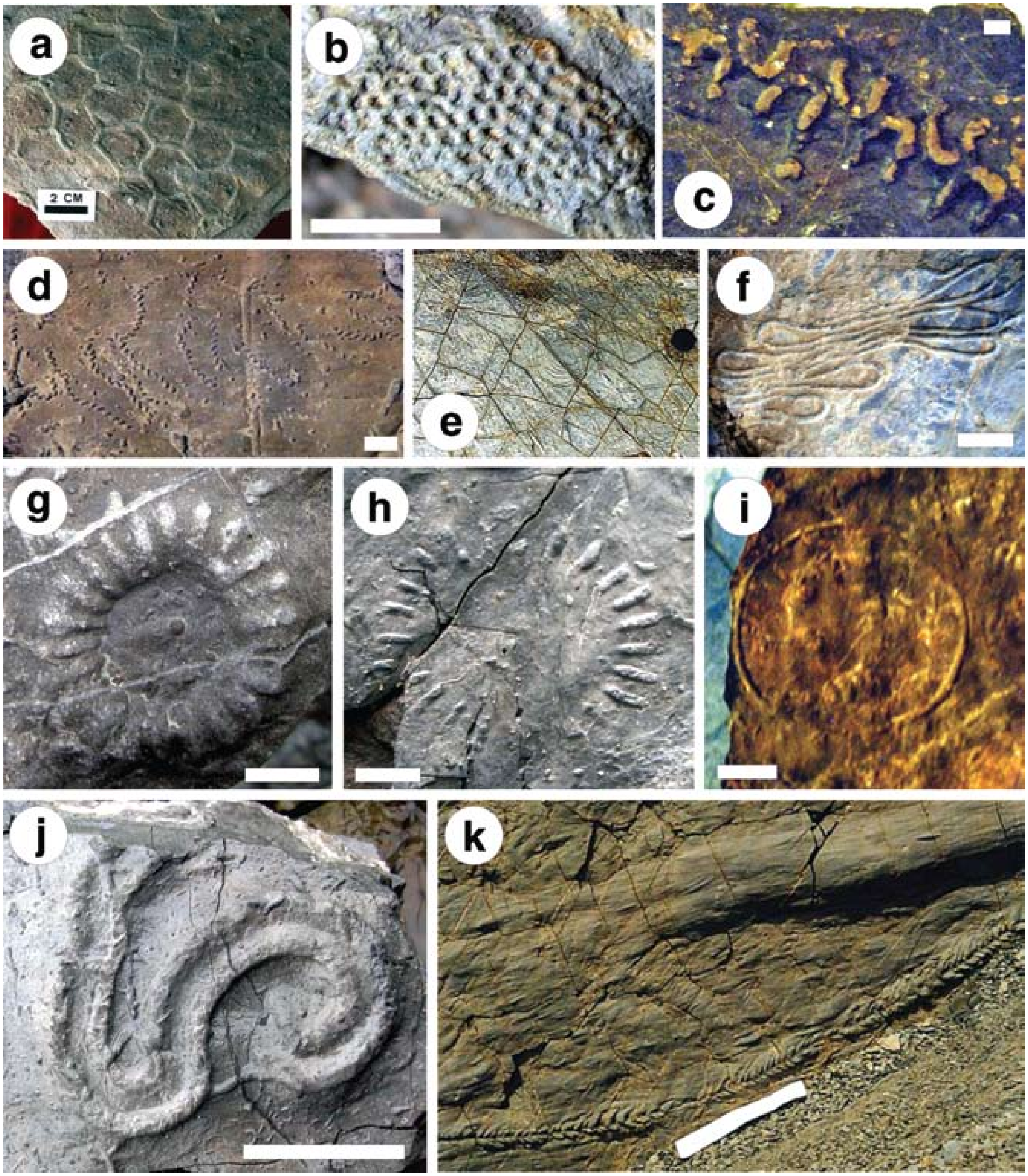

Figure 9.5 Characteristic trace fossils of turbidites in distal areas of frontal splays and fringes of fine-grained turbidite systems. (a) *Paleodictyon gomezi*. Oligocene–Miocene, Campo de Gibraltar, southern Spain. (b) *Paleodictyon minimum*. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Scale bar is 1 cm. See Macsotay (1967). (c) *Desmograpton pamiricus*. Upper Triassic, Al Ayn Formation, Oman Mountains. Scale bar is 1 cm. See Wetzel *et al*. (2007). (d) *Helicolithus sampelayoi*. Eocene, Beloveža Beds, Lipnica Mała, Outer Carpathians, Poland. Scale bar is 1 cm. (e) *Spirorhaphe involuta*. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Lens cover is 5.5 cm. See Macsotay (1967). (f) *Helminthorhaphe* isp. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Scale bar is 1 cm. See Macsotay (1967). (g) *Lorenzinia apenninica*. Upper Cretaceous–Paleocene, Ropianka Formation, Słopnice, Outer Carpathians, Poland. Scale bar is 1 cm. See Uchman (2008a). (h) *Lorenzinia carpathica*. Upper Cretaceous–Paleocene, Ropianka Formation, Słopnice, Outer Carpathians, Poland. Scale bar is 1 cm. See Uchman (2008a). (i) *Circulichnis montanus*. Upper Triassic, Al Ayn Formation, Oman Mountains. Scale bar is 1 cm. See Wetzel *et al*. (2007). (j) *Scolicia* isp. Eocene, Variegated Shale, Słopnice, Outer Carpathians, Poland. Scale bar is 5 cm. See Uchman (2008a). (k) *Protovirgularia* isp. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Scale bar is 10 cm. See Macsotay (1967).

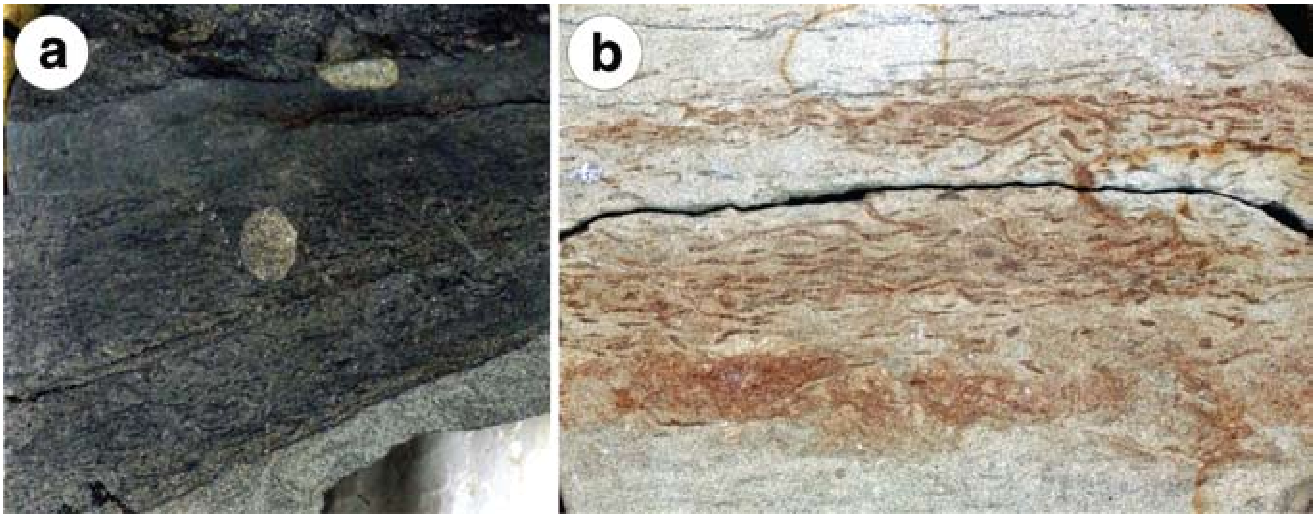

Figure 9.6 Core expression of *Phycosiphon* ichnofabrics in thin-bedded turbidites. (a) High density of *Phycosiphon incertum* at the top of a lobe-fringe turbidite sandstone and in the overlying hemipelagic mudstone. Note also associated firmground *Thalassinoides*. Lower Miocene, La Blanquilla Basin, offshore Venezuela. Core width is 7 cm. (b) Sideritized *Phycosiphon* isp. in overbank turbidite sandstone. Upper Miocene–Lower Pliocene, Carúpano Basin, offshore Venezuela. Core width is 7 cm.

Kern, 1980; Wetzel, 1991; Leszczyński, 1991b, 1992a; Uchman, 1995; Tunis and Uchman, 1996a, b; Wetzel and Uchman, 1997) (Fig. 9.10). The pre-turbidite suite is dominated by graphoglyptids and grazing trails, and is preserved as positive hyporeliefs on the turbidite soles. This suite records the activity of a diverse shallow-tier infaunal community inhabiting pelagic mud. The post-turbidite suite consists of dwelling, feeding, and grazing traces, and is preserved for the most part on the upper surface of the event beds, but also at the base or within turbidites. This suite records opportunistic colonization of the newly emplaced sandy substrate. Accordingly, the base of sandy turbidites represents a palimpsest surface that contain two suites emplaced at different times (Fig. 9.11a–c). Kern (1980) outlined a set of criteria to differentiate between post- and pre-turbidite suites at the base of sandstone. Pre-turbidite trace fossils may show evidence of erosional modification (Fig. 9.11d) and internal lamination preserved within the burrow systems. Post-turbidite trace fossils commonly cross-cut the former suite and show pristine morphologies on surfaces with abundant flute marks. In addition, emplacement of post-turbidite trace fossils may lead to modifications at the sand/mud interface. This author also noted that post-turbidite trace fossils are rare at the base of sandstone thicker than 10 cm. However, Seilacher (1962) documented spectacular specimens of *Ophiomorpha* penetrating to the base of 4 m-thick turbidites.

A number of studies have focused on the tiering structure of ichnofaunas from turbidites and related facies (e.g. Wetzel, 1984, 1991; Leszczyński and Seilacher, 1991; Leszczyński, 1991b, 1992a, b, 1993; Uchman, 1991c, 1995; Orr, 1994; Bak, 1995; Wetzel and Uchman, 1997, 1998). In the case of pre-turbidite suites, two main tiers occur: a very shallow tier consisting of graphoglyptids and a deeper tier consisting of actively filled feeding burrows (Leszczyński, 1991b) (Fig. 9.10). Due to vertical accretion of pelagic and hemipelagic sediment on the sea floor, the deeper-tier fodinichnia migrates upward obliterating the very shallow-tier agrichnia (Werner and Wetzel, 1982; Wetzel, 1991). Therefore, under conditions of suspension fallout background sedimentation, graphoglyptids are not preserved and the resultant ichnofabric is dominated by actively infilled burrows, such as *Zoophycos*, *Scolicia*, *Lophoctenium*, and *Planolites*. Graphoglyptid preservation can only take place if deposition from a turbidity current interrupts background sedimentation and associated bioturbation. Under these conditions, graphoglyptids are preserved as positive hyporelief on the bases of the sandy turbidites (Figs. 9.10). Although it has been traditionally assumed that turbidity currents erode the uppermost millimeters of the muddy substrate and cast with sand the shallow-tier biogenic structures, it has been recently suggested that preservation results from a shock wave immediately prior to deposition (Seilacher, 2007a) (see Section 4.2.5). A micro-tiering structure is developed within the pre-turbidite suite dominated by graphoglyptids. Tiny *Paleodictyon* occupy a shallower-tier position than slightly deeper *Cosmorhaphe* and *Glockerichnus* (Leszczyński and Seilacher, 1991) (Fig. 9.11c). *Spirophycus* tends to emplaced deeper into the sediment cross-cutting shallower trace fossils (Fig. 9.11e). The depth of erosion of the subsequent turbidity current controls which tier becomes preserved (Leszczyński, 1993).

Post-turbidite colonization of the event sand starts after the depositional event is complete (Leszczyński, 1991b, 1993). Some post-turbidite colonizers are adapted to specific sandy substrates, and are typically unable to migrate upward during pelagic and hemipelagic vertical accretion of the sea floor. On the other hand, those infaunal organisms that are less substrate-specific (e.g. producers of *Chondrites* and *Planolites*) may move upward into the background mud (Fig. 9.10). Penetration depth and intensity of bioturbation as a function of oxygen content, rate of

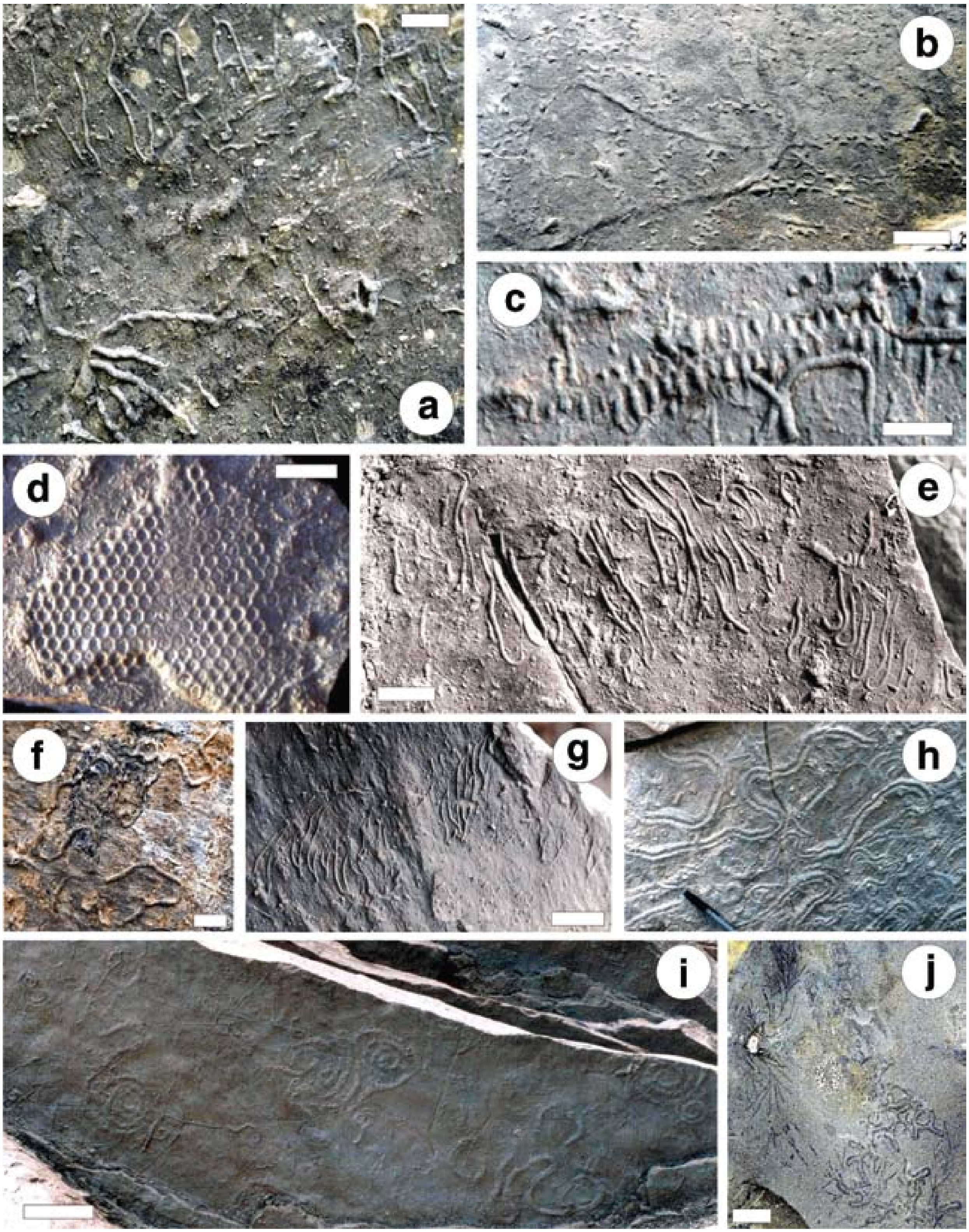

Figure 9.7 Characteristic trace fossils of overbank turbidite deposits in fine-grained turbidite systems. (a) *Helminthorhaphe* isp and *Glockerichnus* isp. Paleocene, Gurnigel Flysch, Zollhaus, Swiss Alps. Scale bar is 5 cm. See Crimes *et al*. (1981). (b) *Paleomeandron* isp. Eocene, Ganei Slates, Ganei, Swiss Alps. Scale bar is 1 cm. See Wetzel and Uchman (1997). (c) *Desmograpton pamiricus*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (d) *Paleodictyon minimum*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (e) *Helminthorhaphe flexuosa*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (f) *Megagrapton submontanum*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (g) *Urohelminthoida dertonensis*. Lower to Middle Eocene, Tarcau Sandstone, Gramaticu Valley, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (h) *Scolicia strozzi*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Pen is 15 cm. See Buatois *et al*. (2001). (i) *Spirophycus involutissimus*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 10 cm. See Buatois *et al*. (2001). (j) *Phycosiphon incertum* and *Chondrites* isp. Paleocene, Gurnigel Flysch, Zollhaus, Swiss Alps. Scale bar is 1 cm. See Crimes *et al*. (1981).

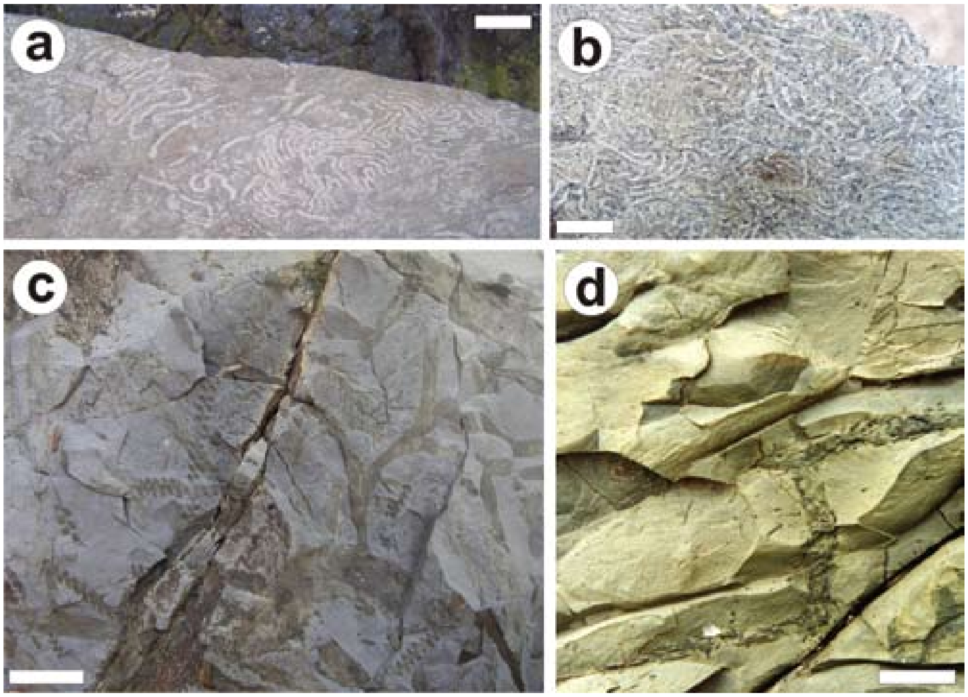

Figure 9.8 Characteristic trace fossils of distal muddy turbidites in fine-grained turbidite systems. (a) *Nereites irregularis* in distal marly turbidites. Paleocene, Głębieniec Member, Ropianka Formation, Głębieniec stream, Outer Carpathians, Poland. See Uchman and Cieszkowski (2008b). (b) *Nereites irregularis* in distal muddy turbidites. Upper Cretaceous, Helminthoid Flysch, Weissenburg Bad, Dranses Nappe, Swiss Alps. See Wetzel (2003). (c) Distal marly and silty turbidites with large and small *Chondrites* isp and *Helicodromites* isp. Eocene, Bystrica Formation, Zbludza, Outer Carpathians, Poland. See Uchman (2008b). (d) *Chondrites* isp. concentrated within "phantom burrows" and dispersed in the host rock. Upper Cretaceous, Horgazu Formation, Covasna Valley, Romania. All scale bars are 1 cm.

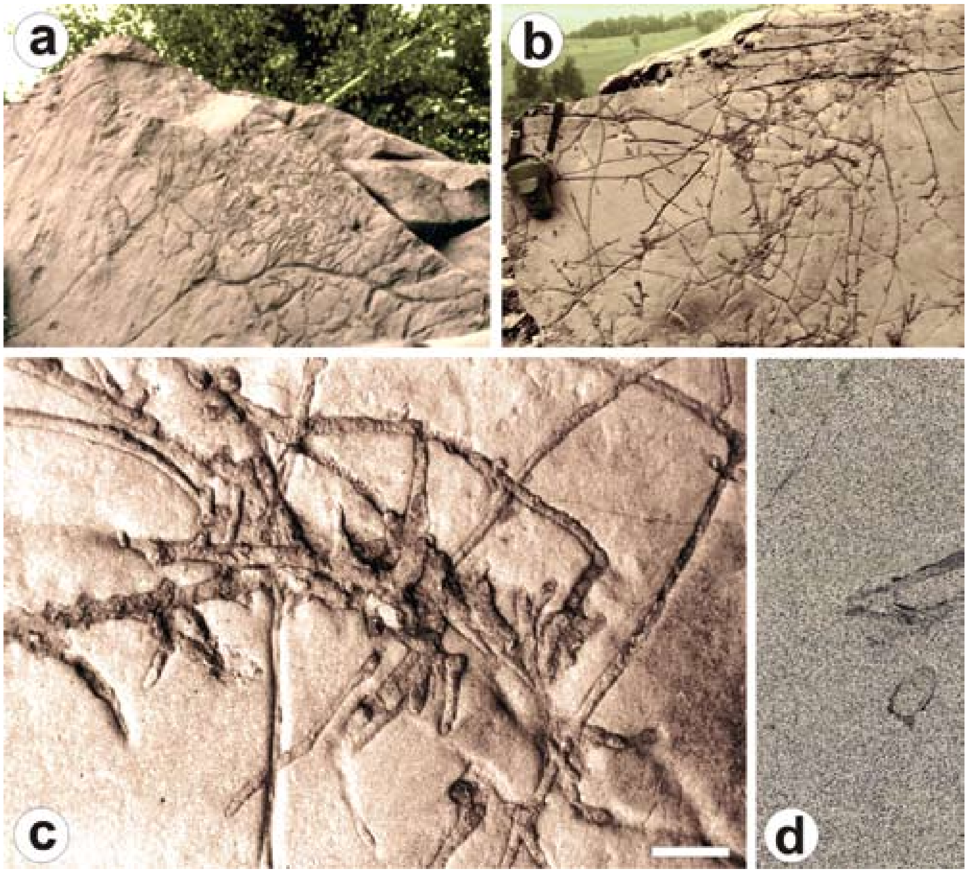

Figure 9.9 Characteristic trace fossils of turbidite-channel deposits in fine-grained turbidite systems. (a) and (b) General views of the top of a channelized sandstone unit with *Ophiomorpha annulata*. (c) Close up of burrow networks of *Ophiomorpha annulata*. Scale bar is 5 cm. (a), (b), and (c) are from outcrops of the Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al.* (2001). (d) Core expression of *Ophiomorpha* isp. in deep-marine high-energy sandstone turbidites. Lower Miocene, La Blanquilla Basin, offshore Venezuela. Core width is 7 cm.

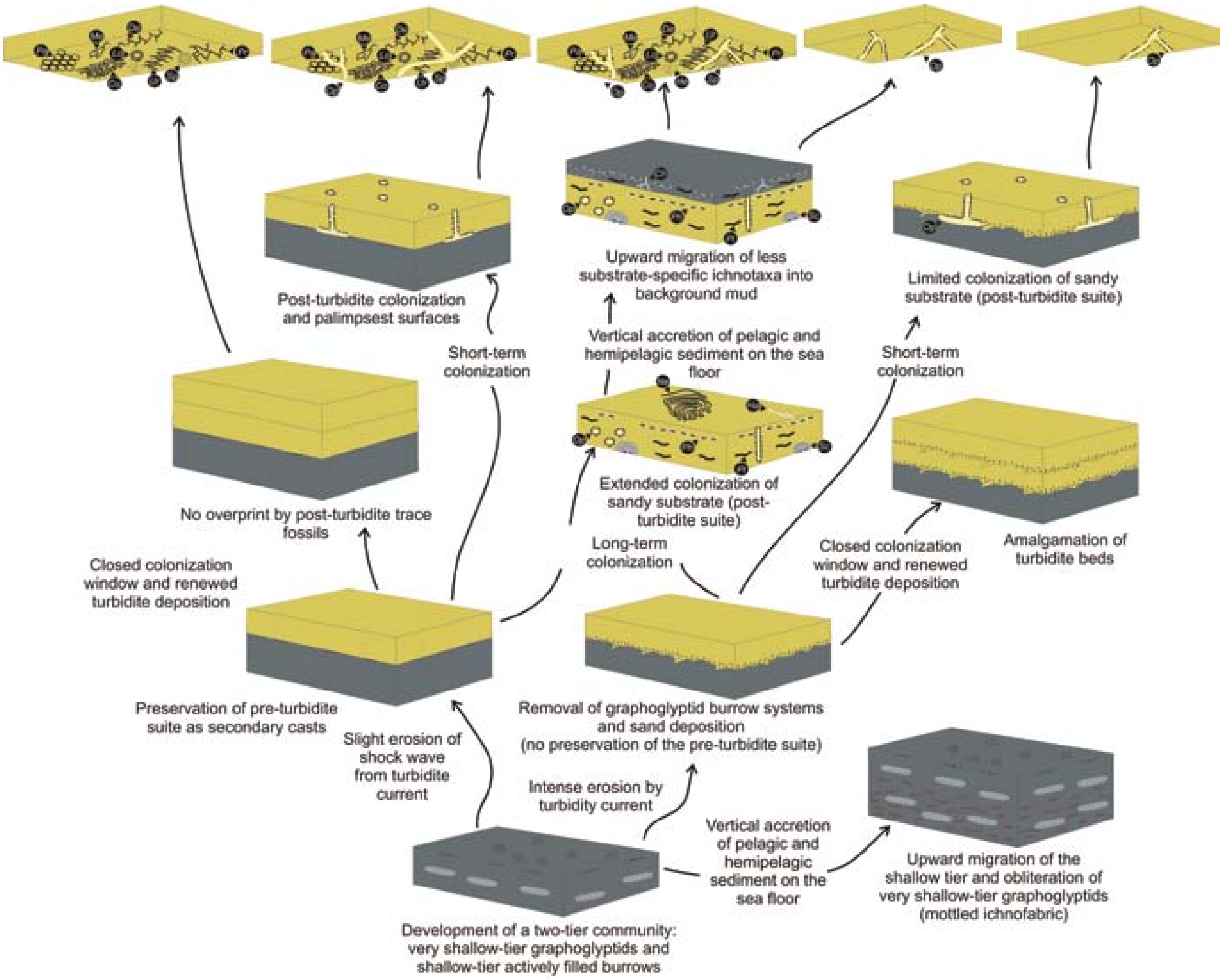

Figure 9.10 Taphonomic pathways of turbidite trace fossils. The preserved ichnofauna is the end-result of a complex array of taphonomic factors. If only hemipelagic suspension fallout takes place, no graphoglyptids are preserved and the resultant product is a mottled ichnofabric that may or may not display discrete trace fossils. If erosion by the turbidity current is too intense, graphoglyptids are not preserved either. Emplacement of post-turbidite colonizers depends on the nature of the colonization window. Under high frequency of highly erosive turbidite events, bed amalgamation occurs and sandstone units are unburrowed. If the frequency of these highly erosive events is lower, limited colonization of the sandy substrate by the post-turbidite suite may occur, being *Ophiomorpha* (*Op*) a typical component. If only slight erosion occurs, graphoglyptids are preserved as positive hyporeliefs on turbidite sandstone beds. Preservation of the graphoglyptid microtiering profile depends on the depth of erosion. Typical elements of the pre-turbidite trace-fossil suite are *Paleodictyon* (*Pa*), *Megagrapton* (*Me*), *Protopaleodictyon* (*Pr*), *Desmograpton* (*De*), *Lorenzinia* (*Lo*), *Cosmorhaphe* (*Co*), *Urohelminthoida* (*Ur*), and *Spirorhaphe* (*Sp*). Under high rates of slightly erosive turbidite events, the colonization window for post-event burrowers remains close and graphoglyptids are not overprinted by the post-turbidite trace-fossil suite. In the case of short-term colonization windows, the post-turbidite trace-fossil suite may occur, but restricted to sand-specific colonizers, typically forming *Ophiomorpha* (*Op*), overprinting the pre-turbidite trace-fossil suite. In the case of long-term colonization windows, pelagic and hemipelagic vertical accretion of the sea floor takes place and even more complex ichnofabrics develop as a result of sequential colonization. In addition to *Ophiomorpha* (*Op*), *Planolites* (*Pl*), *Scolicia* (*Sc*), and *Phycosiphon* (*Ph*) may occur. While post-turbidite sandy-specific colonizers cannot migrate upward during pelagic and hemipelagic sedimentation, less substrate-specific colonizers may move upward into the background mud.

background sedimentation, and the time to next turbidite event are the most important limiting factors (Leszczyński, 1993). Crustacean burrows (e.g. *Ophiomorpha*) are by far the deepest structures, commonly penetrating through several turbidite layers (multilayer colonizers of Uchman, 1995). In the case of muddy turbidites, observations from modern and ancient environments suggest sequential colonization and upward migration in response to geochemical conditions, particularly the re-adjustment and re-establishment of the redox boundary (Wetzel and Uchman, 2001) (Box 9.3). Passive-margin fine-grained turbidite systems tend to be affected by bottom currents (Faugères and Stow, 2008). The ichnologic signatures of contourites (i.e. bottom-current deposits) have been recently explored by Wetzel *et al.* (2008).

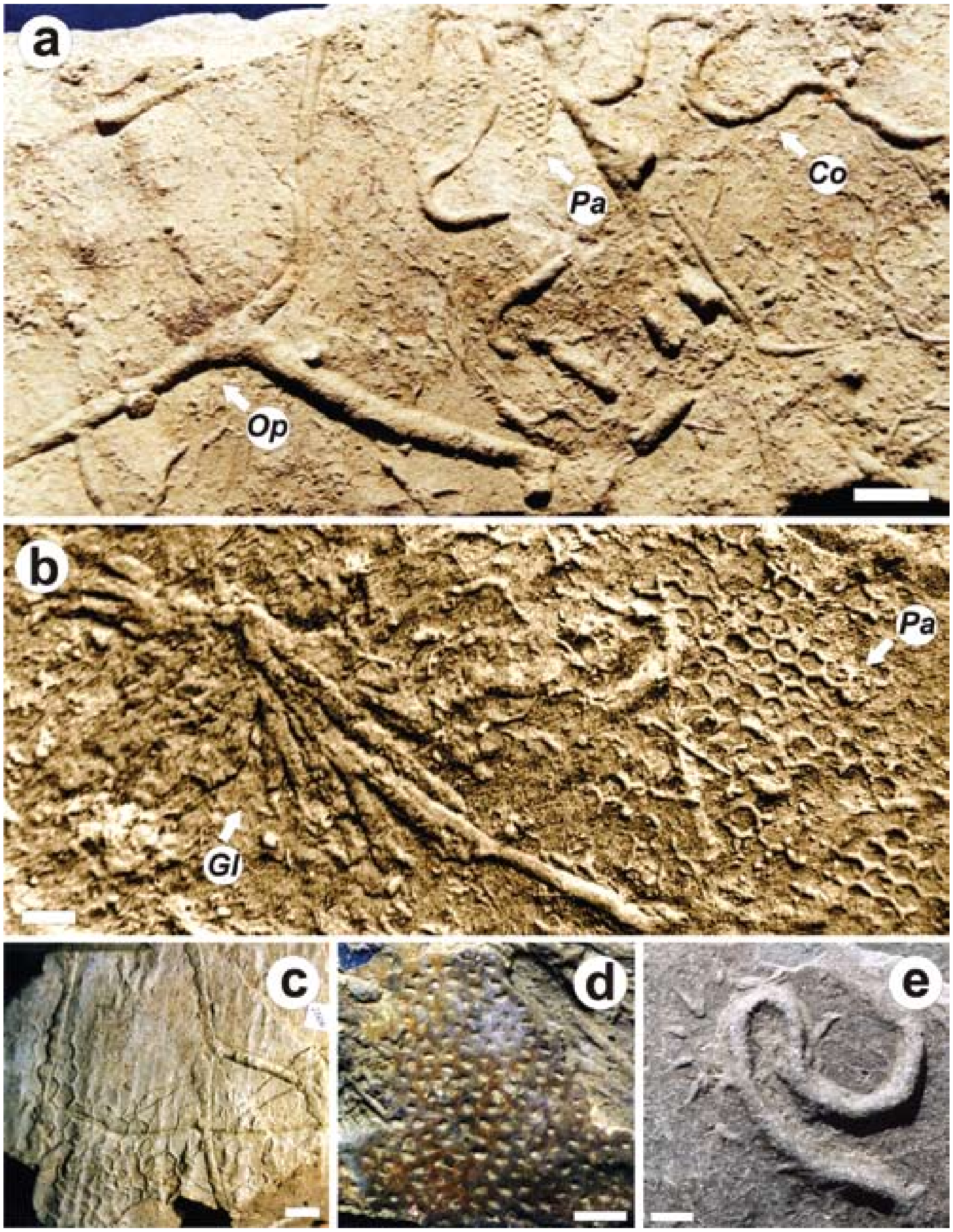

Figure 9.11 Taphonomy of thin-bedded turbidites. (a) Base of a sandstone showing juxtaposition of pre- and post-turbidite suites forming a palimpsest surface. Hexagonal networks (*Paleodictyon minimum*) (*Pa*) and meandering trace fossils (*Cosmorhaphe sinuosa*) (*Co*) belong to the pre-turbidite suite, while superimposed crustacean galleries (*Ophiomorpha annulata*) (*Op*) are part of the post-turbidite suite. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al*. (2001). (b) *Paleodictyon miocenicum* networks (*Pa*) partially modified by erosion. Minimum erosion in some areas allowed preservation of network vertical outlets. The radial trace fossil *Glockerichnus* isp. (*Gl*) occupies a deeper tier, illustrating microtiering in the pre-turbidite community. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al*. (2001). (c) Hexagonal networks (*Paleodictyon maximum*) of the pre-turbidite suite cross-cut by crustacean galleries (*Ophiomorpha annulata*) of the post-turbidite suite. Lower to Middle Eocene, Tarcau Sandstone, Gramaticu Valley, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al*. (2001). (d) *Paleodictyon* cf. *nodosum* showing eroded outlines of vertical components. Lower to Middle Miocene, Shahr Pum Unit, Taherui, Makran Range, Southeastern Iran. See Crimes and McCall (1995). (e) *Spirophycus bicornis* cross-cutting *Lorenzinia pustulosa*. Eocene, Ganei Slates, Ganei, Swiss Alps. See Wetzel and Uchman (1997). All scale bars are 1 cm.

These authors contrasted the role of strong and weak bottom currents. They noted that strong currents may result in intense and deep erosion, formation of non-deposition horizons and/or deposition of sand-dominated contourites. Deep erosion and long-term non-deposition is commonly conducive to the development of the *Glossifungites* ichnofacies in compacted sediment. Sandy contourites tend to be intensely bioturbated, displaying a combination of trace fossils produced by shallow-tier ploughers and deep-tier structures, such as *Skolithos*, *Scolicia* and *Planolites*, as well as deeply emplaced crustacean domiciles (e.g. *Thalassinoides*, *Gyrolithes*).

Weak bottom currents commonly deposit fine-grained particles and abundant organic matter, resulting in the formation of mud-dominated contourites. Because these sediments commonly have anoxic pore waters at very shallow depths, ichnodiversity tend to be low and trace fossils are typically small. *Chondrites* is commonly dominant, and *Nereites* may form along the redox boundary. Low sedimentation rates may be conducive to intense bioturbation, particularly if bottom currents supply additional food. In these cases, distinction from silty/muddy turbidites and hemipelagites may be complicated.

9.2.2 COARSE-GRAINED TURBIDITE SYSTEMS

Coarse-grained turbidite systems are characterized by (1) very high sandstone/shale ratio, including the interchannel areas; (2) medium- and coarse-grained sands with little or no clay minerals; and (3) gradual progradation into the

Box 9.3 Colonization of Eocene muddy turbidites in the Polish Carpathians

Detailed ichnofabric analysis in muddy turbidites of the Eocene Beloveža Formation of the Polish Carpathians allows the reconstruction of the colonization of event beds in the deep sea. Evaluation of cross-cutting relationships demonstrates that colonization was sequential and most likely controlled by changes in geochemical conditions, particularly re-adjustment and re-establishment of the redox boundary. The makers of *Phycosiphon* and *Halopoa* were the first to exploit the newly emplaced substrate. The former is suited to colonize well-oxygenated muds, while the later displayed a preference for sandy substrates. After re-establishment of the redox boundary, *Nereites* was emplaced probably exploiting microbial organic matter right above the redox discontinuity. Next in the sequence was *Chondrites*, which was able to penetrate below the redox boundary, even reaching below the previously emplaced turbidite layer. *Ophiomorpha* and *Scolicia* represent the deepest tier and most likely record permanent bioturbation that was unaffected by the deposition of new turbidites. Both reflect adaptations to burrowing though sand and mud, and to coping with oxygen-restricted conditions. This model is consistent with observations from the modern deep-sea floor that suggest that newly emplaced turbidites contain abundant organic matter and are fully oxygenated. However, because oxygen consumption exceeds oxygen production, the lower part of the turbidite and the buried hemipelagic layer become rapidly depleted in oxygen.

Reference: Wetzel and Uchman (2001).

basin (Bouma, 2000a, b, 2004). Because of the scarcity of very fine-grained sediment, coarse-grained turbidite systems are poorly efficient (Mutti, 1979). These systems are more typical of active margins, and tend to occur in basins with narrow shelves and coastal plains. Submarine channels form at the base of the slope and are typically of a low sinuosity, braided-type. Because of their poor efficiency, lobe deposits are formed relatively close to the base of slope (Fig. 9.12).

As in the case of fine-grained turbidite systems, high-energy channelized areas and the most proximal zones of sheet-sand depositional lobes are typically unbioturbated or may contain trace fossils that are usually common in shallow water, illustrating the *Skolithos* ichnofacies in a deep-marine context (e.g. Kern and Warme, 1974; Buatois and López Angriman, 1992b). However, and in contrast to fine-grained turbidite systems, the *Nereites* ichnofacies (in particular, the *Paleodictyon* ichnosubfacies) is rare to absent in coarse-grained deep-marine systems. The absence or scarcity of graphoglyptids is not a direct result of grain size because off-channel and lobe thin-bedded turbidites of the same grain size occur in both fine-grained and coarse-grained turbidite systems. Rather, the ichnofauna of thin-bedded turbidites in coarse-grained turbidite systems tends to be dominated by feeding traces of deposit feeders, such as *Phycosiphon*, *Chondrites*, *Planolites*, and *Zoophycos*, suggesting affinities with the *Zoophycos* ichnofacies (Buatois and López Angriman, 1992b) (Fig. 9.12) (Box 9.4). The replacement of the *Nereites* ichnofacies by the *Zoophycos* ichnofacies is most likely due to the associated narrow shelf and the close proximity of frontal splays to the base of the slope. This may have promoted a high frequency of sediment gravity flows supplying significant amounts of organic matter to the system, precluding the need for the sophisticated farming strategies that characterize agrichnial structures (Buatois and López Angriman, 1992b). In some cases, it is even possible that the post-turbidite suite displays higher diversity than the pre-turbidite suite (e.g. W. Miller, 1991b). These post-turbidite trace fossils may have exploited abundant plant detritus accumulated within the event-flow sand.

9.3 HYPERPYCNAL SYSTEMS

In recent years, a number of studies have underscored the importance of sustained turbidity currents or hyperpycnal flows as opposed to more classic episodic turbidity currents (Mulder and Syvitski, 1995; Mutti *et al*., 1996; Plink-Björklund and Steel, 2004; Zavala *et al*., 2011). Even more recently, ichnological studies started to focus on the trace-fossil signatures of both modern and ancient deep-marine hyperpycnites (Ponce *et al*., 2007; Wetzel, 2008; Olivero *et al*., 2010; Carmona and Ponce, 2011). Studies from modern deep-sea bottoms indicated that hyperpycnal-flow deposits provide a more appropriate substrate for rapid colonization, particularly in comparison with volcanic ash (Wetzel, 2008). Hyperpycnal flows typically transport larvae, juvenile, and adult organisms, together with benthic food to the deep sea, resulting in deposits commonly containing abundant organic matter. Analysis of Upper Eocene–Lower Oligocene hyperpycnal-flow deposits of Tierra del Fuego, southern Argentina, indicates that bioturbation typically occurs in connection with pause horizons (Ponce *et al*., 2007). This ichnofauna is dominated by *Phymatoderma* (Fig. 9.14a–b) with *Chondrites* (Fig. 9.14c), *Zoophycos* (Fig. 9.14b), *Tasselia* (Fig. 9.14d), and *Paradictyodora* (Fig. 9.14b) also being common. The bioturbated deposits correspond to mudstone accumulated during the backstepping stage of the flow, overlying forestepping-stage unbioturbated sandy-channel and lobe deposits.

Proximal–distal trends in trace-fossil distribution with respect to both the paleoshoreline and the axis of the channel in a deep-marine system dominated by hyperpycnal flows have been evaluated in Miocene deposits of the same region (Carmona and Ponce, 2011). Hyperpycnal-channel and inner-levee deposits

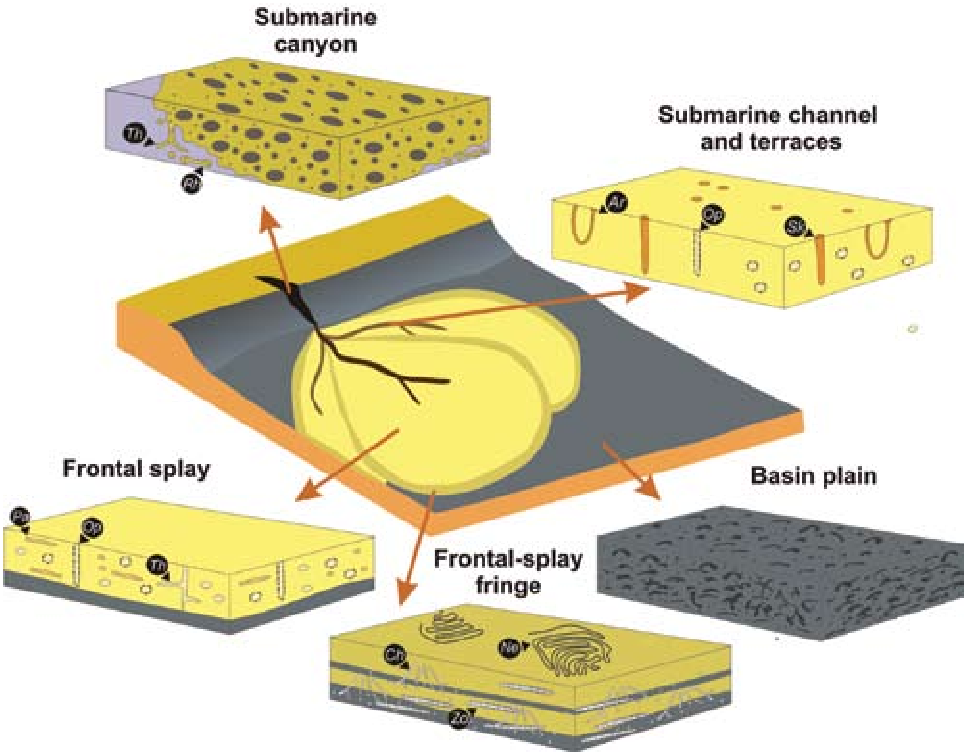

Figure 9.12 Schematic reconstruction of trace-fossil distribution in coarse-grained turbidite systems. As in the case of fine-grained turbidite systems, the base of the incised canyon is characterized by a firmground suite that may contain *Thalassinoides* (*Th*) and *Rhizocorallium* (*Rh*) illustrating the *Glossifungites* ichnofacies. Submarine-channel and terrace deposits typically contain *Ophiomorpha* (*Op*), *Skolithos* (*Sk*), and *Arenicolites* (*Ar*). Frontal-splay deposits may exhibit *Palaeophycus* (*Pa*), *Ophiomorpha* (*Op*), and *Thalassinoides* (*Th*). Frontal-splay fringe deposits may contain *Nereites* (*Ne*), *Zoophycos* (*Zo*), and *Chondrites* (*Ch*). Basin-plain deposits are characterized by an indistinct bioturbated mottling.

Box 9.4 Ichnology of a Cretaceous coarse-grained turbidite system of Antarctica

The Cretaceous Whisky Bay Formation of the James Ross Island, Antarctica, represents part of the infill of a back-arc basin. Deposition occurs in a submarine braided-channel complex comprising a wide variety of subenvironments, including main and secondary braided channels, adjacent marginal terraces and sandy plains, and muddy and sandy interchannel areas. The main braided channel deposits are unburrowed, but two main ichnocoenoses have been recognized in the other subenvironments. The first ichnocoenose occurs in conglomerate and pebbly sandstone which accumulated in minor braided channels, marginal terraces, and sandy plains. It consists of *Arenicolites*, *Diplocraterion* (Fig. 9.13a), *Skolithos*, *Thalassinoides* (Fig. 9.13b), *Palaeophycus*, and *Planolites*. It is essentially dominated by dwelling trace fossils of suspension feeders, illustrating the *Skolithos* ichnofacies. The second ichnocoenose is present in sandstone and mudstone of the interchannel areas. It consists of *Zoophycos*, *Chondrites*, and *Cylindrichnus*. It is dominated by feeding traces of deposit feeders, representing the *Zoophycos* ichnofacies. The absence of graphoglyptids is attributed to a high frequency of sediment gravity flows that introduced abundant organic material, inhibiting the establishment of complex farming strategies. The Whisky Bay Formation provides a good example of the most relevant ichnological features of a coarse-grained turbidite system.

Reference: Buatois and López Angriman (1992b).

tend to contain dwelling trace fossils of suspension feeders, such as *Diplocraterion*. Outer-levee deposits tend to be dominated by opportunistic grazing and locomotion structures (e.g. *Protovirgularia*, *Gordia*, and *Scolicia*) and concentrically laminated burrows. In the middle positions of the system, at the base of the depositional slope, bivalve escape structures occur in sandstone bodies. High sedimentation rates and fluctuating salinity, together with energy fluctuations and high food supply, may have been the most important limiting factors. The importance of salinity fluctuations is also supported by the presence of synaeresis cracks in levee deposits (Carmona and Ponce, 2011; Ponce and Carmona, 2011). A higher intensity of bioturbation was recorded in distal hyperpycnal-lobe deposits, but ichnodiversity is low to moderate. The distal assemblage is dominated by deposit-feeder structures, such as *Scolicia* and *Nereites*. Salinity fluctuations were apparently less intense than in the more proximal positions (Carmona and Ponce, 2011). Graphoglyptids are virtually absent in these hyperpycnal-flow deposits.

Also in Tierra del Fuego, Olivero *et al.* (2010) analyzed the ichnology of an Eocene channel-levee complex containing both hyperpycnal-flow and turbidity-current deposits. Channel-fill to proximal-levee thick-bedded sandstone is dominated by *Ophiomorpha rudis*. Proximal to distal-levee thinner-bedded

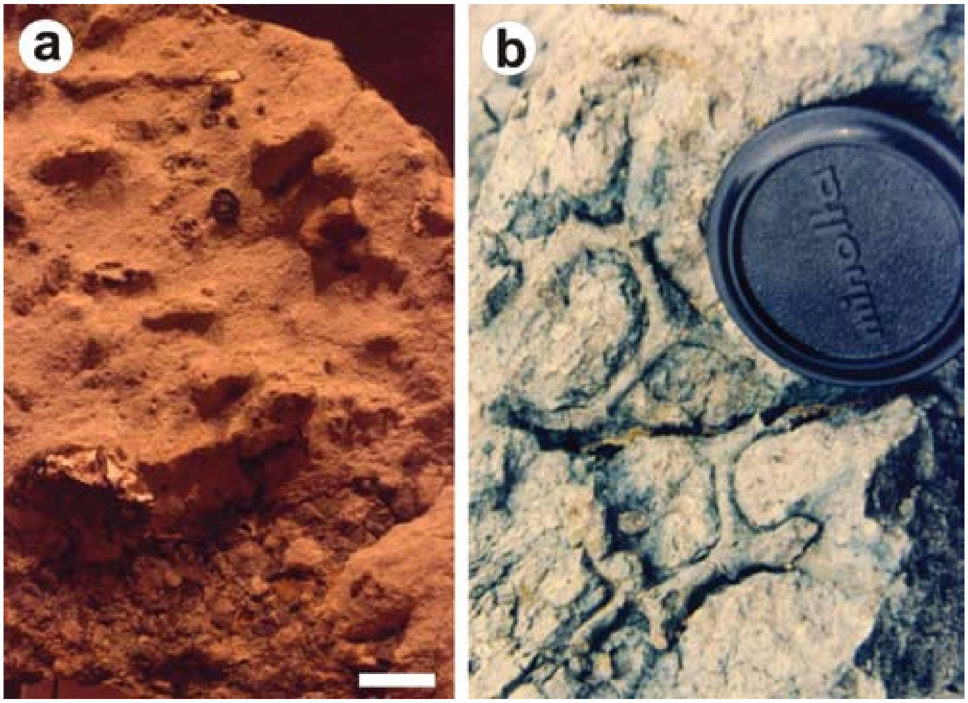

Figure 9.13 Trace fossils from coarse-grained turbidite system deposits in the Lower Cretaceous Whisky Bay formation of James Ross Island, Antarctica. (a) *Diplocraterion* isp. penetrating into an abandoned-channel pebble conglomerate from a mudstone layer mantling the coarse-grained deposit. Scale bar is 1 cm. (b) *Thalassinoides suevicus* in marginal-terrace pebbly sandstone. Lens cover is 5.5 cm. See Buatois and López Angriman (1992b).

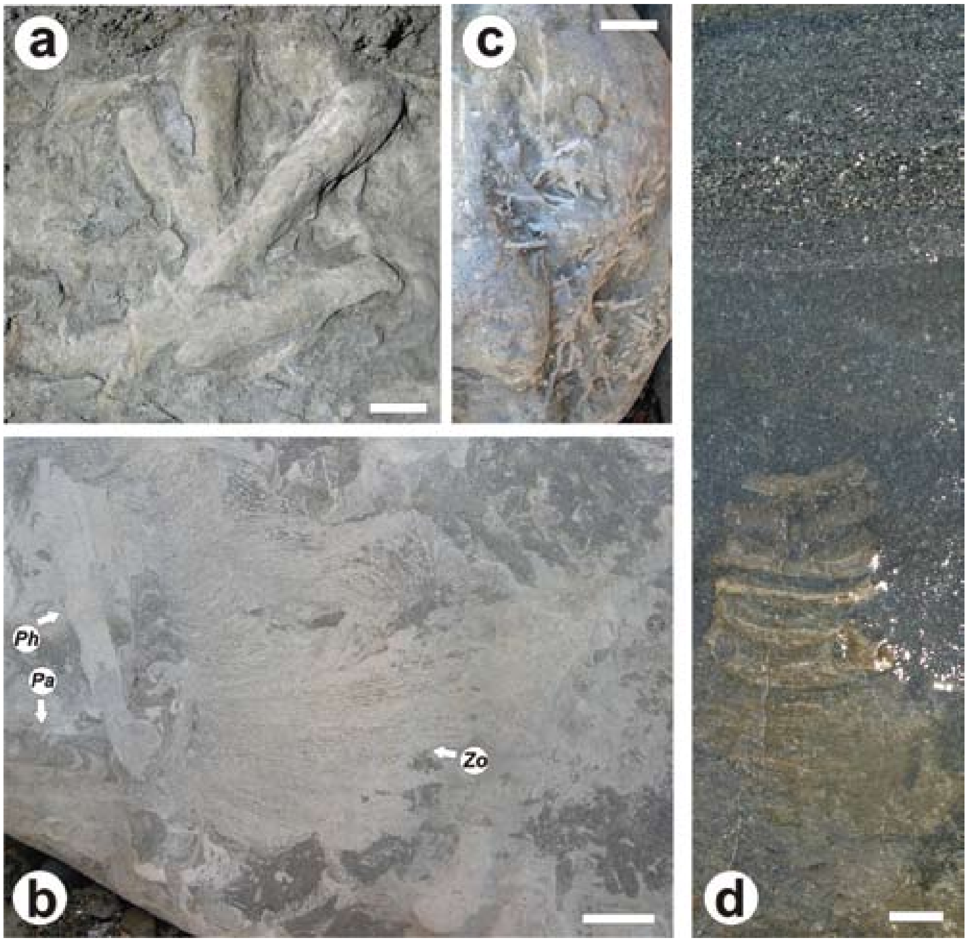

Figure 9.14 Trace fossils from deep-marine hyperpycnal deposits in the Upper Eocene to Lower Oligocene Punta Gruesa Beds, Tierra del Fuego, southern Patagonia, Argentina. (a) *Phymatoderma granulata*. (b) *Phymatoderma granulata* (*Ph*), *Zoophycos* isp. with pelletoidal infill (*Zo*), and *Paradictyodora antarctica* (*Pa*). (c) *Chondrites* isp. (d) *Tasselia* isp. Note overlying erosive surface. All bars are 1 cm. See Ponce *et al*. (2007).

Box 9.5 Biogenic structures in modern deep-sea floors off New Caledonia, southwestern Pacific

Bottom photographs taken in modern deep-sea floors off New Caledonia from water depths of 800 to more than 3000 m documented the presence of a wide variety and complexity of biogenic structures. Most biogenic structures occur over a rather large depth range. Simple holes and mounds are ubiquitous, being abundant along the whole bathymetric range analyzed. However, two main associations were recognized. The deep-slope association is dominated by composite craters having actinarian and enteropneust traces, and horseshoe-shaped traces of an unknown maker. The basin-plain association is dominated by incipient *Asteriacites* and linear grooves. In addition, although other traces show wider bathymetric ranges, they tend to be more abundant at certain water depth ranges. For example incipient *Lorenzinia* is common at 2100–2300 m deep and *Scolicia* at 1600–2200 m. Incipient *Paleodictyon* is apparently present only at water depths below 1700 m and incipient *Urohelminthoida* seems to occur between 1700–2150 m. Overall, holothurians and echinoderms are the most important tracemakers. This study reinforces the idea that deep-tier bioturbation and erosion are detrimental to the preservation of graphoglyptids, underscoring the role of slightly erosive turbidity currents in the preservation of agrichnial structures.

Reference: Gaillard (1991).

turbidites and hyperpycnites contain various ichnotaxa, such as *Nereites*, *Phycosiphon*, *Tasselia*, *Diplocraterion*, and several graphoglyptids, including *Cosmorhaphe*, *Desmograpton*, *Glockerichnus*, *Paleodictyon*, and *Helicolithus*, among other ichnogenera. Some of these deposits display a high content of plant debris. The presence of graphoglyptids in organic-rich deposits that accumulated in an overall high-energy setting is apparently rather unusual, but, in fact, underscores the role of taphonomic controls and times of oligotrophy in graphoglyptid distribution (see Section 9.2.1).

9.4 BASIN PLAINS

The basin plain corresponds to flat and deep areas of the sea bottom (Stow *et al.*, 1996). Here, we specifically address those areas of the basin plain that are removed from turbidity-current or bottom-current supply, and that are dominated by hemipelagic and pelagic sedimentation. Evaluating the role of the fossilization barrier is essential in characterizing the ichnology of basin-plain environments. Complex grazing trails and graphoglyptids have been observed and photographed on modern basin plains during exploration of the deep sea (Ewing and Davis, 1967; Heezen and Hollister, 1971; Hollister *et al.*, 1975; Kitchell *et al.*, 1978a, b; Ekdale and Berger, 1978; Kitchell, 1979; Ekdale, 1980; Gaillard, 1991) (Box 9.5). However, the fossilization potential of these structures is virtually zero because the absence of sand emplaced by turbidity currents precludes their preservation along lithological interfaces. Continuous vertical accretion of the deep-sea floor is conducive to intense reworking of the sediment and destruction of shallow-tier representatives of the *Nereites* ichnofacies by deep-infaunal bioturbators (Ekdale and Berger, 1978; Wetzel, 1983, 1984). Pelagic deposits contain deep-tier dwelling and feeding structures, such as *Zoophycos*, *Thalassinoides*, *Teichichnus*, and *Planolites*. In the distal-most settings, the extremely low sedimentation rates allows complete homogenization of the substrate, and only a mottled texture attributed to *Planolites* is observed (Bromley, 1990, 1996).

10 Ichnology of continental environments

> The prevalent notion that trace fossils are comparatively rare in nonmarine facies is more a reflection of insufficient reconnaissance than of a true dearth of specimens.
>
> Robert Frey and George Pemberton
> "The *Psilonichnus* ichnocoenose, and its relationship to adjacent marine and nonmarine ichnocoenoses along the Georgia coast" (1987)

> Vemos las cosas según como las interpretamos. Lo llamamos previsión: saber de antemano, estar prevenidos. Usted en el campo sigue el rastro de un ternero, ve huellas en la tierra seca, sabe que el animal está cansado porque las marcas son livianas y se orienta porque los pájaros bajan a picotear en el rastro. No puede buscar huellas al voleo, el rastreador debe primero saber lo que persigue: hombre, perro, puma. Y después ver. Lo mismo yo. Hay que tener una base y luego hay que inferir y deducir. Entonces – concluyó – uno ve lo que sabe y no puede ver si no sabe…Descubrir es ver de otro modo lo que nadie ha percibido. Ése es el asunto.. – Es raro, pensó Renzi, pero tiene razón –.
>
> Ricardo Piglia
> Blanco Nocturno (2010)

Historically invertebrate ichnology has focused on marine ichnofaunas. However, studies have gradually moved into freshwater and, more recently, terrestrial environments. As a result, continental ichnology has experienced a remarkable development during the last 15 years, and our perspective on this topic has changed dramatically. Earlier case studies started to show that continental invertebrate ichnofaunas were more varied and abundant than originally envisaged (e.g. Bromley and Asgaard, 1979; Bown, 1982; Pollard *et al.*, 1982; Frey *et al.*, 1984b; Walker, 1985; Ekdale and Picard, 1985; D'Alessandro *et al.*, 1987; Gierlowski-Kordesch, 1991; Pickerill, 1992). It rapidly became clear that continental environments were as numerous and diverse as marine settings, and that such variability was indeed reflected in the ichnological record (Frey and Pemberton, 1987). Subsequent work focused on the expansion of the continental dataset, but more significantly in the proposal of archetypal ichnofacies in addition to the *Scoyenia* ichnofacies (Smith *et al.*, 1993; Buatois and Mángano, 1995b, 2004a, 2007; Bromley, 1996; Genise *et al.*, 2000, 2004b, 2010a). Also, the potential and limitations of the ichnofabric approach to the study of freshwater and terrestrial ichnofaunas have been addressed in a number of studies (e.g. Buatois and Mángano, 1998, 2007; Genise *et al.*, 2004a; Buatois *et al.*, 2007a). More recently, proposals have been made to define continental ichnofacies based on vertebrate trace fossils (Lockley *et al.*, 1994; Hunt and Lucas, 2006a, 2007). There has also been a recent revival of continental neoichnology (e.g. Scott *et al.*, 2007b; Smith and Hasiotis, 2008; Hembree, 2009; Genise *et al.*, 2009). The fields of invertebrate and vertebrate ichnology have evolved independently, and research involves two separate scientific communities to a great extent (Lockley, 2007). This is certainly not a significant problem in marine ichnology, but it has had a negative impact on continental ichnology. The need to integrate vertebrate and invertebrate datasets has long been recognized (e.g. Buatois and Mángano, 1995b, 1996), but little progress has been attained. However, a series of recent papers seem to show that a better articulation between invertebrate and vertebrate ichnology is possible (e.g. Melchor *et al.*, 2006; Lockley, 2007; Hunt and Lucas, 2007; Minter *et al.*, 2007b; Scott *et al.*, 2007b; Krapovickas *et al.*, 2009). Integration of both datasets will be essential to produce more robust depositional models of continental environments.

While most, if not all, of the ichnotaxa from the various terrestrial ichnofacies are produced by insects, and are restricted to continental environments (e.g. *Coprinisphaera*, *Termitichnus*, *Celliforma*, *Eatonichnus*), this is not entirely the case with the ichnogenera commonly recorded from the freshwater *Mermia* and *Scoyenia* ichnofacies (Buatois and Mángano, 2007). With the exception of *Scoyenia*, *Mermia*, *Camborygma*, and some arthropod trackways (e.g. *Stiaria*, *Stiallia*, *Hexapodichnus*), the other components of these ichnofacies are facies-crossing ichnotaxa known from both the continental and marine realm (e.g. *Taenidium*, *Palaeophycus*, *Planolites*, *Gordia*, *Helminthopsis*, *Helminthoidichnites*, *Cochlichnus*, *Treptichnus*). Meniscate trace fossils informally referred to by some authors as "adhesive meniscate burrows" (e.g. Hasiotis, 2004) were subsequently included in a new ichnogenus, *Naktodemasis*, based on meniscate packaging (Smith *et al.*, 2008a). Although this ichnotaxon seems to be exclusive of continental environments, it clearly falls within the diagnosis of *Taenidium* and it is better regarded as a separate ichnospecies, *T. bowni*, rather than a new ichnogenus (Krapovickas *et al.*, 2009). The eolian *Octopodichnus*–*Entradichnus* ichnofacies contain some forms exclusive to continental environments (e.g. *Octopodichnus, Paleohelcura*) associated with other facies-crossing ichnotaxa (e.g. *Palaeophycus*, *Planolites*) (Hunt and Lucas, 2007; Ekdale *et al.*, 2007). *Entradichnus* has also only been recorded in continental environments, but its distinction from *Taenidium* is still unclear (Keighley and Pickerill, 1994; Ekdale *et al.*, 2007).

While subaerial ichnofaunas are overwhelmingly dominated by terrestrial insects and, to a lesser extent, arachnids, freshwater ichnofaunas mostly reveal behavioral convergence of many different groups, including aquatic insects, but also crustaceans and mollusks, to name a few. As a result, freshwater ichnofaunas more closely resemble marine associations than their terrestrial counterparts. Undoubtedly, it is the whole assemblage that should be analyzed in order to distinguish between marine and freshwater ichnofaunas.

Conversely, there is a large number of ichnotaxa that are exclusive of marine settings. These include all the typical elements of the *Nereites* and *Zoophycos* ichnofacies, and most of the ichnotaxa of the *Cruziana* ichnofacies (e.g. *Asterosoma*, *Rosselia*, *Dactyloidites*, *Arthrophycus*, *Asteriacites*, *Curvolithus*, *Psammichnites*, *Teichichnus*). These trace fossils reflect specific behavioral patterns that are exclusive of marine organisms. Some typical marine ichnogenera (e.g. *Paleodictyon*, *Nereites*, *Scolicia*, *Chondrites*) have occasionally been mentioned in continental deposits (e.g. Smith *et al*., 1982; Archer and Maples, 1984; Pickerill, 1990; Hu *et al*., 1998; Hasiotis, 2002, 2004; Kim *et al*., 2005), but they have been misidentified. Re-examination invariably indicates that the forms reported in freshwater settings are much simpler than the marine ichnotaxa, and that they do not display the diagnostic features of those ichnogenera (Buatois and Mángano, 2007). In this chapter, we review the ichnology of different continental environments, from alluvial fans and fluvial systems to lakes and deserts, as well as paleosols.

10.1 ALLUVIAL FANS

Alluvial fans occur where a channel emerges from a mountainous upland to an adjoining valley depositing coarse-grained material at a marked break in the slope, forming a sedimentary body with a form that resembles the segment of a cone radiating downslope (Bull, 1977; Blair and McPherson, 1994; Harvey *et al*., 2005). Alluvial fans typically contain coarse-grained sediment, particularly at their mouths, but display a decrease in grain size towards their edges. Ichnological studies of alluvial-fan successions are virtually non-existent. Rapid rates of sedimentation, high energy and coarse-grained sediments, commonly of gravel-size, make alluvial-fan environments extremely harsh for animal life. As a result, colonization by invertebrate and vertebrate burrowers is unusual, and typically associated with pauses in sedimentation. In addition, the preservation potential of almost any structure produced in alluvial-fan sediments is low because of the strongly erosive nature of depositional events, particularly in the most proximal zones of the systems.

The few studies documenting alluvial-fan ichnofaunas in the fossil record deal with biogenic structures produced in the most distal zones of these systems, particularly in the areas that are transitional with braided-river systems, where both invertebrate (e.g. MacNaughton and Pickerill, 1995; Neef, 2004a; Krapovickas *et al*., 2008), and vertebrate (e.g. García-Ramos and Valenzuela, 1979; Carvalho *et al*., 1995; Carvalho, 1996) trace fossils are preserved in sandstone beds. Invertebrate trace fossils in distal alluvial-fan deposits are remarkably simple, and consist of a few facies-crossing ichnotaxa, such as *Palaeophycus* and *Skolithos*, which commonly reflect progressive consolidation of the substrate due to desiccation (Krapovickas *et al*., 2008). Slightly more diverse ichnofaunas, dominated by arthropod locomotion trace fossils, such as *Cruziana*, *Diplichnites*, *Diplopodichnus*, *Merostomichnites*, and *Palmichnium*, occur in ponded areas where fine-grained sedimentation may be locally important (Neef, 2004a). Vertebrate ichnofaunas recorded in alluvial-fan deposits are scarce, and mostly consist of poorly preserved dinosaur trackways in Mesozoic strata (e.g. García-Ramos and Valenzuela, 1979; Carvalho *et al*., 1995; Carvalho, 1996). In addition, the ichnogenus *Ichniotherium*, probably produced by reptilomorph amphibians (Voight *et al*., 2007), is common in Permian distal alluvial-fan deposits (Hunt and Lucas, 2006a).

In terms of archetypal ichnofacies, alluvial-fan systems display a transition from the *Skolithos* to the *Scoyenia* ichnofacies. The *Skolithos* ichnofacies tends to occur at the top of channel sandstones, reflecting rapid colonization during short breaks in sedimentation. The *Scoyenia* ichnofacies is extremely impoverished, commonly containing one or two ichnotaxa, but a diversity increase may occur in associated ponds. With respect to vertebrates, the so-called *Ichniotherium* sub-ichnocoenosis of the *Batrachichnus* ichnofacies typically occurs in alluvial-fan settings from the Devonian to the Middle Triassic (Hunt and Lucas, 2006a, 2007).

10.2 RIVERS

Fluvial systems include a wide range of lithofacies and architectural elements, representing a complex mosaic of subenvironments, such as channels of variable sinuosity, containing different types of bars, and overbank settings displaying levees, crevasse splays, and floodplains (Miall, 1996). Modern rivers are inhabited by a wide variety of vertebrates (e.g. fish, amphibians, and reptiles) and invertebrates, including aquatic to semiaquatic insects (e.g. ephemeropterans, trichopterans, dipterans, coleopterans, hemipterans); several groups of crustaceans, such as ostracodes, branchiopods (e.g. conchostracans), and malacostracans (e.g. amphipods, decapods), as well as oligochaete annelids, nematodes, nematomorphs, and mollusks (Chamberlain, 1975; Ratcliffe and Fagerstrom, 1980; Hasiotis and Bown, 1992; Giller and Malmqvist, 1998; Cushing and Allan, 2001). Many of these organisms are able to produce a relatively wide variety of biogenic structures. However, trace fossils are not abundant in fluvial successions. In a classic study, Ratcliffe and Fagerstrom (1980) demonstrated that modern floodplains are very rich in invertebrate structures, although relatively few of the forms documented by these authors have been reported from the fossil record. This fact suggests that the problem of scarcity of trace fossils in continental successions is, at least in part, one of preservation potential.

Although it is sometimes assumed that fluvial ichnofaunas have not been frequently reported from the fossil record,

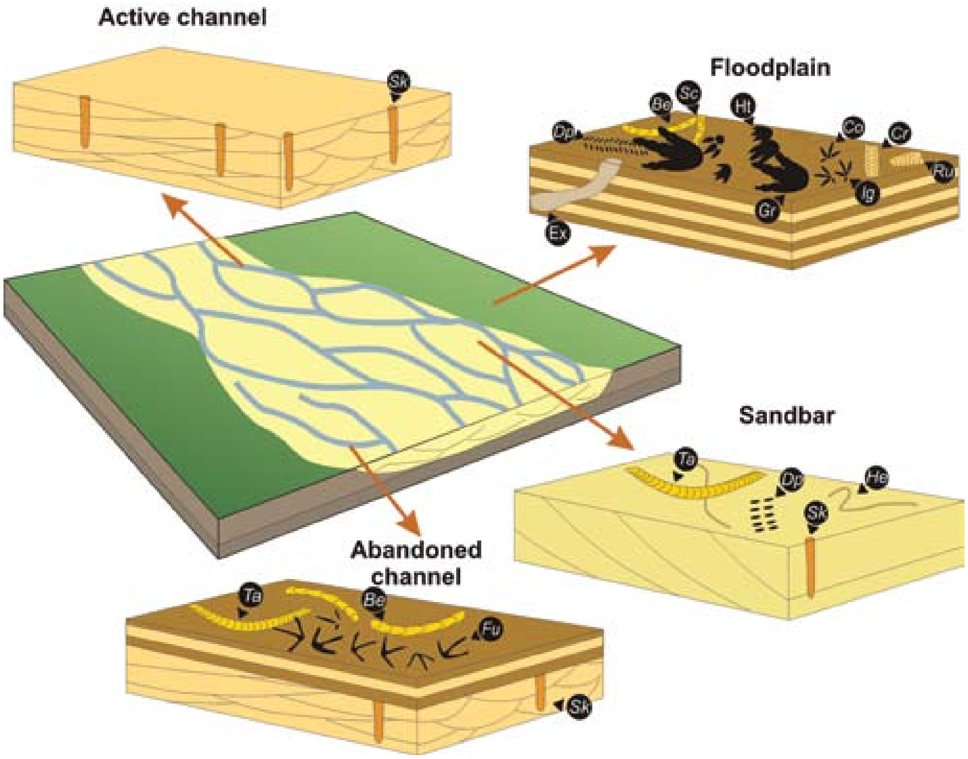

Figure 10.1 Schematic reconstruction of trace-fossil distribution in braided river systems. Composition of vertebrate ichnofaunas is highly variable according to geological age. Active-channel deposits contain *Skolithos* (*Sk*). Abandoned-channel deposits may display the meniscate trace fossils *Taenidium* (*Ta*) and *Beaconites* (*Be*), as well as vertebrate trace fossils such as the bird trackway *Fuscinapeda* (*Fu*). Sandbar deposits may exhibit *Skolithos* (*Sk*), *Taenidium* (*Ta*), *Helminthopsis* (*He*), and *Diplichnites* (*Dp*). Floodplain deposits typically host *Scoyenia* (*Sc*), *Beaconites* (*Be*), *Cochlichnus* (*Co*), *Diplichnites* (*Dp*), *Cruziana* (*Cr*), and *Rusophycus* (*Ru*). Vertebrate trackways and excavations (Ex) are typically abundant and diverse in floodplain deposits. Examples include the theropod ichnogenera *Grallator* (*Gr*) and the shorebird ichnotaxa *Ignotornis* (*Ig*) in the Mesozoic. Various types of heteropod trackways (Ht) are common in the Cenozoic. Vertebrate and invertebrate trace fossils not to scale.

recent compilations have shown that several examples have been documented (Buatois and Mángano, 2007; Minter *et al.*, 2007b). Abundance and diversity of trace fossils in fluvial successions are highly variable from one subenvironment to the other. Thick successions of fluvial deposits are commonly unburrowed or display trace fossils only in discrete beds. Suites are typically monospecific or contain few ichnotaxa. In contrast, the density of biogenic structures may be quite high locally. Ichnofossil distribution in fluvial environments largely depends on the variability in stream discharge and the amount of time between depositional episodes (D'Alessandro *et al.*, 1987). Recent work indicates that ichnofossils have been recorded more commonly in meandering rather than in braided deposits (Buatois and Mángano, 2007). Only a few examples are known in anastomosing and ephemeral deposits, but this sparse record probably reflects lack of studies rather than true absence. Overall, more favorable preservational conditions occur in abandoned channels and associated floodplain settings, instead of active channels (Figs. 10.1 and 10.2). The *Scoyenia* ichnofacies occurs in deposits of any fluvial style, but the *Mermia* ichnofacies is more common in floodplain deposits of meandering systems (Buatois and Mángano, 2007). The *Skolithos* ichnofacies seems to be more common in channel sandstones of braided rivers (e.g. Fitzgerald and Barrett, 1986; Zawiskie *et al.*, 1983), but has also been recorded in ephemeral systems (Sarkar and Chaudhuri, 1992). Buatois and Mángano (2004a) distinguished between ichnofaunas from channel and overbank deposits, a classification framework that is followed here. The ichnology of the subaerial portion of the alluvial plain characterized by soil development is discussed elsewhere (see Section 10.5).

10.2.1 CHANNELS

Fluvial channels display high to relatively high energy, rapid fluctuations in flow velocity and rates of sedimentation and erosion, unstable banks and floors, and coarser-grain sizes than associated overbank environments. Running water or lotic habitats represent stressful and unstable environments for colonization by a benthic fauna. Accordingly, production and/or preservation of biogenic structures are commonly inhibited. Buatois and Mángano (2004a, 2007) noted that some fluvial-channel ichnofaunas seem to have been emplaced when the channel is still active, while others reflect colonization after channel diversion ("abandonment"), or during periods of low discharge characterized by non-deposition ("inactive").

Active-channel deposits tend to have a meager trace-fossil record (Fig. 10.3). These deposits are characterized by low-diversity suites (typically monospecific), and dominance of simple vertical burrows and escape traces (e.g. Bradshaw, 1981; Zawiskie *et al.*, 1983; Fitzgerald and Barrett, 1986; Woolfe, 1990; Sarkar and Chaudhuri, 1992). The degree of bioturbation is commonly low, although dense assemblages of moderately deep to deep *Skolithos* are known (e.g. Fitzgerald and Barrett, 1986) (Figs. 10.1 and 10.2). Affinities with the *Skolithos* ichnofacies are consistent with the associated environmental scenario, although the identity of the tracemakers and the functional significance of these vertical structures are poorly understood (Buatois and

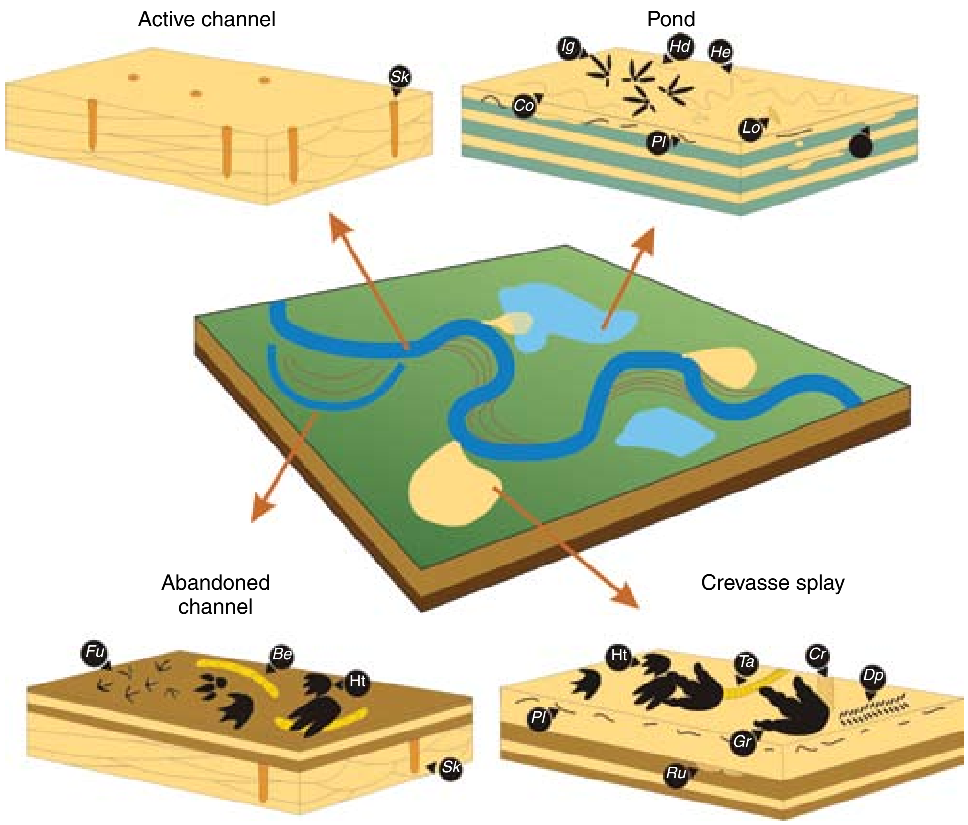

Figure 10.2 Schematic reconstruction of trace-fossil distribution in meandering river systems. Composition of vertebrate ichnofaunas is highly variable according to geological age. As in the case of braided rivers, active-channel deposits contain *Skolithos* (*Sk*). Abandoned-channel deposits commonly display *Beaconites* (*Be*), as well as vertebrate trace fossils such as the bird trackway *Fuscinapeda* (*Fu*) and a variety of heteropod trackways (Ht). Crevasse-splay deposits may exhibit *Taenidium* (*Ta*), *Planolites* (*Pl*), *Cruziana* (*Cr*), *Rusophycus* (*Ru*), and *Diplichnites* (*Dp*). Examples of vertebrate trace fossils in crevasse-splay deposits include the theropod ichnogenera *Grallator* (*Gr*) in Mesozoic strata and various types of heteropod trackways (Ht) in Cenozoic strata. Pond deposits may host *Cochlichnus* (*Co*), *Planolites* (*Pl*), *Lockeia* (*Lo*), *Palaeophycus* (*Pa*), *Helminthopsis* (*He*), and *Helminthoidichnites* (*Hd*). Vertebrate trackways are abundant and diverse in pond deposits including, for example, the shorebird ichnogenus *Ignotornis* (*Ig*) in Mesozoic strata. Vertebrate and invertebrate trace fossils not to scale.

Mángano, 1998, 2004a, 2007; White and Miller, 2008). In other situations, colonization of omission surfaces may have occurred (Netto *et al.*, 2007). More rarely, vertebrate swim tracks, such as those produced by turtles (e.g. *Chelonipus*), are preserved in channel deposits (Lockley and Foster, 2006).

Abandoned- or inactive-channel deposits contain meniscate trace fossils (*Beaconites* and *Taenidium*), vertical to inclined burrows (*Skolithos* and *Cylindricum*), arthropod trackways (*Diplichnites*), and simple horizontal burrows (*Palaeophycus*) (e.g. Allen and Williams, 1981; Graham and Pollard, 1982; Bamford *et al.*, 1986; Sarkar and Chaudhuri 1992; Miller and Collinson, 1994; Miller, 2000; Keighley and Pickerill, 2003; Morrissey and Braddy, 2004; Lucas *et al.*, 2006a; Buatois *et al.*, 2007a) (Fig. 10.3). Vertebrate (e.g. dinosaur and bird) tracks may occur locally in profuse densities at the top of abandoned-channel deposits (e.g. Lockley *et al.*, 2003, Falcon-Lang *et al.*, 2007) (Figs. 10.1 and 10.2). Ichnodiversity is typically low, but relatively high when compared to active channels. The degree of bioturbation is highly variable. Low to moderate intensities of bioturbation are common, but high bioturbation indexes are locally measured, more commonly at the top of channel-sandstone units (e.g. Buatois *et al.*, 2007a). Meniscate trace fossils reflect the activity of vagile organisms that excavate while searching for food, most likely revealing a combination of bypassing and ingestion. Vertical to inclined burrows may serve several functions, such as permanent domiciles, semi-permanent shelters, nests, and passageways (Stanley and Fagerstrom, 1974). Insect nesting trace fossils may also be present, reflecting the ability of these organisms to colonize various types of substrates (Genise *et al.*, 2000) (see Section 10.5). Tracemakers that colonize abandoned or inactive channels are regarded as behavioral generalists that record an opportunistic strategy (Miller and Collinson, 1994). Ichnofaunas of abandoned- or inactive-channel deposits are similar in taxonomic composition to those from overbank deposits, because abandoned channels lead to the formation of ponded areas (Fig. 10.3). In terms of archetypal ichnofacies, abandoned- or inactive-channel ichnofaunas belong to the *Scoyenia* ichnofacies. If channels are reactivated, the *Skolithos* ichnofacies is re-established.

10.2.2 OVERBANK

Overbank settings encompass a wide variety of subenvironments, including floodplains, crevasse splays and levees, which comprise complex riparian ecosystems (Naiman *et al.*, 2005). These represent quite unique habitats in which a link is established between aquatic and terrestrial realms (Malanson, 1993). Ecological studies suggest that the lateral water flow that characterizes these settings near river channels ranks among one of the most important controlling factors in riparian ecology (e.g. Brown *et al.*, 1979; Malanson, 1993). Overbank flooding helps to define terrestrial–aquatic gradients, from perennially inundated wetlands through frequently inundated wetlands to occasionally and infrequently flooded areas.

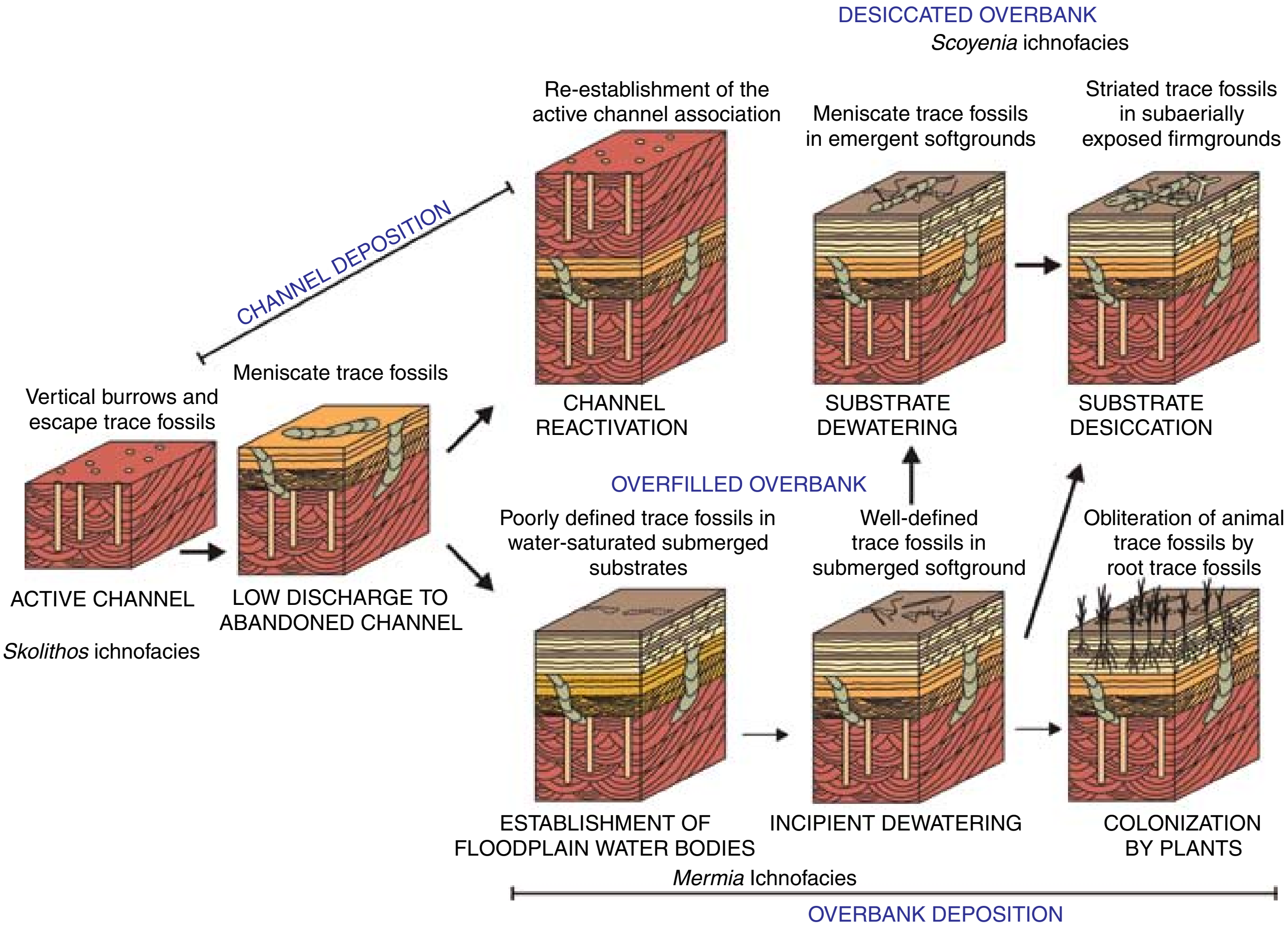

Figure 10.3 Taphonomic pathways of fluvial ichnofaunas showing transitions between different channel and overbank trace-fossil suites. Substrate consolidation plays a major role in controlling ichnofacies occurrence (after Buatois and Mángano 2004a, 2007).

Box 10.1 Ichnology of Miocene fluvial deposits of the Sub-Andean region of Bolivia

Cenozoic deposits with thicknesses up to 7.5 km accumulated in the Chaco foreland basin of the Sub-Andean region of Bolivia, mostly recording sedimentation in fluvial environments. Bioturbation is widespread in anastomosed fluvial deposits of the Upper Miocene Tariquia Formation. This unit is dominated by *Taenidium barretti*, illustrating the *Scoyenia* ichnofacies. Ichnodiversity is remarkably low and trace-fossil composition does not change significantly throughout the succession, but ichnofabric analysis reveals some degree of variability as a result of various taphonomic pathways (Fig. 10.4). Abandoned main-channel deposits are sparsely bioturbated, while medium- to very fine-grained crevasse sandstone and overbank mudstone display intense and deep bioturbation (bi = 6), showing complete destruction of the primary sedimentary fabric. Main-channel and crevasse-splay sandstones both display upward increases in degree of bioturbation. The tops of the channel and crevasse-splay sandstones represent colonization surfaces, therefore, allowing direct measurements of maximum burrowing depth. Some specimens of *Taenidium barretti* may extend up to 2.2 m into the crevasse sand sheets. Depth and intensity of bioturbation of the main-channel and crevasse sandstones are a reflection of the colonization window (i.e. time between depositional events). Main-channel and crevasse sandstones that underlie thick packages of bioturbated overbank mudstones are intensely bioturbated, as a result of prolonged periods of low-energy sediment fall-out between crevassing events. Conversely, the lowest degree of bioturbation occurs in amalgamated channel sandstone units underlying thin intervals of overbank mudstones, reflecting high-frequency depositional episodes.

Reference: Buatois *et al.* (2007a).

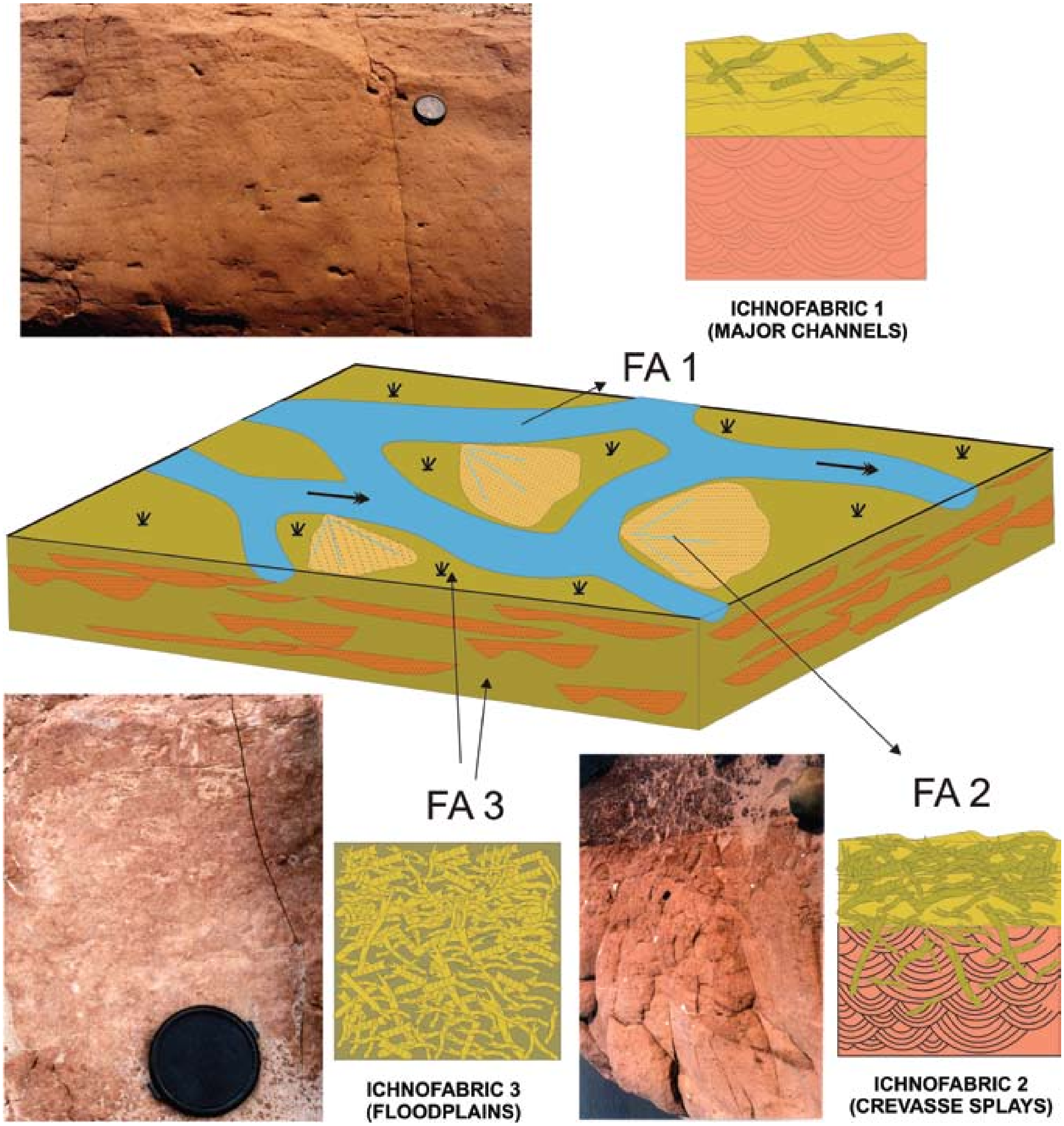

Figure 10.4 Ichnofabric distribution in anastomosed fluvial systems from the Upper Miocene Tariquia Formation of Bolivia (modified from Buatois *et al*., 2007a).

Trace fossils are more abundant and varied in overbank deposits, particularly where standing bodies of water are established (e.g. Fordyce, 1980; D'Alessandro *et al*., 1987; Buatois *et al*., 1997a; Buatois and Mángano, 2002, 2004a; Keighley and Pickerill, 2003). Although in some cases no increase in ichnodiversity is observed, overbank deposits are more intensely bioturbated than their associated channel deposits (Buatois *et al*., 2007a) (Box 10.1). In many cases, the only trace fossils present in a fluvial succession are found in fine-grained overbank intervals interbedded with unbioturbated, coarser-grained stacked-channel deposits, recording taphonomic and colonization windows (Buatois *et al*., 1997a).

Maples and Archer (1989) outlined a number of conditions that enhance the preservation potential of biogenic structures in overbank settings, namely: (1) deposition of fine-grained heterogeneous sediment; (2) little or no reworking; and (3) enough time between depositional events to allow colonization, but not so much time that plant colonization obliterates

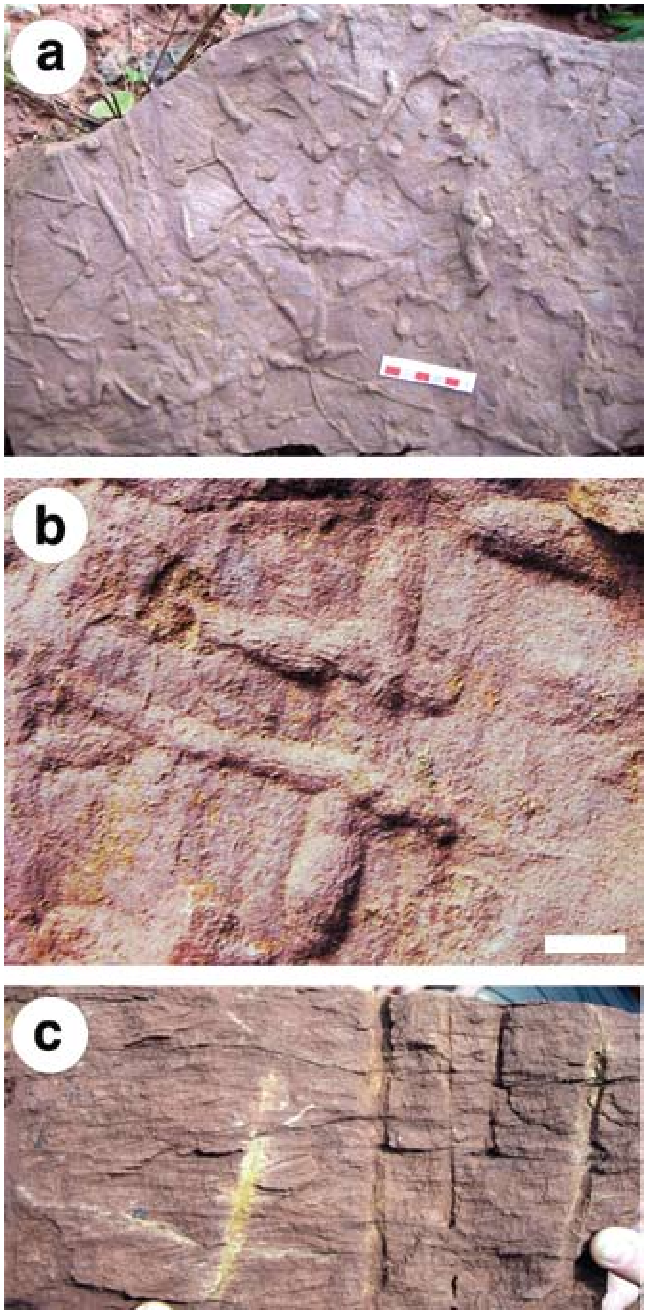

Figure 10.5 Invertebrate and plant trace fossils in crevasse-splay deposits of braided rivers Lower Triassic, Baranów Formation, Baranów Quarry, Holy Cross Mountains, Poland. (a) General view of bedding plane with *Scoyenia gracilis*, displaying both horizontal and vertical components and desiccation cracks. Scale bar is 5 cm. (b) Close-up of *Scoyenia gracilis* with well-developed scratch marks. Scale bar is 1 cm. (c) Vertical root trace fossil. See Bujok *et al*. (2008).

animal traces. These conditions allow the preservation of delicate biogenic structures in protected ponded areas. Buatois and Mángano (2004a, 2007) noted that some overbank ichnofaunas are emplaced in water bodies that have been progressively desiccated (desiccated overbank), while others record subaqueous colonization in water bodies filled by the vertical accretion of overbank deposits without experiencing desiccation (overfilled overbank). These two ichnofaunas commonly display contrasting characteristics and are discussed separately.

Desiccated-overbank deposits contain arthropod trackways (*Diplichnites*, *Protichnites*, *Hexapodichnus*, *Trachomatichnus*), meniscate trace fossils (*Scoyenia*, *Taenidium*, *Beaconites*) (Fig. 10.5a–b), ornamented burrows (*Spongeliomorpha*, *Tambia*), and bilobate trace fossils with scratch marks (*Cruziana*, *Rusophycus*) (e.g. Bromley and Asgaard, 1979; Bracken and Picard, 1984; Squires and Advocate, 1984; D'Alessandro *et al*., 1987; Debriette and Gand, 1990; Sarkar and Chaudhuri, 1992; Smith, 1993; Kim and Paik, 1997; Gand *et al*., 1997; Eberth *et al*., 2000; Savrda *et al*., 2000; Gierliński *et al*., 2004; Buatois *et al*., 2007a; Lucas *et al*., 2010a). Vertical burrows (*Skolithos*, *Cylindricum*) and insect and arachnid nesting structures may also be present (Figs. 10.1 and 10.2).

Desiccated-overbank deposits commonly contain superbly preserved vertebrate trackways. Late Paleozoic floodplain deposits may host abundant basal amniote trackways including a variety of sauropsids and synapsids (e.g. Smith, 1993). Mesozoic examples are dominated by dinosaur (e.g. theropods, ornithopods, sauropods), amphibian (e.g. temnospondyls), reptile (e.g. archosaurs, lepidosaurs), and bird trackways (e.g. Calafat *et al*., 1986; Lockley and Conrad, 1989; Fuglewicz *et al*., 1990; Currie *et al*., 2003; Gierliński *et al*., 2004; Gangloff *et al*., 2004; Foster and Lockley, 2006; Hunt and Lucas, 2006b; Zhang *et al*., 2006; Smith *et al*., 2009) (Figs. 10.1 and 10.2). Formation of densely crowded tracked surfaces by chiroteriids and rhychosauroids resulted from a complex taphonomic history in which flooding may have led to the concentration of reptiles on narrow land patches (Fuglewicz *et al*., 1990) (Fig. 10.6a–d). During low water levels, footprints were impressed on muddy substrate and subsequently cast by sand during the next flooding event. Wide varieties of bird (e.g. ciconiiforms, charadiiforms), reptile (e.g. turtles), and mammal (e.g. artiodactyls, perissodactyls, proboscideans, liptoterns, megatheriids, carnivores,) trackways occur in Cenozoic river-margin deposits (Aramayo and Manera de Bianco, 1996; Mustoe, 2002; Krapovickas *et al*., 2009).

In addition to trackways, floodplain deposits may contain tetrapod burrows (Fig. 10.1). Permian–Triassic examples were produced by therapsids, such as *Diictodon* (Fig. 10.7a–c), *Trirachodon*, and *Thrinaxodon* (Smith, 1987; Groenewald *et al*., 2001; Damiani *et al*., 2003; Sidor *et al*., 2008), while similar structures in the Neogene are attributed to medium to small mammals, such as the primitive beaver *Paleocastor* (Martin and Bennet, 1977). Helicoidal burrows have been commonly placed in the ichnogenus *Daimonelix*, while other tetrapod burrows have not received formal ichnotaxonomic assignation. Amphibian burrows attributed to the lysorophid *Brachydectes elongates* were produced in Permian pond deposits, probably during episodic droughts (Hembree *et al*., 2004). Also, the finding of dinosaur skeletal remains in the expanded distal chamber of a burrow suggests that some dinosaurs were able to excavate (Varricchio *et al*., 2007).

Invertebrate ichnodiversity is low to rarely moderate in desiccated-overbank deposits, but vertebrate trace fossils may be relatively diverse. The degree of bioturbation is highly variable, ranging from low to intense; some floodplain deposits may

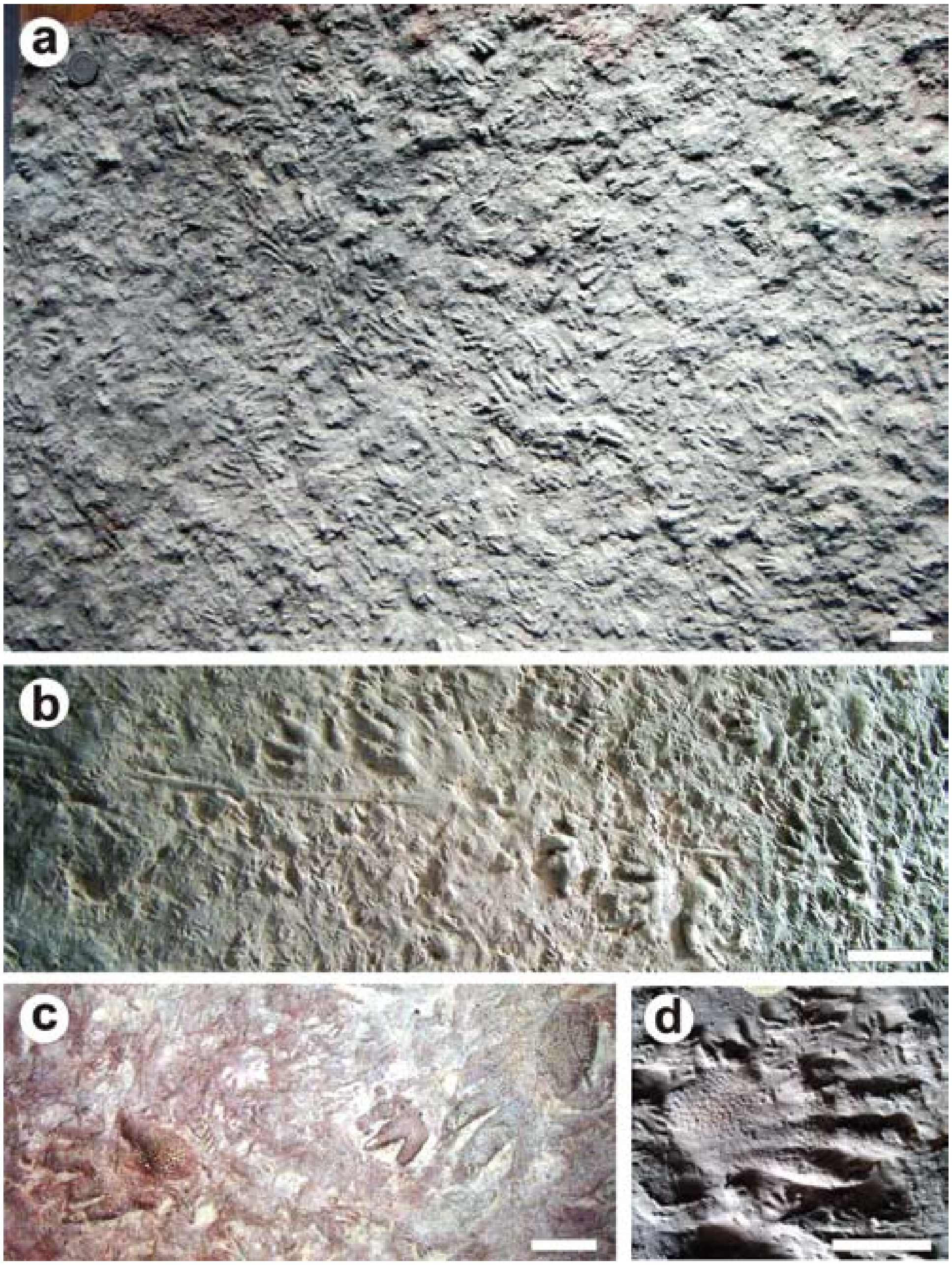

Figure 10.6 Vertebrate trackways in crevasse-splay deposits of braided rivers. Lower Triassic, Wióry Formation, Wióry site, Holy Cross Mountains. (a) General view of a surface having a large density of labyrinthodontid trackways, including both *Isochirotherium* and *Rhynsochauroides*. Scale bar is 10 cm. (b) Surface with *Isochirotherium* (large tracks) and *Rhynsochauroides* (small tracks). Tail marks are associated with *Isochirotherium* tracks. Scale bar is 10 cm. (c) Close-up of *Isochirotherium* trackway. Scale bar is 5 cm. (d) Skin textures preserved in *Isochirotherium* track. Scale bar is 5 cm. See Fuglewicz *et al.* (1990).

be totally bioturbated (e.g. Buatois *et al.*, 2007a). Ichnofossils are associated with physical structures that indicate periodic subaerial exposure (e.g. desiccation cracks, raindrop imprints) (Fig. 10.5a). Root trace fossils occur locally (Fig. 10.5c). Depths of bioturbation up to 2.2 m have been measured for *Taenidium barretti* from colonization surfaces at the top of crevasse-splay sandstones (Buatois *et al.*, 2007a). Deep bioturbation may reveal avoidance of stressful conditions caused by extreme desiccation. Morrissey and Braddy (2004) suggested that the *Beaconites* producer, most likely a myriapod, burrowed to the water table in search of moisture during the dry season. In terms of archetypal ichnofacies, desiccated-overbank suites illustrate the *Scoyenia* ichnofacies (Buatois and Mángano, 2002, 2004a, 2007). With respect to vertebrate ichnofacies, these fluvial deposits contain examples of the so-called *Amphisauropus* sub-ichnocoenosis of the *Batrachichnus* ichnofacies from the Devonian to the Middle Triassic (Hunt and Lucas, 2006a, 2007).

Trace-fossil morphology and burrow-wall characteristics suggest common emplacement in firm substrates (Fig. 10.3). For example, striated walls in *Scoyenia* (Fig. 10.5a–b) and *Spongeliomorpha*, sharp scratch marks in *Tambia*, *Cruziana*, and *Rusophycus* and well-defined appendage imprints in arthropod trackways all indicate a cohesive substrate that has experienced desiccation due to subaerial exposure. This “desiccation suite” commonly cross-cuts an earlier, “pre-desiccation suite”,

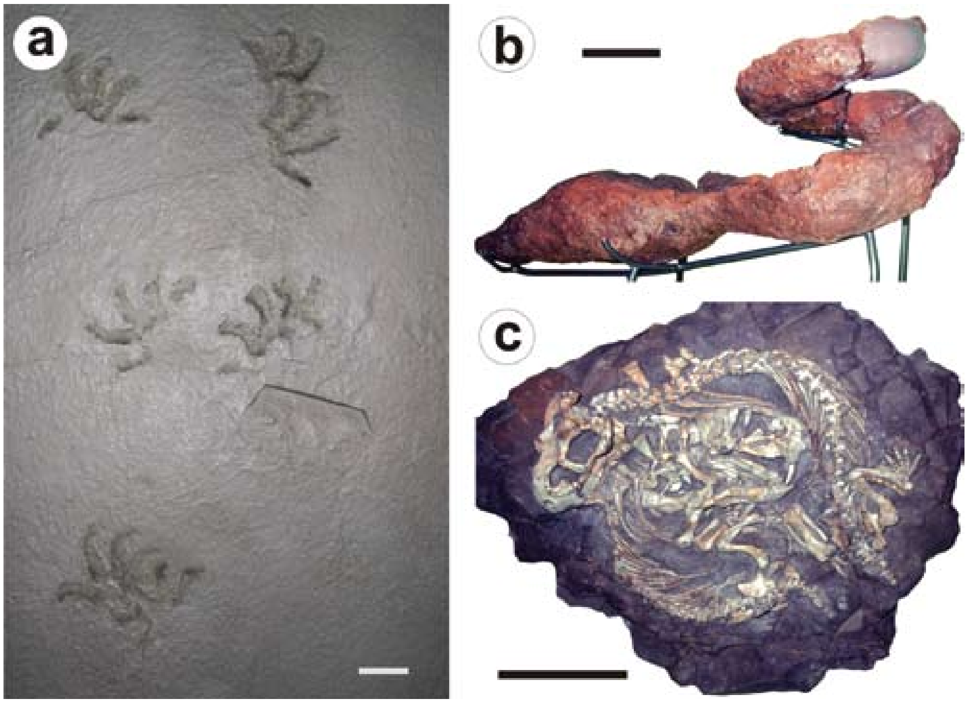

Figure 10.7 The small dicynodont *Diictodon* and its ichnological record. Upper Permian, Teekloof Formation, Beaufort Group, southwestern Karoo basin, South Africa. (a) Trackways formed along the shoreline of a floodplain water body. Scale bar is 3 cm. (b) Sand-filled helicoidal burrows containing at the base a terminal chamber. Scale bar is 10 cm. (c) Articulated skeletons found within the terminal chambers and spirals of burrows. Scale bar is 10 cm. Specimens exhibited at the South African Museum, in Cape Town. See Smith (1987).

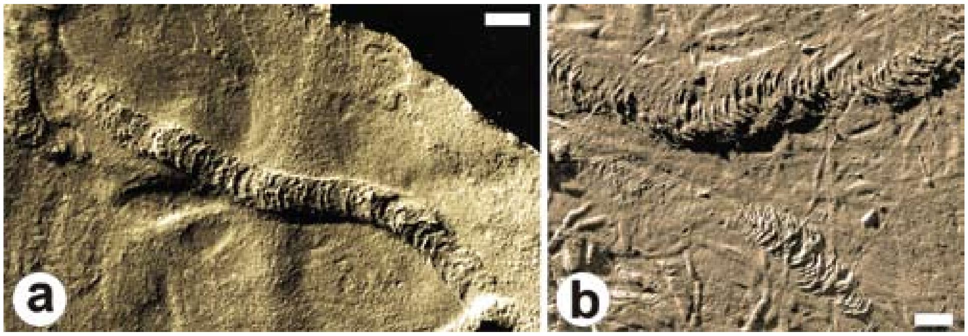

Figure 10.8 Two suites of the *Scoyenia* ichnofacies in desiccated overbank deposits. Lower Permian, La Colina Formation, Los Colorados de Patquia, western Argentina. (a) *Beaconites barretti*. Meniscate backfilled trace fossils lacking striated walls, suggesting emplacement in a softground. (b) Firmground meniscate striated trace fossils cross-cutting the softground suite. See Buatois *et al.* (1996a). Scale bars are 1 cm.

which is typically characterized by meniscate, backfilled structures without ornamentation (e.g. *Taenidium* and *Beaconites*) developed in soft substrates (Buatois *et al.*, 1996a; Savrda *et al.*, 2000; Buatois and Mángano, 2002, 2004a) (Fig. 10.8a–b). Both suites belong to the *Scoyenia* ichnofacies, which in desiccated-overbank deposits may form palimpsest surfaces or composite ichnofabrics that record taphonomic pathways showing progressive desiccation of floodplain sediments (see Section 6.2). Desiccated-overbank ichnofaunas are common in distal zones (comprising occasionally to infrequently flooded areas) and/or arid to semiarid settings.

Overfilled-overbank deposits contain simple grazing trails (*Helminthopsis*, *Helminthoidichnites*), locomotion trails (*Cochlichnus*), horizontal dwelling burrows (*Palaeophycus*), dwelling burrow systems (*Ctenopholeus*), and bivalve resting (*Lockeia*) and equilibrium (*Calceoformites*) traces (e.g. Turner, 1978; Fordyce, 1980; Miller, 1986; Pollard and Hardy, 1991; Gluszek, 1995; Buatois *et al.*, 1997a; Buatois and Mángano, 2002; Keighley and Pickerill, 2003; Uchman *et al.*, 2004b; Pieńkowski and Niedźwiedzki, 2009) (Fig. 10.9a–c). Fish trails (*Undichna*) may be preserved in floodplain bodies of water (e.g. Morrissey *et al.*, 2004; Wisshak *et al.*, 2004). Arthropod and tetrapod trackways, meniscate trace fossils, and bilobate structures with scratch marks are typically absent; where present, they are subordinate elements (Buatois and Mángano, 2002, 2004a, 2007). Ichnodiversity is low to rarely moderate. With rare exceptions (e.g. *Ctenopholeus*), most of the ichnofossils are oriented parallel to the bedding plane, and reflect very shallow-tier emplacement, so intensity of bioturbation is low. Physical structures indicating subaerial exposure are absent, reflecting overbank vertical accretion rather than desiccation of the water body. Root trace fossils may be common in associated waterlogged paleosols (Fig. 10.10a–d).

In these settings, morphological details of the trace fossils are commonly very poorly preserved, suggesting that they were formed in a water-saturated substrate (e.g. Buatois *et al.*, 1997a). Overall features of these overbank ichnofaunas indicate subaqueous emplacement (Fig. 10.3). Poorly preserved trace

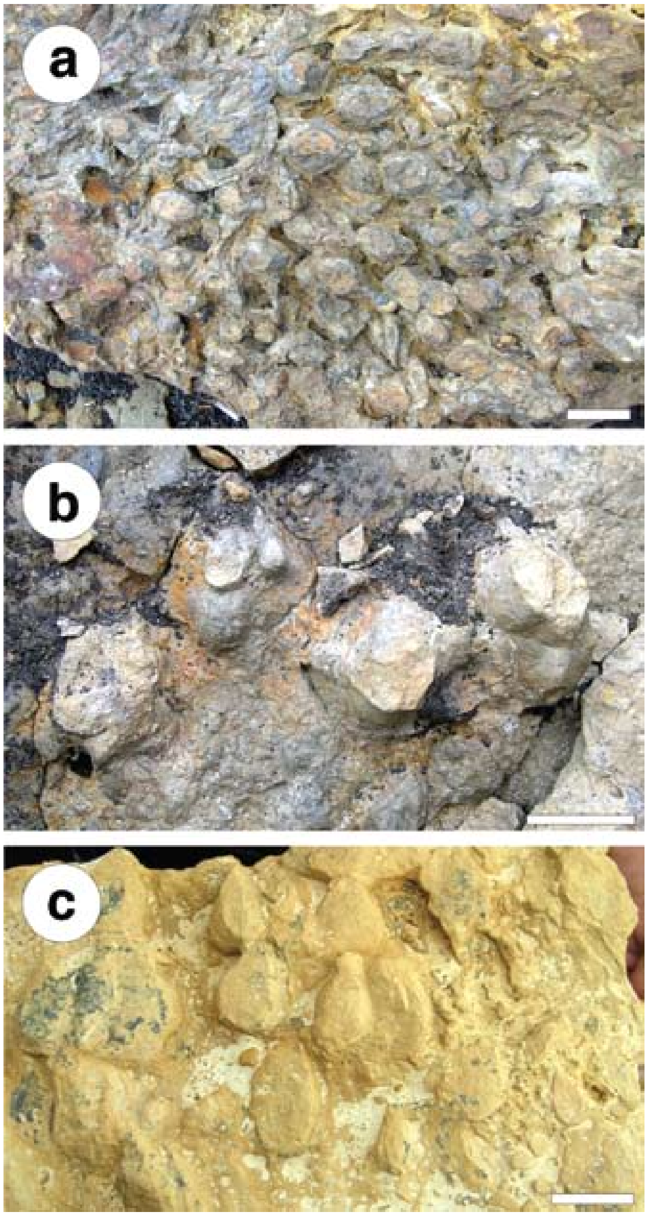

Figure 10.9 Bivalve trace fossils in crevasse-splay deposits of meandering rivers. Lower Jurassic, Zagaje Formation, Sołtyków Nature Reserve, Holy Cross Mountains, Poland. (a) General view of a sandstone base showing high density of the equilibrium structure *Calceoformites uchmani*. Scale bar is 3 cm. (b) Close-up of *Calceoformites uchmani*. Note spreite in the specimen on the right revealing re-positioning of the bivalve in response to sedimentation. Scale bar is 2 cm. (c) The dwelling/resting trace *Lockeia*. Scale bar is 2 cm. See Pieńkowski and Niedźwiedzki (2009).

fossils may be cross-cut by better-defined softground ichnofossils reflecting improving taphonomic conditions due to increasing consolidation of the substrate. In any case, burrow walls are unornamented indicating that substrates never attained firmground stage. These ichnofaunas lack most of the diagnostic features of the *Scoyenia* ichnofacies and are regarded as examples of the impoverished *Mermia* ichnofacies (Buatois and Mángano, 2002, 2004a, 2007). The lower ichnodiversity of the *Mermia* ichnofacies in these overbank deposits in comparison with their equivalents from lakes results from the temporary nature of floodplain bodies of water and their less-stable conditions. Overfilled-overbank ichnofaunas are dominant in the proximal-overbank settings of meandering systems (comprising perennially to frequently inundated wetlands) and/or temperate and humid settings (Buatois and Mángano, 2004a, 2007).

10.3 LAKES

Modern lake systems contain a wide variety of benthic organisms that produce biogenic structures, including annelids (e.g. oligochaetes, leeches), aquatic to semiaquatic insects (e.g. dipterans and coleopterans), crustaceans (e.g. ostracodes), and mollusks (e.g. bivalves, gastropods) (Cohen, 2003; White and Miller, 2008). Some vertebrates, mostly fish, amphibians, and aquatic reptiles, although nektonic, may occasionally interact with the substrate to produce biogenic structures. Biogenic structures emplaced in lacustrine sediments have the highest preservation potential of all continental ichnofossils. Unsurprisingly, recent compilations demonstrated that there is a large volume of literature documenting examples of lacustrine ichnofaunas (Buatois and Mángano, 2007; Minter *et al.*, 2007b). Cohen (2003) listed a number of abiotic and biotic factors that control animal distribution in lakes. Abiotic factors include energy, light, oxygen, temperature, salinity, substrate, and nutrients, while biotic factors, such as competition, grazing, predation, and symbiosis, have complex feedback loops and are difficult to interpret (see also Miller and White, 2007).

Species diversity results from a complex interplay of these different factors. Overall, larger lakes contain more species than small ones, because they are more persistent, encompass a great variety of habitats, and are located closer to centers of species origin (Cohen, 2003). As a general trend, ichnofaunas from large lakes are typically more diverse than those in small lakes or fluvial ponds (Buatois and Mángano, 2007). The density and diversity of benthic fauna usually reach a maximum in the oxygenated sublittoral zone (the concentration zone of Mackie, 2001). In most lakes, this zone occurs between 2 and 4 m deep, but it may as deep as 18 m in large oligotrophic lakes (Mackie, 2001, Martin *et al.*, 2005; White and Miller, 2008).

Taphonomic factors also play a major role in controlling ichnodiversity. The highest preservation potential of biogenic structures is in low-energy areas of lacustrine systems. Low-energy conditions may occur both in the deep zones of the lake, and in shoreline areas in systems that are weakly affected by wave action. In deep-lake environments, alternation of very fine-grained sandstone and mudstone deposited from underflow or turbidity currents promotes the preservation of delicate and tiny surface trails, as well as very shallow trace fossils (Buatois and Mángano, 1995c, 1998, 2007). In low-energy shoreline areas, preservation of biogenic structures commonly results from rapid influx of sand via non-erosive sheet floods (e.g. Zhang *et al.*, 1998; Minter *et al.*, 2007b). Although monospecific trace-fossil assemblages are present, moderately

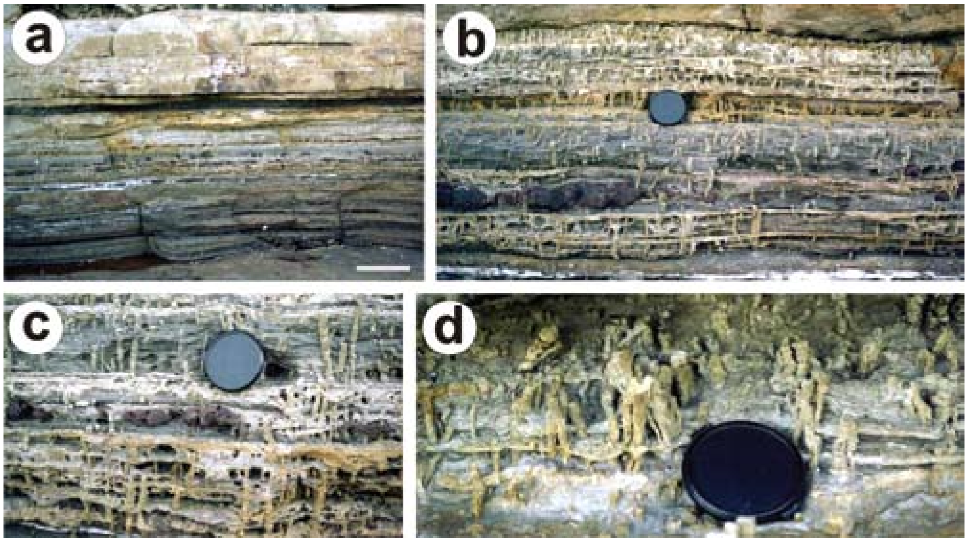

Figure 10.10 Plant trace fossils from floodplain deposits of meandering rivers. Lower Triassic, Newport Formation, St. Michaels Cave, Sydney Basin, eastern Australia. (a) General view of intensely rooted deposits. Scale bar is 50 cm. (b) Close-up showing dominance of vertically oriented root trace fossils. Lens cap is 5.5 cm. (c) and (d) Close-ups of root trace fossils. Note that the root trace fossils are filled with sand, and no carbonaceous wall or infill is present.

Box 10.2 Ichnology Oligocene fluvial-fan-lacustrine systems of Spain

The Ebro Basin of northeastern Spain was characterized by fluvial fans attached to the basin margins grading towards the central-basin areas into hydrologically closed, shallow lakes. Trace fossils have been recorded in one such complex, the Oligocene Solsona–Sanaüja Fluvial Fan and the Noguera Lacustrine System. Bioturbation is absent in the lacustrine deposits, most likely as a reflection of the closed hydrology that may have caused hypersalinity. Fluvial-fan terminal-lobe deposits formed in low wetland areas around the lake contain a moderately diverse trace-fossil assemblage dominated by *Taenidium barretti*, *Cochlichnus anguineus*, and the bird footprint *Gruipeda* isp. Medial fluvial-fan areas include crevasse-splay deposits, which contain most of the ichnotaxa present in the terminal lobes, except for the bird tracks, plus abundant vertical burrows (*Taenidium barretti* and ornamented burrows). The presence of deep-tier traces in this assemblage was linked to the greater relief and lower mean groundwater position in the more proximal fan with respect to the lowland areas. Fluvial-channel deposits only contain irregularly clustered tunnels of unknown affinity formed after abandonment of the channel. The distribution of trace-fossil assemblages was essentially controlled by the position and fluctuations of water tables, which also promoted their composite nature.

Reference: Gibert and Sáez (2009).

diverse ichnofaunas are common in lacustrine deposits. Gore (1989) subdivided lacustrine systems into hydrologically open and hydrologically closed. Buatois and Mángano (1998, 2004a, 2007) used this scheme to frame ichnological observations and, accordingly, this classification is used here.

10.3.1 CLOSED LAKES

Hydrologically closed lakes lack an outlet, and are characterized by high salinity and rapidly fluctuating shorelines (Gore, 1989). As a result, they represent extremely stressful ecosystems, in which faunal diversity is very low. Trace fossils formed under permanent subaqueous conditions are scarce or absent because of hypersalinity (e.g. Price and McCann, 1990; Uchman and Álvaro, 2000). However, moderately diverse ichnofaunas, both produced by invertebrates and vertebrates, may occur at the lake margins, in subaerially exposed littoral to mud-flat environments, recording the activity of terrestrial rather than aquatic faunas (e.g. Zhang *et al.*, 1998; Minter *et al.*, 2007b; Scott *et al.*, 2007b; Gibert and Sáez, 2009) (Boxes 10.2 and 10.3) (Fig. 10.11). Species diversity increase is most evident at the lake margins due to rising lake levels and the associated decrease in salinity, while low diversity levels are maintained in the central part of the lake due to continuous accumulation of saline groundwater and chemical stratification (Cohen, 2003). Ichnofaunas from hydrologically closed lakes mostly consist of plant traces, arthropod trackways (*Diplichnites*, *Umfolozia*, *Lithographus*), meniscate trace fossils (*Scoyenia*, *Taenidium*), bilobate structures (*Cruziana*, *Rusophycus*), chironomid, coleopteran, and annelid dwelling and feeding traces (*Fuersichnus*, *Labyrintichnus*, and *Beaconites filiformis*), and vertebrate traces (e.g. Bromley and Asgaard, 1979; Gierlowski-Kordesch, 1991; Dam and Stemmerik, 1994; Kozur and Lemone, 1995; Rodríguez-Aranda and Calvo, 1998; Zhang *et al.*, 1998; Clemmensen *et al.*, 1998; Uchman and Álvaro, 2000; Schlirf *et al.*, 2001; Lucas *et al.*, 2002; Melchor and Sarjeant, 2004; Minter *et al.*, 2007b; Scott *et al.*, 2007b). Chironomid (Diptera) larvae are highly tolerant to saline conditions, and are regarded

Box 10.3 Ichnology of Triassic lacustrine deposits of western Argentina

Spectacular outcrops of the continental Middle to Upper Triassic Agua de la Peña Group of the Ischigualasto-Villa Unión Basin of western Argentina allow careful analysis of trace-fossil distribution in lacustrine systems of contrasting characteristics. The Chañares Formation and the lowermost part of the Ischichuca Formation represent deposition in mildly saline to playa lakes surrounded by mud flats. Tetrapod trackways occur in the mud-flat deposits associated with desiccation cracks. These units reveal the stressful conditions dominant in hydrologically closed lakes, but also highlight the potential for trackway preservation in lake-margin areas. However, most of the Ischichuca Formation represents deposition in alternating shallow- and deep-water conditions, fluctuating from hydrologically open to closed. Lacustrine strata are stacked forming coarsening-upward parasequences due to progradation of wave- and river-dominated deltas. Offshore underflow current deposits do not contain trace fossils, most likely as a result of anoxia in the hypolimnion of freshwater stratified lakes. However, delta-plain channel deposits contain escape trace fossils, recording rapid sedimentation in a river-dominated context. Lower delta-plain deposits contain a moderately diverse ichnofauna dominated by locomotion trace fossils (*Cruziana problematica*, *Undichna britannica*, *Diplichnites* isp., *Stiaria* isp.), together with resting (*Rusophycus stromnessi*) and grazing (*Cochlichnus anguineus*) trace fossils. The pattern of trace-fossil distribution in the succession reveals the complex interplay of environmental conditions in lakes of fluctuating hydrological regime. The most diverse ichnological record is present in the Los Rastros Formation, with coarsening-upward parasequences as a result of deltaic progradation. Upper delta-plain deposits contain simple dwelling trace fossils (e.g. *Palaeophycus striatus*) and vertebrate trackways (*Rhynchosauroides* isp.). Upper delta-front to lower delta-plain deposits are sparsely bioturbated and only contain a few ichnotaxa, mostly dwelling trace fossils (*Palaeophycus tubularis*, *Skolithos* isp.), although *Cochlichnus anguineus* is also present. Some of the delta-front trace fossils are present in hummocky cross-stratified sandstone, recording opportunistic colonization after storm events. Middle delta-front deposits display a relatively diverse association dominated by simple grazing trails (*Helminthoidichnites tenuis*, *Helminthopsis abeli*, *Gordia indianaensis*, *Archaeonassa fossulata*, *Cochlichnus anguineus*), with fish locomotion trails (*Undichna britannica*) and simple facies-crossing dwelling trace fossils (*Palaeophycus tubularis*) as subordinate components. Underflow-current deposits of the distal delta front are the most diverse in terms of trace-fossil content, hosting a wide variety of simple grazing trails (*Helminthoidichnites tenuis*, *Gordia marina*, *Archaeonassa fossulata*, *Cochlichnus anguineus*) and fish trails (*Undichna britannica*, *U. bina*, *U.* cf. *insolentia*), with subordinate occurrences of feeding structures (*Treptichnus pollardi*), horizontal dwelling structures (*Palaeophycus tubularis*), and arthropod trails (*Cruziana problematica*, *Diplopodichnus biformis*, *Didymaulichnus lyelli*), resting traces (*Rusophycus stromnessi*, *Avolatichnium* isp.) and trackways (*Bifurculapes* isp., *Diplichnites* isp., *Protichnites* isp.). The Los Rastros Formation is an excellent example illustrating patterns of trace-fossil distribution in a hydrologically open lake affected by wave-dominated deltaic progradation.

References: Melchor (2001, 2004, 2007); Melchor *et al.* (2003).

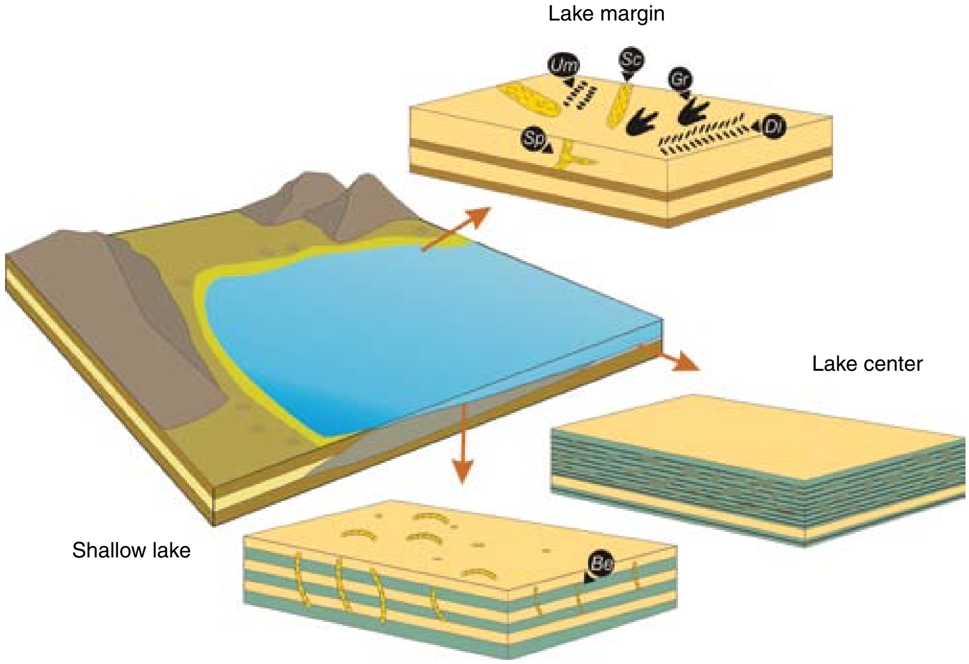

Figure 10.11 Schematic reconstruction of trace-fossil distribution in hydrologically closed lakes. Composition of vertebrate ichnofaunas is highly variable according to geological age. This type of lake typically displays sparse bioturbation, particularly in subaqueous settings. Lake-margin deposits tend to have the highest diversity and density of trace fossils, including the striated burrow system *Spongeliomorpha* (*Sp*), the striated meniscate trace fossil *Scoyenia* (*Sc*), arthropod trackways, such as *Umfolozia* (*Um*) and *Diplichnites* (*Di*), and a wide variety of vertebrate trackways, such as *Grallator* (*Gr*) in Mesozoic examples. The salinity-tolerant ichnotaxon *Beaconites filiformis* (*Be*) may be present in shallow-lake areas, while lake-center deposits are commonly unburrowed or may show local bioturbation in gypsum deposits. Desiccation cracks, and vertebrate and invertebrate trace fossils not to scale.

as the producer of *Beaconites filiformis* in saline lacustrine deposits (Uchman and Álvaro, 2000). However, large meniscate trace fossils filled with gypsum and micrite may occur in relatively high densities in some saline lake deposits (Rodríguez-Aranda and Calvo, 1998; Ortí *et al*., 2003).

Basal amniote trace fossils, particularly sauropsid trackways (*Erpetopus*, *Dromopus*, *Varanopus*, *Hyloidichnus*) and, to a lesser extent, "amphibian" trackways (*Amphisauropus*) may be particularly common in late Paleozoic ephemeral lake deposits (Haubold and Lucas, 2003; Melchor and Sarjeant, 2004; Minter *et al*., 2007b) (Fig. 10.11). Mesozoic vertebrate tracksites are typically dominated by dinosaur trackways, which have high preservation potential around ephemeral- and playa-lake environments (Lockley and Hunt, 1995). The theropod ichnogenera *Eubrontes*, *Anchisauripus*, *Grallator* are typical components (e.g. Lockley and Hunt, 1995; Getty, 2005). Cenozoic lake margins of closed lakes may contain abundant bird and mammal tracks (e.g. Scrivner and Bottjer, 1986; Cohen *et al*., 1991, 1993; Lockley and Hunt, 1995; Lockley and Meyer, 2000; Lucas *et al*., 2002).

Associated physical structures (e.g. desiccation cracks, raindrop imprints) indicate subaerial exposure. Under appropriate taphonomic conditions, omission surfaces totally covered by trackways may be preserved (Zhang *et al*., 1998) (Fig. 10.12a–b). Due to the progressive desiccation of the substrate, better-defined trackways emplaced in compacted sediment commonly cross-cut those with less-defined imprints that were formed in less-firm substrates (Uchman and Álvaro, 2000; Buatois and Mángano, 2004a, 2007; Scott *et al*., 2009).

The distribution and preservation of biogenic structures in saline lakes is controlled by a series of factors, some of which are related to the evolved fluid compositions resulting from evaporation (Cohen *et al*., 1991; Scott *et al*., 2010), and in many saline lakes, by the presence of thermal springs (Scott *et al*., 2007a, b). Relatively fresh areas of lake margins, such as springs and ephemeral streams, favor the concentration of many species of insects, mammals, birds, and reptiles that may contribute to the ichnological record. In addition, local development of microbial mats, associated with hypersaline conditions and/or hot springs, may favor burrowing by certain insects (e.g. staphylinid, heterocerid beetles). In turn, matgrounds help to stabilize the substrate or contribute to its early cementation, increasing the preservation potential of biogenic structures produced by both vertebrates and invertebrates (Scott *et al*., 2007b). Lake-margin trace-fossil assemblages of closed lakes are typical examples of the *Scoyenia* ichnofacies. No examples of the *Mermia* ichnofacies have been documented in closed-lake deposits. In terms of vertebrate ichnofacies, lake-margin trackway suites commonly belong to the *Grallator* ichnofacies from the Late Triassic to the Recent (Hunt and Lucas, 2007).

10.3.2 OPEN LAKES

Hydrologically open lakes have an outlet, and are characterized by low salinity and relatively stable shorelines (Gore, 1989). Accordingly, they represent less stressful ecosystems than closed lakes. Open lakes contain more varied ichnofaunas, and a distinction can be made between those established along the lake margin and those formed subaqueously further into the lake (Buatois and Mángano, 2004a, 2007) (Fig. 10.13; Box 10.3).

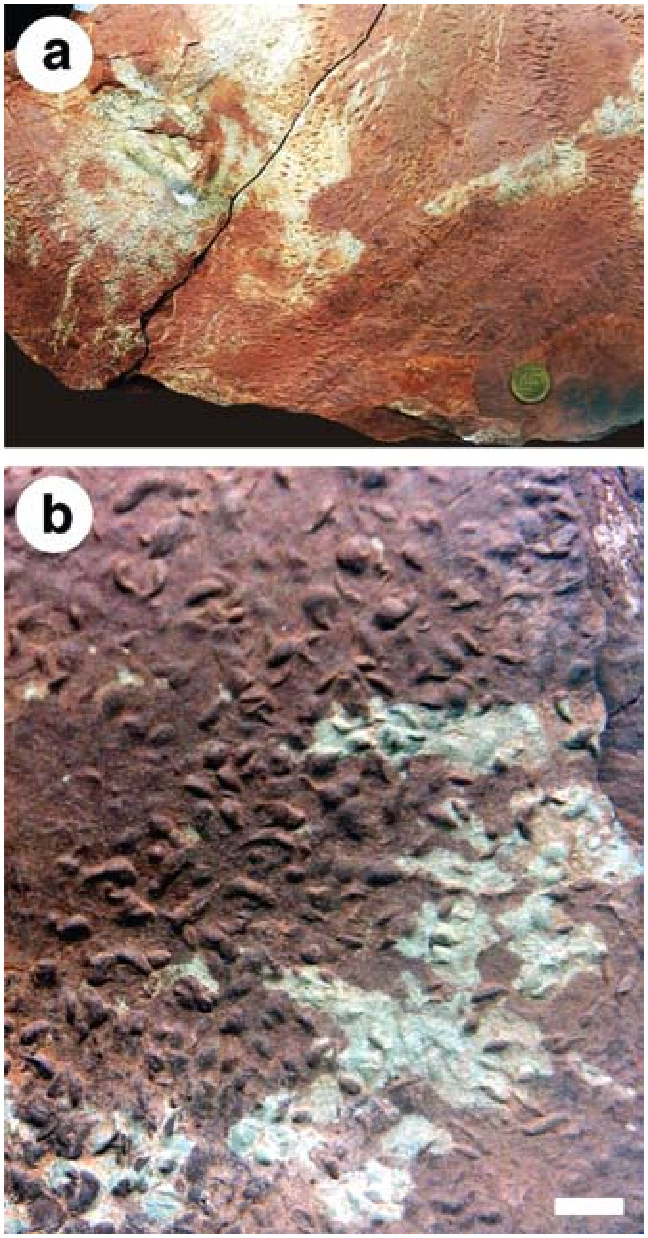

Figure 10.12 Trackway overlap in marginal deposits of playa lakes. Lower Permian, Patquía Formation, Bordo Atravesado, western Argentina. See Zhang *et al*. (1998). (a) General view of a sandstone top exhibiting high density of arthropod trackways. Coin is 1.6 cm. (b) Close-up of the tracked surface. Scale bar is 1 cm.

Lake-margin ichnofaunas of hydrologically open lakes can be in turn subdivided into two main environmental settings: those of protected, low-energy sites under weak wave action and those in comparatively higher-energy environments either due to wave action or influence of distributary channels. Low-energy

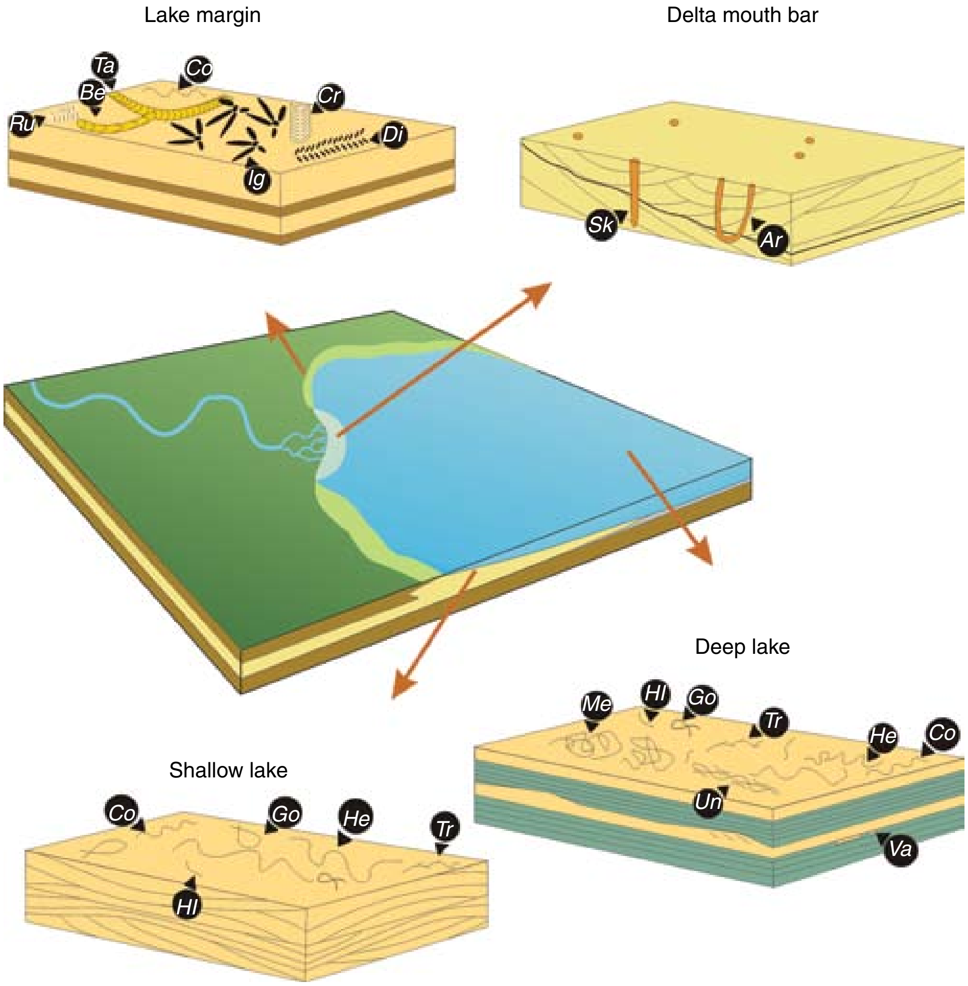

Figure 10.13 Schematic reconstruction of trace-fossil distribution in hydrologically open lakes. Composition of vertebrate ichnofaunas is highly variable according to geological age. This type of lake typically contains more diverse ichnofaunas. Protected lake-margin deposits are characterized by meniscate trace fossils, namely *Beaconites* (*Be*) and *Taenidium* (*Ta*), bilobate trace fossils, such as *Cruziana* (*Cr*) and *Rusophycus* (*Ru*), arthropod trackways, such as *Diplichnites* (*Di*), and the sinusoidal trail *Cochlichnus* (*Co*). Vertebrate trackways are abundant and diverse in the subaerial portion of the lake margin. In particular, shorebird tracks are common, including the ichnogenus *Ignotornis* (*Ig*) in Mesozoic strata. Vertical burrows, including *Skolithos* (*Sk*) and *Arenicolites* (*Ar*), tend to dominate in high-energy shoreline areas, such as mouth bars. Shallow- and deep-lake areas are very similar in taxonomic composition. Both are dominated by grazing trails, such as *Gordia* (*Go*), *Cochlichnus* (*Co*), *Helminthopsis* (*He*), and *Helminthoidichnites* (*Hl*). The simple burrow system *Treptichnus* (*Tr*) is also common. The grazing trail *Mermia* (*Me*) and the fish trail *Undichna* (*Un*) are more common in deep-lake deposits. *Vagorichnus* (*Va*) may occur in deep-lake turbidites. Vertebrate and invertebrate trace fossils not to scale.

conditions tend to predominate in sheltered shorelines or in small lakes. Ichnofaunas from low-energy lake margins consist of meniscate trace fossils (*Scoyenia*, *Taenidium*), arthropod trackways (e.g. *Diplichnites*, *Kouphichnium*), simple horizontal burrows (*Palaeophycus*), bivalve resting structures (*Lockeia*), and bilobate trails (*Cruziana*, *Rusophycus*) (e.g. Daley, 1968; Pollard *et al.*, 1982; Smith *et al.*, 1982; Pollard and Walker, 1984; Walker, 1985; Cook and Bann, 2000; Hester and Lucas, 2001; Kim *et al.*, 2005; Lucas and Lerner, 2006; Lucas *et al.*, 2006b). Associations dominated by *Lockeia* seem to be common in carbonate lake shorelines (Lucas *et al.*, 2010a).

Vertebrate trackways are also extremely common in low-energy marginal-lake deposits, including traces produced by amphibians, reptiles, dinosaurs, mammals, and birds (e.g. Olsen *et al.*, 1978; Alonso, 1985; Lockley *et al.*, 1986; Lim *et al.*, 1989; Prince and Lockley, 1989; Abbassi and Lockley, 2004; Kim *et al.*, 2006; Lockley *et al.*, 2006). Shorebird tracks are particularly common in lake-margin deposits, with *Ignotornis*, *Jindongornipes*, *Koreanaornis*, and *Aquatilavipes* the most commonly ichnogenera preserved (Fig. 10.13). In fact, dinosaur and bird tracks have been used to recognize paleoshorelines in lacustrine successions; tracked horizons typically occur at the top of shallowing-upward successions (e.g. Olsen *et al.*, 1978; Alonso, 1985; Lockley *et al.*, 1986; Prince and Lockley, 1989). Multiple horizons with dinosaur tracks allowed delineation of cycles of expansion and contraction of the water body (Lockley, 1986, 1989). Fossil human footprints have also been documented in lake-margin deposits (Zavala *et al.*, 1992; Bayón and Politis, 1996). Other vertebrate trace fossils include lungfish burrows, which may have served as aestivation chambers and breeding tunnels (e.g. Gobetz *et al.*, 2006).

Even freshwater, open lakes can experience periods of relatively low lake levels, with exposure of littoral deposits and desiccation of lake-margin areas. Accordingly, trace fossils are commonly associated with physical structures that indicate subaerial exposure. These ichnofaunas are examples of the *Scoyenia* ichnofacies, which occurs in low-energy, lake-margin areas, and records adaptations of a benthos to either very slightly submerged sediments that are periodically desiccated or to waterside subaerial substrates that are periodically submerged (Frey and Pemberton, 1987). Because of desiccation of lake-margin deposits, firmground ichnofaunas dominated by striated meniscate trace fossils (*Scoyenia*) and burrow galleries (*Spongeliomorpha*) may be present (e.g. Metz, 1993). Bioerosion

Figure 10.14 Vertebrate trace fossils in lacustrine deposits. Upper Carboniferous, Radnice Member, Kladno Formation, Bohemia, Czech Republic. See Turek (1989). (a) The fish trail *Undichna britannica*. (b) The amphibian trackway *Gracilichnium* (?) *chlupaci*. Scale bars are 1 cm.

in stromatolites has been recorded also, but it is relatively rare (Ekdale *et al.*, 1989). Vertebrate ichnofacies in these low-energy shorelines typically represent the *Grallator* ichnofacies from the Late Triassic to the Recent (Hunt and Lucas, 2007).

Moderate- to high-energy conditions are more common in large lakes affected by strong waves or near the mouth of distributary channels. These zones are characterized by strong turbulence and a mobile substrate, complicating colonization by the macrobenthos (Cohen, 2003). The ichnofauna of these lakes is dominated by simple vertical burrows (*Skolithos*), U-shaped vertical burrows (*Arenicolites*), and escape structures (e.g. Mángano *et al.*, 1994; Melchor *et al.*, 2003; Buatois and Mángano, 1998, 2004a, 2007) (Fig. 10.13). These trace-fossil assemblages show affinities with the *Skolithos* ichnofacies (Buatois and Mángano, 1998, 2004a; Melchor *et al.*, 2003) (see Section 10.2.1). Overall, ichnofaunas dominated by vertical burrows are less common than the typical lake-margin *Scoyenia* assemblages.

The subaqueous zones of hydrologically open lakes are characterized by low energy and relative environmental stability. The most important controls on trace-fossil distribution in these areas are oxygen content, energy, food supply, and substrate (Buatois and Mángano, 2007). Oxygenation is a first-order limiting factor because in lakes with thermal stratification, the hypolimnion becomes anoxic/dysoxic and bioturbation is commonly suppressed. Turbidity and underflow currents may provide oxygen to lake bottoms, favoring the establishment of benthic faunas. In addition, episodic or sustained flows help to increase food supply by transporting organic detritus from adjacent alluvial plains and lacustrine-shoreline areas. On the other hand, in areas strongly affected by high-energy sediment gravity flows, bioturbation may be inhibited. The degree of consolidation of the substrate also plays a role because trace-fossil preservation is precluded in soupy substrates.

Feeding (*Treptichnus*, *Vagorichnus*, and *Tuberculichnus*) and grazing traces (e.g. *Mermia*, *Gordia*, *Helminthopsis*, and *Helminthoidichnites*) of detritus and deposit feeders are commonly dominant in subaqueous zones of open lakes (Fig. 10.13), most commonly in siliciclastic (e.g. Walter, 1985; Pickerill, 1992; Buatois and Mángano, 1993a; Miller *et al.*, 1991; Buatois *et al.*, 1996b; Walter and Suhr, 1998; Melchor *et al.*, 2003; Melchor, 2004), but also in carbonate deposits (e.g. Buatois *et al.*, 2000; Gibert *et al.*, 2000). Although arthropod trackways may occur, they are comparatively rare. Vertebrate trace fossils are represented by the fish trail *Undichna* and the amphibian trackways *Lunichnium* and *Gracilichnium* (Higgs, 1988; Turek, 1989; Gibert *et al.*, 1999; Trewin, 2000; Minter and Braddy, 2006b) (Figs. 10.13 and 10.14a–b).

Pleistocene varves seem to contain a very distinctive ichnofauna (e.g. Gibbard and Stuart, 1974; Gibbard, 1977; Gibbard and Dreimanis, 1978; Walter and Suhr, 1998; Gaigalas and Uchman, 2004; Uchman *et al.*, 2009; Benner *et al.*, 2009; Knecht *et al.*, 2009). Glacial varves contain not only simple grazing trails (e.g. *Gordia*, *Cochlichnus*, and *Helminthoidichnites*) and fish traces (e.g. *Undichna*, *Pisichnus*, and *Broomichnium*), but also arthropod trackways (e.g. *Glacichnium* and *Warvichnium*).

Ichnological evidence is useful to distinguish between deposits from sustained density underflows and episodic turbidity currents (Buatois and Mángano, 1998, 2004). Both processes commonly operate in open lakes and are difficult to differentiate based on physical sedimentary structures alone. As discussed by Pharo and Carmack (1979), turbidites are deposited by episodic currents that involve redeposition of sediment initially emplaced under unstable conditions, while underflow currents are relatively continuous and represent the uninterrupted transport of river-borne sediment into the lake. Turbidites commonly display ichnofossils at the top of layers or, more rarely, at the base of layers. In both cases, the trace-fossil suite records colonization of opportunistic organisms after episodic emplacement of the event bed (Buatois and Mángano, 1998) (Fig. 10.15). Where preserved at the base, a post-depositional origin is indicated by the presence of trace fossils cross-cutting inorganic sole marks (e.g. Buatois *et al.*, 1996b). Almost invariably pre-depositional suites are more diverse than post-depositional suites. Underflow-current deposits contain distinctive suites of ichnofossils in each lamina or lamina set (e.g. Buatois and Mángano, 1993a; 1998; Melchor *et al.*, 2003), reflecting that they were produced contemporaneously with sedimentation, rather than after a major break in deposition as is typical of turbidites (Fig. 10.16).

Trace fossils also help to distinguish between marine and lacustrine turbidites, which are identical in terms of physical sedimentary structures (Buatois and Mángano, 1998, 2004a). Deep-marine turbidites display diverse ichnofaunas dominated by ornate grazing trace fossils and graphoglyptids that reflect highly specialized feeding strategies recorded by the *Nereites* ichnofacies (see Section 4.3.5). In contrast, lacustrine turbidites are characterized by non-specialized grazing and feeding trace fossils (Buatois and Mángano 1998, 2004a) (Fig. 10.17a–e). These

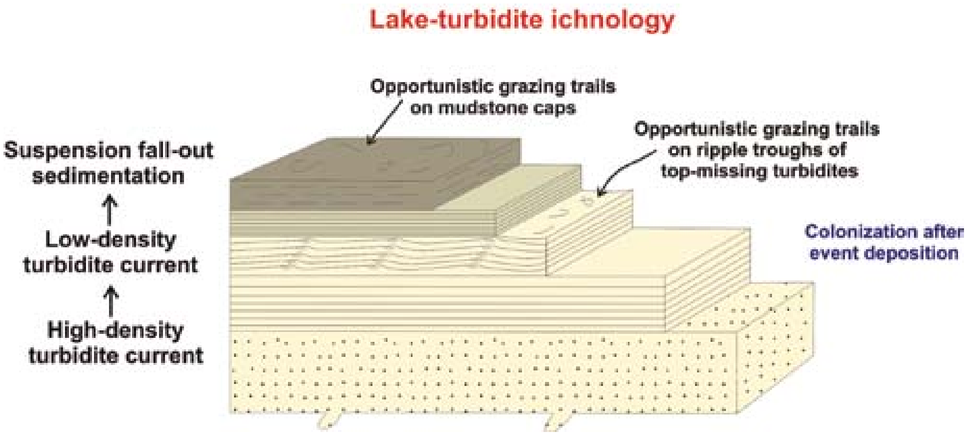

Figure 10.15 Ichnology of lacustrine turbidites. Ichnofossils typically occur at the top of turbidite layers (e.g. simple grazing trails) or, more rarely, at the base of layers (e.g. *Vagorichnus*), recording opportunistic colonization after episodic emplacement of the event bed. Modified from Buatois and Mángano (1998).

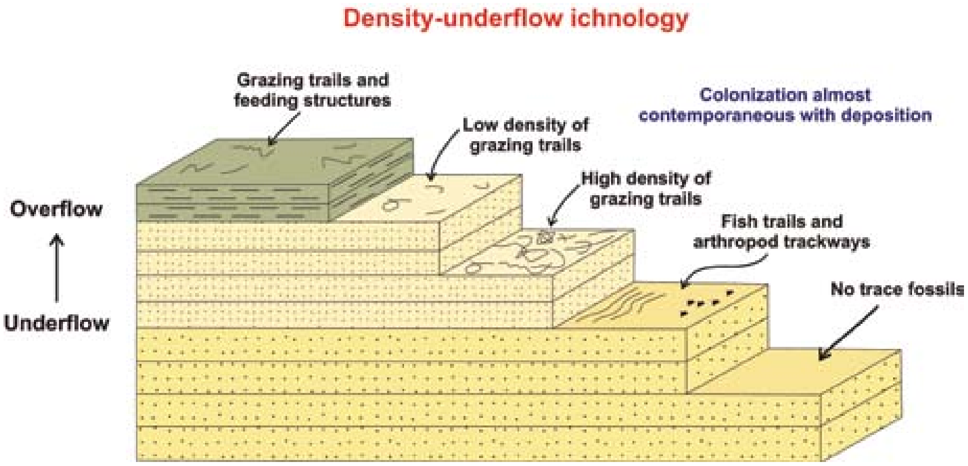

Figure 10.16 Ichnology of underflow-current deposits. These deposits may contain distinctive suites of ichnofossils in each lamina or lamina-set, recording animal activity contemporaneous with sedimentation. Modified from Buatois and Mángano (1998).

non-specialized feeding patterns are illustrated by the ichnogenus *Mermia*, which shows looping and a high level of self-overcrossing, revealing the repeated passage of the tracemaker across the same portion of sediment. Other examples of unsophisticated feeding strategies are the simple grazing trails *Helminthopsis* and *Helminthoidichnites*. Such non-specialized feeding strategies most likely reflect the abundance and accessibility of food in lacustrine systems (Buatois and Mángano, 2004a). The comparatively lower ichnodiversity of lakes in comparison with deep-marine environments results from the more ephemeral nature of the continental bodies of water (Buatois and Mángano, 1998).

Although oxygen-depleted lacustrine sediments are commonly unbioturbated, some organisms have developed adaptations to deal with dysaerobic to anoxic settings (Cohen, 2003). In modern lakes, chironomid larvae construct oxygen-mining burrows similar to *Polykladichnus* and *Thalassinoides* to exploit food in suboxic and anoxic sediment (Gingras *et al.*, 2007). Similar structures have been rarely documented in the fossil record (e.g. Smith *et al.*, 1982).

Permanent subaqueous lacustrine zones of hydrologically open lakes are characterized by the *Mermia* ichnofacies, which extends from shallow to deep areas of the lake (Buatois and Mángano, 1995a, 1998). No archetypal trace-fossil associations can be defined at present to distinguish between shallow-and deep-lacustrine subenvironments. Virtually all of the same assemblages that occur in shallow areas of some lakes (e.g. Pickerill, 1992) occur in the deep areas of others (e.g. Buatois and Mángano, 1993a; Buatois *et al.*, 1996b). Both examples belong to the same archetypal ichnofacies, the *Mermia* ichnofacies. These variations in ichnofossil content from one lake to the other probably reflect the wide variability of lacustrine basins. Although there are no recurrent ichnofacies that distinguish shallow-versus deep-lacustrine subenvironments, zonations can be made at the scale of individual lacustrine basins (e.g. Metz, 1996; Walter and Suhr, 1998; Melchor *et al.*, 2003; Melchor, 2004) (Box 10.3). In general, traces of deposit and detritus feeders dominate in deeper areas of the lake, while suspension-feeder traces may occur in littoral zones, a pattern consistent with distribution of these trophic types in modern lakes (Cohen, 2003).

10.4 DESERTS

Deserts develop in areas where rainfall rarely exceeds evaporation and, as such, impart significant stress on their biotas. In

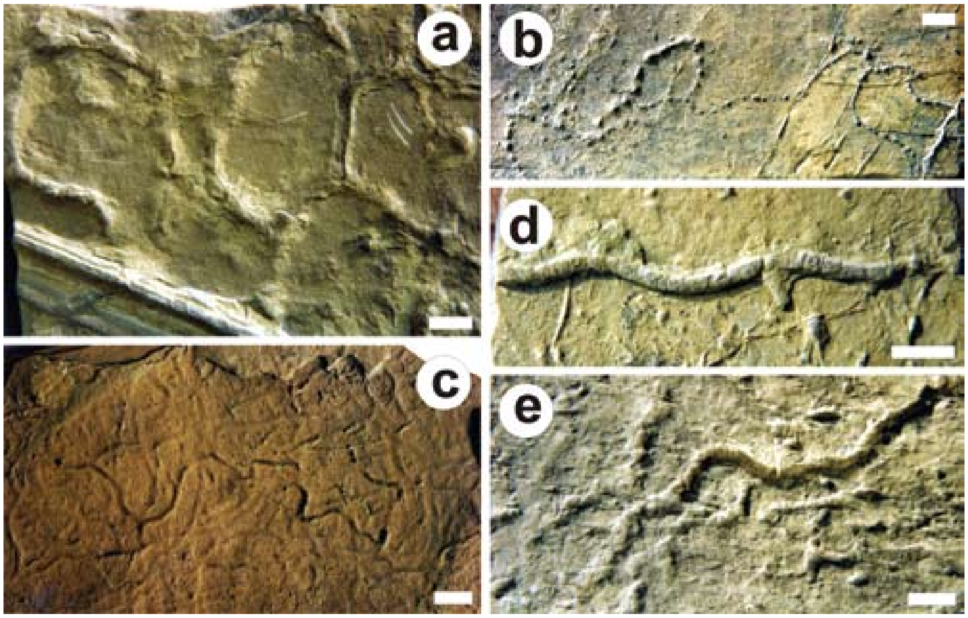

Figure 10.17 Trace fossils preserved at the base of lacustrine turbidites. Lower Jurassic, Anyao Formation, Jiyuan–Yima Basin, central China. (a) *Vagorichnus anyao* cross-cutting sole mark. (b) *Tuberculichnus vagans*. (c) *Paracanthorhaphe togwunia*. (d) *Cochlichnus anguineus*. (e) *Helminthopsis abeli*. Scale bars are 1 cm. See Buatois *et al*. (1996b).

particular, the interaction between rainfall and nutrient availability is essential in controlling desert dynamics and ecology (Whitford, 2002). Episodic events, such as flash floods and wind storms, also have a huge impact in desert ecosystems. Animals inhabiting deserts have a series of adaptive physiological traits and behavioral mechanisms that allow them to maintain a survivable thermal energy balance and water balance (Whitford, 2002). In this regard, the role of benign microclimates within desert areas is of paramount importance.

In contrast with other continental environments, the ichnology of eolian systems is less well understood. However, in recent years there has been a renewed interest in eolian trace fossils (e.g. Fornós *et al*., 2002; Hunt and Lucas, 2007; Ekdale *et al*., 2007; Loope, 2008). Available information derives from both modern environments and some case studies from the fossil record. In modern eolian systems, a moderate diversity of biogenic structures, mostly produced by arthropods (in particular arachnids and insects), has been documented (e.g. Ahlbrandt *et al*., 1978). More specifically, tracemakers in inland dunes and interdune areas include burrowing wasps, crickets, beetles, spiders, scorpions, millipedes, termites, and ants. In the case of coastal eolian dunes, dwelling burrows of the crab *Ocypode quadrata*, producer of *Psilonichnus* in the fossil record, are common (Frey *et al*., 1984a; Curran, 1992, 1994).

Burrowing commonly represents an efficient strategy to escape from the harsh conditions at the surface. In hot deserts most arthropods live underground during the day and leave their burrows at night, while under warmer conditions some may be diurnal (Cloudsey-Thompson, 1991). However, some arthropods (e.g. millipedes, mites) lack morphological and physiological water-conservation adaptations, and are only able to live at the surface after rainfall events (Tevis and Newell, 1962; Whitford, 2002). Termites and ants live mainly in underground nests and galleries that may extend up to 2–3 m below the surface (Whitford, 2002). Burrows not only offer protection from high temperatures and desiccation, but they are also an integral part of the feeding strategies of passive predators, such as spiders, scorpions, and tiger beetle larvae, which prey on different insects and even small vertebrates, adopting a "sit and wait" strategy (Main, 1982; Pearson, 1988; Whitford, 2002). Many insects (e.g. crickets, most beetles) are detritus and deposit feeders that exploit sites of preferential accumulation of wind-blown detritus (Crawford, 1988). Overall, desert ichnofaunas reflect the activity of feeding generalists.

In addition, a number of vertebrates, mostly mammals and reptiles, inhabit desert systems, and may produce biogenic structures. The majority of small mammals (e.g. squirrels, kangaroo rats) live in their own burrows during the day, where they experience more favorable microclimates. Intermediate-size mammals (e.g. rabbits, foxes) either construct their own burrows, or enlarge those constructed by other animals (Whitford, 2002). Reptiles also burrow into the sediment, although their efficient thermoregulatory behavior allows them to experience less stress due to high temperatures (Whitford, 2002). Experiments with sand-swimming snakes (the Kenyan sand boa *Eryx colubrinus*) indicate that these organisms produce a wide variety of biogenic structures (Hembree and Hasiotis, 2007). Amphibians are rare, but they may occur in ephemeral water bodies, which serve as breeding sites (Whitford, 2002). They typically burrow into the sediment to absorb moisture from the soil and avoid the desiccating environment of the surface. Although vegetation is typically sparse to non-existent, plant traces may occur around water bodies.

Ahlbrandt *et al*. (1978) noted that the preservation potential of most eolian biogenic structures is low. Wind erosion is pervasive and detrimental for preservation of plant or animal structures. Most of the traces seen in modern environments occur in the erosional stoss side of dunes and, therefore, have very low preservational potential (Ekdale *et al*., 2007). The presence of temporarily wetted and cohesive substrates, rapid burial, emplacement in the depositional slip phase, lined burrow walls, preferential cementation, and stabilization by biological crusts are among the factors that promote preservation of biogenic structures. In particular, Seilacher (2008) emphasized the importance of microbial participation (bioglues) in the preservation of delicate arthropod and vertebrate trackways in eolian-dune deposits. Animal burrowing removes and disaggregates large volumes of sediment, contributing to its deflation by wind (Whitford and Kay, 1999; Whitford, 2002).

Eolian ichnofaunas typically show low diversity in the fossil record, mainly because of their low preservation potential (Fig. 10.18). In general, trace-fossil diversity is directly linked to the position of the water table and the predominant climatic conditions. In hyper-arid climatic settings, the regional water table lies well below the accumulation surface in most areas of the desert (Mountney, 2004). Under these conditions, dry eolian systems, characterized by large and extensive dunes are formed. Associated dry interdunes are characterized by accelerating airflow and are subject to intense erosion. As a consequence, dunes grow and expand at the expense of the interdune flats (Mountney, 2006). Typically, dry eolian systems are sparsely vegetated at best, and contain few or no trace fossils due to the absence of near-surface moisture. However, trace-fossil suites may occur in grain-flow layers of the dune slip faces, reflecting preferential preservation in damp sand during rainy seasons (Sadler, 1993; Loope, 2006; Ekdale *et al*., 2007).

Under arid climates, wet eolian systems tend to dominate (Mountney, 2004). In these systems the water table or its capillary fringe is in contact with the accumulation surface and, therefore, moisture influences sedimentation (Mountney, 2006). The presence of damp sand restricts sediment availability for transport. Complex patterns of dunes and wet and damp interdunes are common. Vegetated zones may occur along interdunes corridors, leading to the local formation of rooted layers. Elevated water tables result in local concentrations of track, trails, and burrows in interdune settings. In addition, the preservation potential of biogenic structures is enhanced particularly in wet interdunes. Large burrows probably formed by insectivorous vertebrates have been documented on the flanks of actively migrating, compound dunes, in moist sand that most likely formed due to seasonal rainfall (Loope, 2008).

In semiarid climatic settings, large parts of deserts become stabilized (Mountney, 2004). In stabilized eolian systems, vegetation and surface cementation play a major role in accumulation by restricting sediment availability (Mountney, 2006). Due to extended vegetation cover, root traces may be abundant and incipient paleosols may develop. Water tables are typically high, promoting the formation and preservation of invertebrate and vertebrate structures. Rooted and burrowed horizons commonly occur at several stratigraphic levels. These horizons reflect bypass supersurfaces that form where the water table remains static (Mountney, 2004).

Interestingly, Paleozoic and post-Paleozoic eolian ichnofaunas are remarkably different (see Sections 4.5.4 and 14.2.6). Trackways produced by scorpions (*Octopodichnus*, *Paleohelcura*) are particularly common in Paleozoic eolianites (e.g. Brady, 1947; Sadler, 1993; Hunt and Lucas, 2007). Although ichnodiversity may reach moderate levels particularly in post-Paleozoic eolian deposits, many ichnotaxa (e.g. *Arenicolites*, *Palaeophycus*, *Skolithos*) may have been produced by the same burrower (Ekdale *et al*., 2007). During the Permian, the fossil track record is dominated by different ichnospecies of *Chelichnus* (Fig. 10.18), possibly produced by non-mammalian synapsids (McKeever and Haubold, 1996). Mesozoic eolianites contain carnivore dinosaur trackways (e.g. *Grallator*) rather than those produced by herbivore dinosaurs, suggesting that carnivorous dinosaurs fed on smaller carnivores, mammals and invertebrates (Leonardi, 1989; Lockley, 1991). In addition, some of these trackways are of small size, which may indicate dwarfism in response to the harsh conditions of deserts (Leonardi, 1989). In addition to trackways, vertebrate burrows attributed to tritylodontid cynodonts have been recorded in interdune deposits (Fig. 10.18), probably reflecting colonization during periods of high rainfall (Lucas *et al*., 2006c). Preferential preservation of trackways has been noted in certain eolian settings, such as cliff-front coastal echo dunes (Fornós *et al*., 2002). The preservation potential of biogenic structures is enhanced in echo dunes because deflation erosion is reduced against the cliff. Extensively trampled horizons may alternate with intervals preserving the primary sedimentary fabric. Associated biogenic structures include root traces at the margins of dune deposits and horizontal insect galleries similar to the ichnospecies *Gracilichnus sinualis* (Fornós *et al*., 2002).

Eolian dune ichnofaunas are attributed to the recently introduced *Octopodichnus–Entradichnus* ichnofacies (Hunt and Lucas, 2007; Ekdale *et al*., 2007). In terms of vertebrate ichnofacies, they belong to the *Chelichnus* ichnofacies (Hunt and Lucas, 2007). Vegetated dunes may contain the *Coprinisphaera* or the *Celliforma* ichnofacies in connection to incipient paleosols, while the *Scoyenia* ichnofacies typically occur in wet and, less commonly, damp interdunes (Buatois and Mángano, 1996; Genise *et al*., 2000).

10.5 PALEOSOLS

Paleosols represent an important element of alluvial successions and its associated ichnofaunas have received significant attention during the last decade (e.g. Bown and Laza, 1990; Hasiotis *et al*., 1993b; Genise and Bown, 1994b; Smith *et al*., 2008b; Genise *et al*., 2000, 2004b, 2010a) (Box 10.4). The nature of paleosol ichnofaunas is shaped by a number of factors, such as the intensity of soil processes, the position of the water table, climate, the duration of subaerial exposure, and the evolution of bioturbating insects (Genise *et al*., 2000, 2004b). Needless to say, most of these factors are not independent, but are closely interrelated.

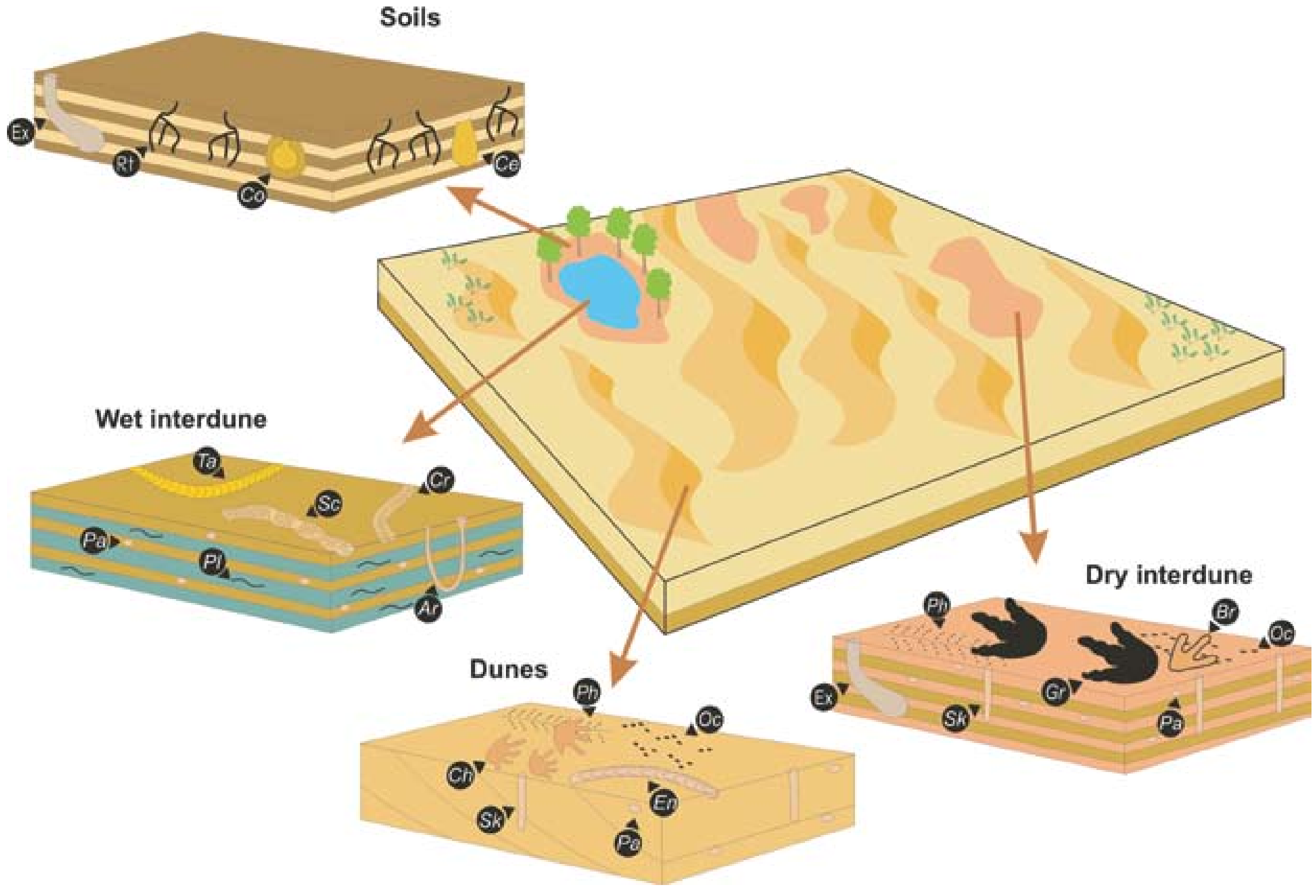

Figure 10.18 Schematic reconstruction of trace-fossil distribution in deserts. Composition of vertebrate ichnofaunas is highly variable according to geological age. Dune areas display a low diversity and density of trace fossils, including scorpion trackways, such as *Octopodichnus* (*Oc*) and *Paleohelcura* (*Ph*), meniscate trace fossils, such as *Entradichnus* (*En*), simple vertical and horizontal burrows, such as *Skolithos* (*Sk*) and *Palaeophycus* (*Pa*), and various vertebrate trackways, including *Chelichnus* (*Ch*) in Permian examples. Dry-interdune deposits commonly contain a few trace fossils, such as *Octopodichnus* (*Oc*), *Paleohelcura* (*Ph*), *Skolithos* (*Sk*), and *Palaeophycus* (*Pa*) and tetrapod excavations (Ex). In Mesozoic assemblages dune and dry-interdune deposits may contain trackways produced by theropod dinosaurs (e.g. *Grallator* (*Ga*)) and synapsids (e.g. *Brasilichnium* (*Br*)). Wet-interdune deposits may contain slightly more diverse ichnofaunas, including the ichnogenera *Taenidium* (*Ta*), *Scoyenia* (*Sc*), *Cruziana* (*Cr*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*) and *Arenicolites* (*Ar*). Some areas may be vegetated with moderate soil development. Trace fossils in these soils may include *Coprinisphaera* (*Co*), *Celliforma* (*Ce*), tetrapod excavations (Ex), and root traces (Rt). Vertebrate and invertebrate trace fossils not to scale.

Box 10.4 Ichnology of Lower-Middle Miocene paleosols of Patagonia, Argentina

Mesozoic and Cenozoic paleosols preserved in Patagonia, southern Argentina, have become a natural laboratory from which some of the most comprehensive studies of terrestrial ichnology have resulted. These studies include the detailed characterization of a large number of ichnotaxa, careful analysis of their producers, and evaluation of the resulting ichnofabrics. In particular, the Lower to Middle Pinturas Formation has been the subject of a number of studies. This pyroclastic unit contains abundant fossil mammals (including platyrrhine primates) and trace fossils of insects and rodents. Analysis of its insect trace fossils has provided valuable information to explain changes in paleoenvironmental conditions during deposition of this unit. Mature paleosols from the lower part of the Pinturas Formation contain the termite nest *Syntermesichnus fontanae*, which is locally associated with the scarabid beetle nest *Coprinisphaera frenguellii*. These paleosols were formed in a marginal habitat between forested areas and more open country. Associated primate body fossils also point towards the presence of nearby forested areas. These mature paleosols alternate with immature ones containing the bee cells *Celliforma rosellii* and *Celliforma pinturensis*, together with *Coprinisphaera frenguellii*. While primate body fossils are absent, skeletons of large herbivorous mammals (e.g. *Astrapotherium* and *Astrapothericulus*) are abundant. Large herbivores most likely provided the dung that was exploited by the scarabid beetles. The presence of burrowing bees is consistent with arid conditions and moderate plant growth. Integration of sedimentological, ichnological, and paleontological evidence suggests that the Pinturas Formation reveals a succession of ash-fall events, deforestation, drying, and establishment of eolian-dune fields, followed by the return of humid conditions, forest development, and the formation of mature paleosols.

References: Bown and Laza (1990); Genise and Bown (1994a).

Soil processes affect the primary sedimentary fabric and may also disrupt biogenic structures. For example, laterization may strongly affect paleosol ichnofabrics, only allowing preservation of insect nests with thick constructed walls (Genise *et al.*, 2004b). In addition, laterization disrupts ichnofabrics by randomly reorienting insect nests. These authors noted that soil features that disrupt the primary fabric of terrestrial deposits are in some cases independent of bioturbation and, therefore, proposed that the pedofabric should be evaluated independently from the ichnofabric (see Section 5.5).

The position of the water table strongly controls the type of trace fossils present in soils (e.g. Hasiotis *et al.*, 1993b; Genise *et al.*, 2004b). While bee and dung beetle nests commonly occur in environments characterized by low water tables, ant and termite nests are present in well-drained to seasonally flooded soils, and earthworms typically burrow in moist substrates, such as gleyed paleosols (Genise *et al.*, 2004b) (see Section 6.1.10). The water table preferences of coleopteran pupal chambers are less understood, although available information indicates that they occur above the water table (Genise *et al.*, 2002). Waterlogged soils are commonly reducing, precluding insect nesting (Retallack, 1990).

Climate ranks as one of the most significant controls in paleosol ichnofaunas, and this is clearly reflected in recently developed models of paleosol ichnofacies (Genise *et al.*, 2000, 2004a, 2010a). As a result, ichnofacies show a close correspondence with the plant formations identified by Mueller-Dombois and Ellenberg (1980). In particular, the *Coprinisphaera* ichnofacies occurs in paleosols developed in paleoecosystems of herbaceous communities, ranging from dry and cold to humid and warm conditions, while the *Termitichnus* ichnofacies is present in paleosols formed in closed forests with plant growth under warm and humid conditions and the *Celliforma* ichnofacies typifies carbonate-rich paleosols (see Sections 4.4.3, 4.4.5, and 4.4.6).

The importance of climate as a limiting factor on paleosol ichnofaunas is due to their overwhelming dominance by insect nests, which contain larvae provisioned with organic matter. Larvae and provisions are strongly sensitive to microclimatic conditions (e.g. moisture and soil temperature) because an excess of moisture inside cells leads to decay of provisions and insufficient moisture is conducive to larval dehydration (see Section 6.1.9). Overall, dung beetles, bees and, to a lesser extent, ants nest in bare soil exposed to sun rather than in humid tropical areas (Batra, 1984; Michener, 1979; Genise and Bown, 1994a). In contrast, most termite nests typically characterize more humid soils (Grassé, 1984). Some termites (e.g. Macrotermitinae), however, exhibit a wider range and are able to live from tropical rain forests to semiarid steppes.

Duration of subaerial exposure strongly impacts soil maturity and trace-fossil diversity. Extended periods of subaerial exposure are commonly associated with mature soils that contain abundant and diverse insect nests. Termite colony growth by apposition of chambers and contemporaneous formation of new colonies reflect long periods of subaerial exposure (Genise and Bown, 1994b). In contrast, nests of solitary insects require shorter periods of subaerial exposure. Finally, soils formed around water bodies or in swamps lack insect nests and contain only root traces.

11 Ichnology of carbonate environments, rocky shorelines, and volcanic terrains

> The pillars are forty-two feet in height; their surface is smooth and uninjured to the height of about twelve feet above their pedestals. Above this, is a zone, twelve feet in height, where the marble has been pierced by a species of marine perforating bivalve – *Lithodomus*, Cuv. The holes of these animals are pear-shaped, the external opening being minute, and gradually increasing downwards. At the bottom of the cavities, many shells are still found, notwithstanding the great numbers that have been taken by the visitors. The perforations are so considerable in depth and size, that they manifest a long continued abode of the Lithodomi in the columns; for, as the inhabitant grows older and increases in size, it bores a larger cavity, to correspond with the increasing magnitude of its shell. We must, consequently, infer a long continued immersion of the pillars in sea-water, at a time when the lower part was covered up and protected by strata of tuff and the rubbish of buildings, the highest part at the same time projecting above the waters, and being consequently weathered, but not materially injured.
>
> Charles Lyell
> *Principles of Geology* (1830)

> Estoy sentado aquí en el atolón. Estoy sentado y plantado aquí en el atolón.
>
> Luis Alberto Spinetta
> *Holanda* (1996)

As mentioned in previous chapters, our ichnological knowledge of the different depositional environments is highly variable. For example, carbonates have received less attention than siliciclastics. Also, volcanic terrains have been little explored from an ichnological perspective. On the other hand, rocky shorelines, which fall within the realm of bioerosion, have been the focus of a number of detailed ichnological studies, both on modern and ancient shorelines. In fact, the study of bioerosion has a long history, starting with Lyell's (1830) observation of borings produced by the lithophagid bivalve *Lithodomus*, which actually belongs in the ichnogenus *Gastrochaenolites*, pervasively bioeroding the marble pillars of the Temple of Serapis. In this chapter, we will explore the ichnology of this last set of environments. First, we will focus on carbonate rocks, addressing shallow-marine tropical carbonates, reefs, shelf and deep-sea chalk, and carbonate turbidites. Second, we will review our present knowledge of rocky shorelines. Finally, we will explore the ichnology of environments strongly affected by volcanism.

11.1 CARBONATE SYSTEMS

Notwithstanding some exceptions (e.g. fluvial and glacial), almost all siliciclastic environments have carbonate counterparts (Kennedy, 1975). Carbonates have certain peculiarities that distinguish them from siliciclastics, and impact on production and preservation of biogenic structures. Among these peculiarities, the role of early cementation (leading to ample development of firm and hard substrates), the influence of organisms on early diagenesis, the role of color contrast, and the heterogeneity in sediment composition and texture rank among the most important (Kennedy, 1975; Ekdale *et al.*, 1984; Curran, 1994, 2007). Early cementation is widespread in carbonate substrates (e.g. Wilson, 1975). In fact, lithification can take place even before burrow abandonment by the producers, or after abandonment but before infill of the structures (Shinn, 1968; Kennedy, 1975). Early cementation is conducive to the establishment of hardgrounds, and is the driving force behind development of substrate-controlled ichnofacies and associated bioerosion (e.g. Bromley, 1967, 1975; Goldring and Kaźmierczak, 1974; Palmer, 1978; Gruszczynski, 1979; Bottjer, 1985; Landing and Brett, 1987; Mángano and Buatois, 1991; Bromley and Allouc, 1992) (Fig. 11.1a–b). In turn, early diagenesis is influenced by burrowing activities, and diagenesis influences preservation of biogenic structures (e.g. Mason, 1980; Archer, 1984; Narbonne, 1984; Fillion *et al.*, 1990). For example, diagenesis may lead to the formation of dolomite haloes surrounding burrow systems contributing to the formation of mottling textures (e.g. Pak and Pemberton, 2003; Pemberton and Gingras, 2005) (Fig. 11.2a–b). Carbonate sediment Eh/pH is strongly affected by the activity of deposit and detritus feeders. For example, Taylor (1964) demonstrated that between 80 and 90% of carbonate sands at a study area in the Bahamas have passed through the digestive tract of echinoderms. Virtually every single chalk particle is thought to have been ingested by organisms (Ekdale and Bromley, 1991). In addition, pellet production plays a major role in substrate consistency, sometimes reducing substrate stability (Pryor, 1975; Ekdale *et al.*, 1984). Several factors contribute to the somewhat decreased preservation potential of biogenic structures in carbonates. Although common in siliciclastics, contrasts between trace fossils and the host sediment are rare in carbonates, complicating visualization of ichnofossil forms (Curran, 1994, 2007). Furthermore, the degree of heterogeneity in composition and texture also impacts on preservation potential. Carbonates with high textural and compositional contrasts tend to favor preservation of discrete biogenic structures (Archer, 1984; Maples and Archer, 1986).

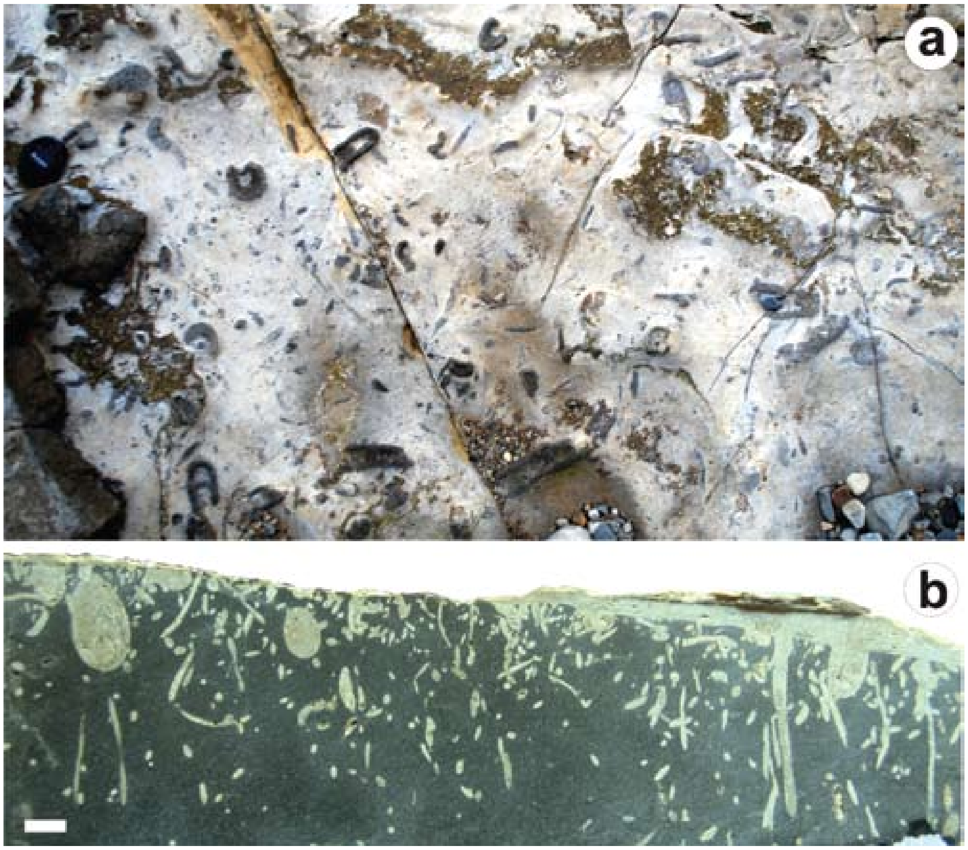

Figure 11.1 Substrate-controlled ichnofaunas in carbonate rocks. (a) High density of firmground *Rhizocorallium* isp. Upper Jurassic, Rodiles Formation, El Puntal Cliffs, San Martín del Mar, Villaviciosa, Asturias, northern Spain. Lens cap is 5.5 cm. (b) *Trypanites* isp. and *Gastrochaenolites* isp. in a hardground. Contact between the Middle Jurassic Upper Inferior Oolite and underlying Carboniferous limestone. Nunney Quarry, Somerset, England. Scale bar is 1 cm. See Bromley (1975).

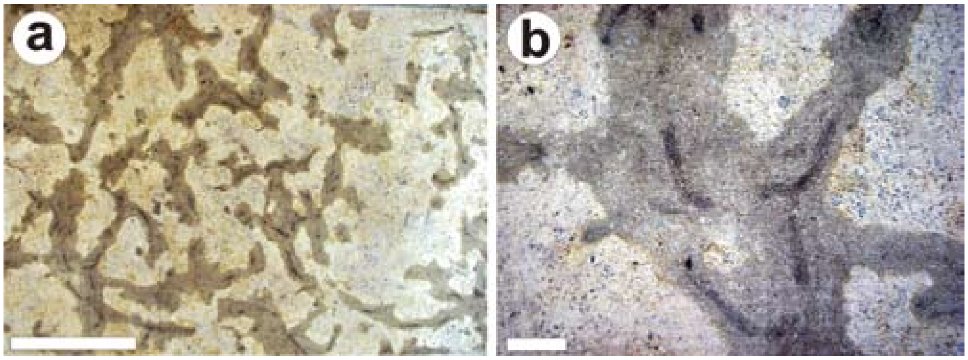

Figure 11.2 *Thalassinoides*-like burrow systems in a mottled limestone, Upper Ordovician, Red River Formation of Manitoba, Canada. This limestone is known as Tyndall stone. Wall at the entrance to the Department of Geological Sciences of the University of Saskatchewan. (a) General view of branching burrow systems. Scale bar is 10 cm. (b) Close-up showing branching and dolomitic halo surrounding the burrow; only the darker inner core is the actual burrow. Scale bar is 1 cm. See Pak and Pemberton (2003).

However, Pemberton and Jones (1988) indicated that differences between carbonate and siliciclastic ichnology have been overstated. These authors pointed out that in many instances carbonate components are transported rather than produced *in situ* and, therefore, they are subjected to the same hydrodynamic principles as siliciclastics. This situation has been illustrated by Wu (1982), who documented colonization suites in carbonate tempestites. In the same vein, Pickerill *et al.* (1984) described a carbonate ichnofauna in which diagenetic processes, albeit important, did not mask the original environmental distribution of trace fossils.

Present knowledge of the ichnology of different carbonate environments is uneven, with most studies focused on shallow-marine tropical carbonates, reefs, and pelagic carbonates (i.e. chalk). A smaller proportion of studies have dealt with the ichnology of carbonate turbidites.

11.1.1 SHALLOW-MARINE TROPICAL CARBONATES

Most ichnologic studies on shallow-marine tropical carbonates have been based on Pleistocene and recent examples in the carbonate factories of Florida, the Bahamas Archipelago, the Seychelles Islands, and the Persian Gulf (e.g. Shinn, 1968; Farrow, 1971; Braithwaite and Talbot, 1972; Pemberton and Jones, 1988; Curran, 1992, 1994, 2007). In particular, San Salvador Island in the Bahamas has been the focus of intense

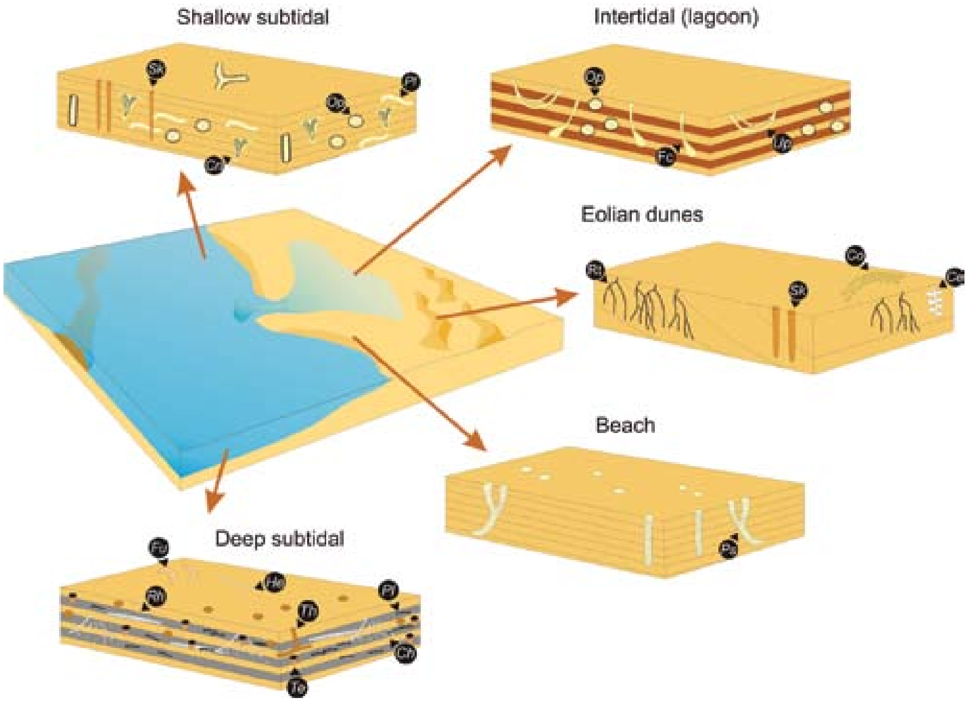

Figure 11.3 Schematic reconstruction of trace-fossil distribution in shallow-marine tropical carbonate environments. Coastal eolian-dune deposits contain *Cellicalichnus* (*Ce*), *Coenobichnus* (*Co*), *Skolithos* (*Sk*), and root traces (Rt). Sandy-beach deposits are dominated by *Psilonichnus* (*Ps*). Intertidal-lagoonal deposits may exhibit *Ophiomorpha* (*Op*), fiddler crab burrows (Fc) and *Upogebia* burrows (*Up*). Shallow-subtidal calcarenites may contain *Ophiomorpha* (*Op*), *Skolithos* (*Sk*), *Conichnus* (*Cn*), and *Planolites* (*Pl*). Deep-subtidal deposits host *Fuersichnus* (*Fu*), *Helicodromites* (*He*), *Planolites* (*Pl*), *Rhizocorallium* (*Rh*), *Thalassinoides* (*Th*), *Teichichnus* (*Te*), and *Chondrites* (*Ch*).

scrutiny (e.g. Curran, 1984, 1992, 1994, 2007; Curran and White, 1991, 2001). These studies allow comparisons between Pleistocene and Holocene deposits and their modern analogues, and documented distribution of biogenic structures from coastal dunes to sandy beaches, and intertidal and shallow-subtidal environments (Fig. 11.3). As noted by Curran (2007), tropical carbonate environments are extremely rich in biodiversity. However, their ichnological record is of relatively low diversity, probably as a result of taphonomic overprints, such as domination of burrows (*Ophiomorpha*) of deep-tier callianassids.

Coastal-dune deposits in tropical settings consist of large-scale, planar cross-stratified calcarenite with multiple truncation surfaces (Carew and Mylroie, 2001). In the Bahamas, the dunal ichnocoenosis is the most diverse of all trace-fossil suites (Curran and White, 2001; Curran, 2007). Root traces (Fig. 11.4a) are the most abundant, and may lead to complete obliteration of the primary fabric in the case of vegetated dunes showing paleosol development. Animal traces are represented by many different arthropod structures, including cluster burrows attributed to sphecid wasps, stellate burrows (*Cellicalichnus*) of halictid bees (Fig. 11.4b), and vertical insect or spider burrows (*Skolithos*) (Fig. 11.4c), as the most common structures. Land hermit crab trackways (*Coenobichnus*) are present also (Walker *et al.*, 2003), together with burrows constructed by the land crab *Gecarcinus lateralis* (Seike and Curran, 2010). Terrestrial ichnofaunas from tropical carbonates illustrate the *Celliforma* ichnofacies discussed by Genise *et al.* (2000, 2010a) and Melchor *et al.* (2002).

Beach deposits typically consist of calcarenite with abundant shell fragments, with surfaces gently dipping landwards behind the berm. These deposits contain vertical J-, Y-, and U-shaped burrows assigned to *Psilonichnus* and constructed by ghost crabs, such as *Ocypode quadrata* (Frey *et al.*, 1984a; Curran, 1984, 1994, 2007). In contrast to siliciclastic settings, the ghost crab *Ocypode quadrata* typically does not inhabit dunes in the tropics, being restricted to the unvegetated beach backshore zone (Curran and White, 1991; Curran, 2007) (Fig. 11.5a–b). Similar burrows have been documented not only in the backshore calcarenite of the Bahamas Archipelago but also in Bermuda (Curran, 1994) and the Persian Gulf (Knaust, 1997). It has been suggested that some of these crustacean burrows may have been later modified by a hymenopteran which constructed brooding chambers (Martin, 2006). Ichnofaunas from beach-backshore tropical carbonates represent the *Psilonichnus* ichnofacies (Curran, 1994, 2007). Towards the foreshore, high energy is detrimental to infaunal activity, and also reduces the preservation potential of biogenic structures.

Intertidal lagoons under slightly hypersaline conditions and fringed landwards by mangroves are common in the Bahamas (Curran, 1994; Curran and Martin, 2003). Deposits mostly consist of carbonate sands and minor amounts of mud, forming extensive tidal flats that display a topography of mounds and craters produced by the callianassid shrimp *Glypturus acanthochirus* (Curran, 1994, 2007; Curran and Martin, 2003) (see Section 6.6). *Glypturus acanthochirus* burrows are deep, large, and complex, with a downward spiraling morphology. Microbial growth allows mound stabilization and colonization by the shrimp *Upogebia vasquezi* and the fiddler crab *Uca major*, which produce U-shaped, commonly paired, burrows (Fig. 11.6a) and simple obliquely vertical burrows (Fig. 11.6b) with a basal bulbous turnaround, respectively. *Uca* trackways are common also (Fig. 11.6b). Large amounts of pellets (fecal, feeding, and excavation) are typically produced (Curran, 1994,

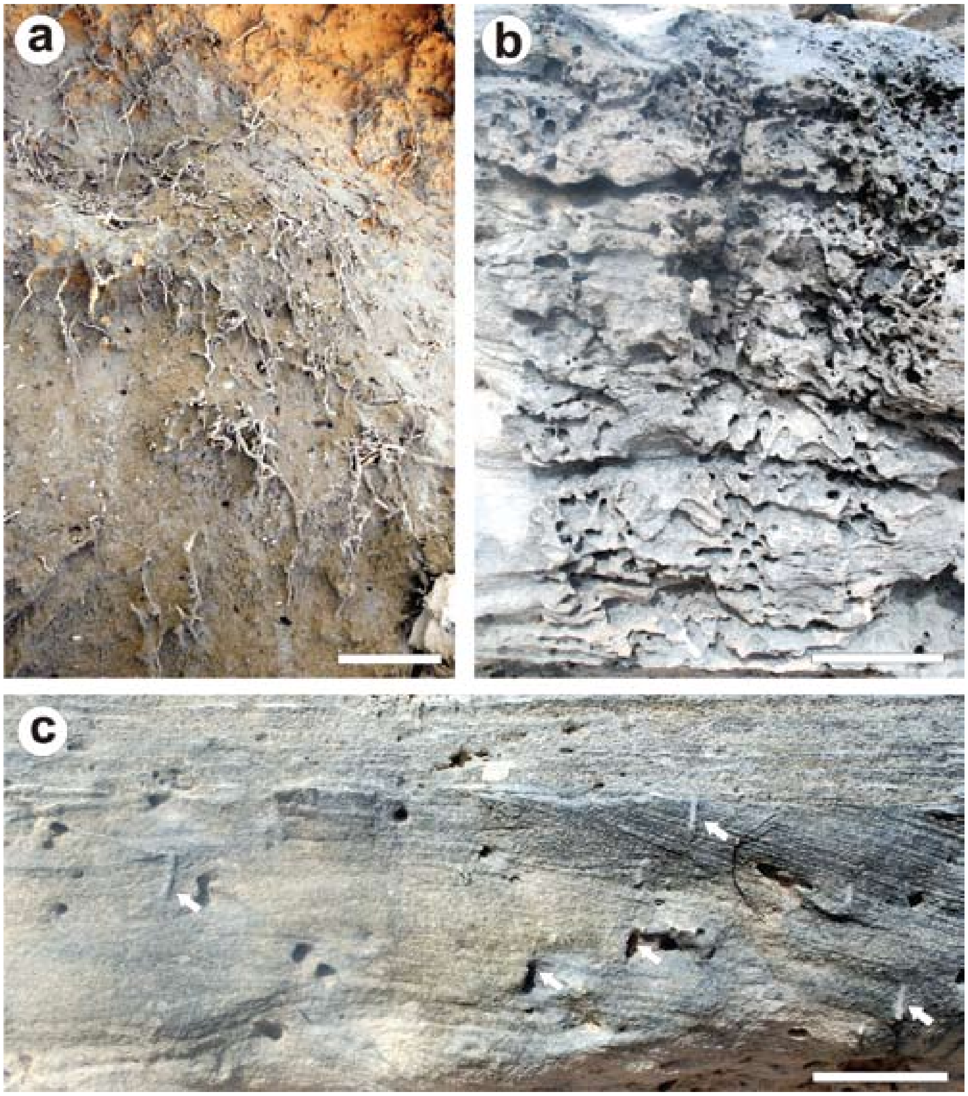

Figure 11.4 Characteristic trace fossils of coastal-dune deposits in tropical settings. (a) High density of rhizomorphs (or rhizoliths). Pleistocene, Cockburn Town Member, Grotto Beach Formation of San Salvador Island, Bahamas. Scale bar is 20 cm. (b) Stellate burrows (*Cellicalichnus*) probably produced by halictid bees Holocene, Hanna Bay Member, Rice Bay Formation of San Salvador Island, Bahamas. Scale bar is 10 cm. (c) Vertical insect or arachnid burrows attributed to *Skolithos* (arrows). Holocene, Hanna Bay Member, Rice Bay Formation of San Salvador Island, Bahamas. Scale bar is 10 cm. See Curran and White (2001).

Figure 11.5 Cast of modern Y-shaped burrows constructed by the ghost crab *Ocypode quadrata* in beach backshore deposits. These burrows would be assigned to *Psilonichnus upsilon* in the fossil record. Specimens housed at the Gerace Research Station of San Salvador Island, Bahamas. Scale bars are 10 cm. See Curran and White (1991) and Curran (2007).

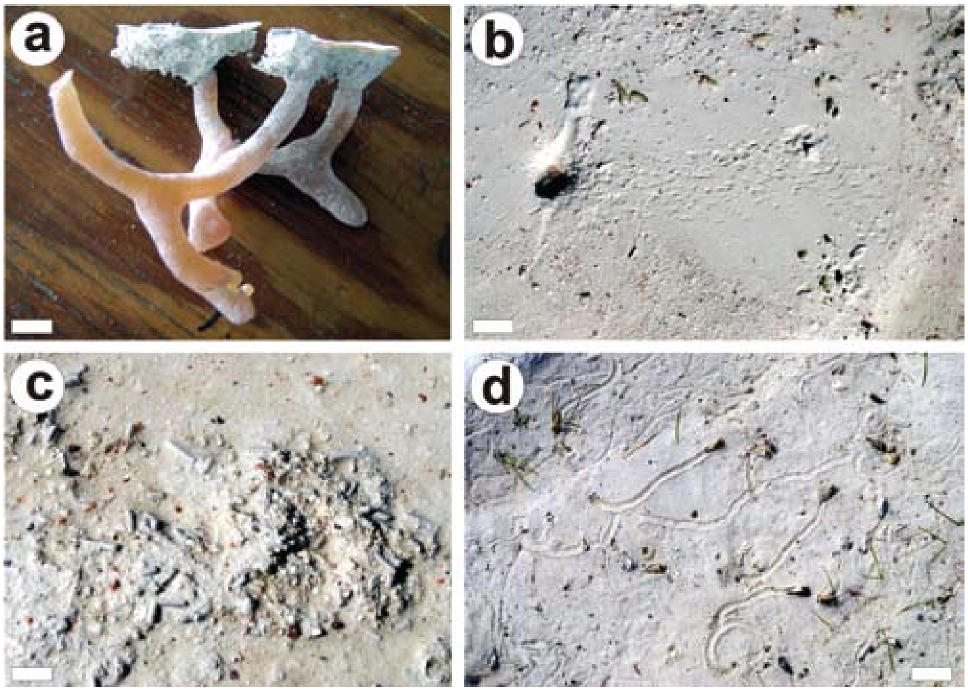

Figure 11.6 Biogenic structures in a modern carbonate lagoon flanked by mangroves. Pigeon Creek, San Salvador Island, Bahamas. (a) U-shaped, paired burrows of the shrimp *Upogebia vasquezi*. Scale bar is 1 cm. (b) Opening of simple vertical burrows and associated trackway of the fiddler crab *Uca major* Scale bar is 2 cm. (c) Concentration of *Uca major* feeding pellets. Scale bar is 1 cm. (d) Grazing trails of batillarid gastropods that in the fossil record would be assigned to the ichnogenus *Archaeonassa*. Scale bar is 2 cm. See Curran and Martin (2003).

2007; Curran and Martin, 2003) (Fig. 11.6c). During low tide, batillarid gastropods produce grazing trails in mangrove areas (Fig. 11.6d). Similar lagoonal ichnofaunas have been documented in the Seychelles (Farrow, 1971) and Belize (Dworschak and Ott, 1993). Large spiraling callianassid burrows occur in the Seychelles. In Belize, the mounded topography occurs in intertidal channels and subtidal zones of the lagoon, and is also the result of *Glypturus acanthochirus*. Mangrove channels include U- and Y-shaped vertical burrows of the shrimps *Alpheus floridanus* and *A. heterochaelis*. Burrows of the shrimp *Neocallichirus grandimana* occupy shallow tiers in intertidal zones. Other structures in Belize lagoonal deposits are J- and U-shaped burrows of *Corallianassa longiventris* and simple burrows of *Axiopsis serratifrons*.

In the fossil record, a common ichnotaxon in calcarenites of subtidal, higher energy settings is *Conichnus conicus* (Pemberton and Jones, 1988; Curran, 1994; Curran and White, 1997). This ichnotaxon is commonly present in planar cross-bedded calcarenites formed in back-reef and shallow-subtidal shoaling bar and tidal-channel settings. *Conichnus conicus* has often been attributed to the upward escape-burrowing activity of sea anemones, although other possibilities exist and should be considered (Curran and White, 1997; Buck and Goldring, 2003). Fossil burrows of *Upogebia vasquezi* also occur in Pleistocene lagoonal-margin deposits of the Bahamas (Curran and Martin, 2003). Extensive *Thalassinoides* systems can also be common, as described by Monaco and Giannetti (2002) from the Jurassic of the Southern Alps, Italy. Although Pleistocene lagoonal ichnofaunas are of low diversity, those in lagoonal calcarenites of Grand Cayman Island are more diverse, including *Bergaueria*, *Ophiomorpha*, and *Skolithos*, among other ichnogenera, illustrating the *Skolithos* ichnofacies (Pemberton and Jones, 1988; Jones and Pemberton, 1989). Jurassic lagoonal lithographic limestones of the Cerin fossil site (France) show a more complex pattern of trace-fossil distribution, in which unburrowed intervals alternate with beds containing polychaete (*Tubularina lithographica*) and crustacean burrows (*Rhizocorallium irregulare* and *Thalassinoides suevicus*) (Gaillard *et al*., 1994). Also, a relatively diverse ichnofauna containing *Polarichnus*, *Palaeophycus*, *Skolithos*, *Bergaueria*, and *Helicodromites*, among other forms, was documented in Silurian intertidal deposits (Narbonne, 1984).

Open-marine shallow-subtidal carbonates in tropical environments host an incredibly diverse array of planktonic, nektonic, and benthic organisms. However, the preservation potential of the traces of many of these organisms is low. In fact, the ichnological record of Bahamian Pleistocene subtidal calcarenites is one of rather low diversity, with a clear bias towards deep-infaunal vertical burrows, such as *Ophiomorpha* (Fig. 11.7a–b) and, more rarely, *Skolithos*, representing the *Skolithos* ichnofacies (Curran, 1992, 1994, 2007). Similar ichnofaunas occur in high-energy shoals where *Ophiomorpha* and *Diplocraterion* dominate (Fürsich, 1998). In areas of relatively low energy during fair-weather times, but sporadically affected by storms, two contrasting suites occur as in the case of storm-influenced siliciclastic settings (see Section 7.1). *Ophiomorpha* is common in tempestites, while *Thalassinoides*, *Zoophycos*, and *Planolites* predominate in background deposits (Fürsich, 1998).

Under lower-energy conditions, such as those in distal carbonate ramps and platforms, more diverse suites dominated by horizontal trace fossils may be preserved, including *Thalassinoides*,

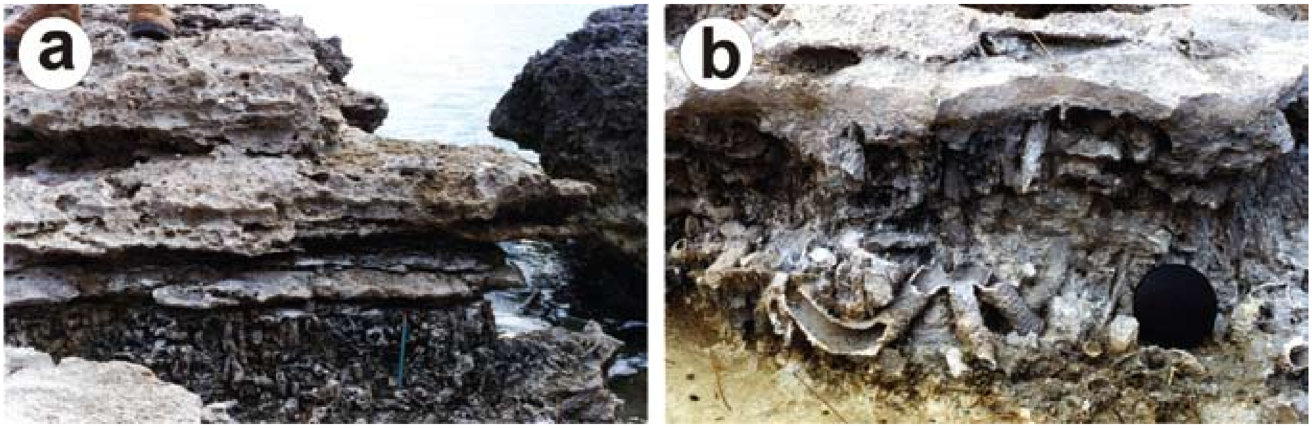

Figure 11.7 *Ophiomorpha nodosa* in carbonate sandy patches formed between reef areas. Pleistocene, Cockburn Town Member, Grotto Beach Formation of San Salvador Island, Bahamas. (a) General view. Pencil (lower center) is 16 cm. (b) Close-up showing dense mazes of *Ophiomorpha nodosa*. Lens cap is 5.5 cm. See Curran (1994, 2007).

Figure 11.8 Bioerosion by sea urchin in beachrock, French Bay, San Salvador Island, Bahamas. Scale bar is 2 cm.

Rhizocorallium, *Fuersichnus*, *Protovirgularia*, *Helicodromites*, *Palaeophycus*, *Teichichnus*, *Cruziana*, and *Chondrites*, among other ichnogenera (e.g. Narbonne, 1984; Maples and Archer, 1986; Fraaye and Werver, 1990; Fürsich, 1998). *Thalassinoides* is a common elite trace fossil in subtidal carbonates (e.g. Mángano and Buatois, 1994). These low-energy settings are represented by the *Cruziana* ichnofacies. *Chondrites* and, to a lesser extent, *Planolites* and *Thalassinoides*, are common in marly-limestone rhythmites formed under low-energy, dysaerobic conditions (e.g. Olóriz and Rodríguez-Tovar, 1999a).

Bioerosion is also important in shallow-marine carbonate settings. In particular, beachrock, which typically occurs discontinuously in the intertidal zone (Ginsburg, 1953), provides a substrate for many bioeroding organisms. These include sea urchins (Fig. 11.8), clionid sponges, polychaetes, bivalves, and sipunculans, among other organisms (e.g. Moran and Reaka, 1988; Stearley and Ekdale, 1989). Beachrock bioeroders may be highly variable depending on the complexity of the intertidal area (Stearley and Ekdale, 1989). On gently dipping regular surfaces, endolithic populations tend to be of higher density and lower diversity than those in more stepped and complex beachrock, comprising a network of pools and channels. In addition, cavities produced by bioeroders provide a shelter for a sessile and motile cryptic fauna that protect themselves from predation and physical stress (Moran and Reaka, 1988).

11.1.2 REEFS

Reefs are one of the most appropriate ecosystems for the establishment of bioeroding organisms (Warme, 1977; Bromley, 1978; Perry and Hepburn, 2008). Bioeroders play two main roles in reefs: (1) they effectively weaken the substrate, making it more susceptible to weathering and erosion, and (2) they may produce large amounts of sediment as a by-product (Perry and Hepburn, 2008). Sponges (e.g. *Cliona*) are typically the most important infaunal bioeroders, substantially contributing to substrate degradation. Sponges produce dense networks of inter-connected chambers up to several centimeters deep, included in the ichnogenus *Entobia* (Bromley and D'Alessandro, 1990). Bivalves, although producers of single discrete boreholes (ichnogenus *Gastrochaenolites*), are also effective agents of bioerosion in reefs (Perry and Hepburn, 2008). Boring polychaetes, producers of the ichnogenus *Trypanites* among other ichnotaxa, are small and, in comparison with sponges and bivalves, do not extract significant amounts of $CaCO_3$ (Perry and Hepburn, 2008). However, they may modify the substrate, facilitating bioerosion by other agents (Perry and Hepburn, 2008) and, in some cases, they have been documented to contribute significantly to bioerosion (Hein and Risk, 1975; Klein *et al.*, 1991). Other common bioeroders, albeit volumetrically of less impact, are chitons, cirripedians, and gastropods. Also, because coral reefs are living substrates, they are ideal for bioclaustration structures (see Section 1.4.14). Examples of these include cirripedian, bivalve, gastropod, and polychaete borings (Ekdale *et al.*, 1984).

Earlier studies in Bermuda did not detect bathymetric zonations of bioerosion structures in modern reefs (Bromley, 1978). However, subsequent work in the Mediterranean Sea demonstrated that shallow-water coral reefs display a higher diversity of borings than their deep-water equivalents, although no changes in abundance were detected (Bromley and D'Alessandro, 1990). Some differences in boring distribution occur at ichnospecific level. For example, *Entobia paradoxica* is abundant only in deep reefs, while *E. volti* and *E. gigantea* are restricted to coastal environments.

Although most bioerosion studies on reefs have been undertaken in modern environments, there are a few detailed analyses dealing with fossil material. James *et al.* (1977) documented the ichnogenus *Trypanites* in Lower Cambrian archaeocyatid reefs. Bertling (1997) identified 24 ichnospecies in a Jurassic reef. This highly diverse ichnofauna includes sponge (*Entobia*), polychaete (*Caulostrepsis*, *Maeandropolydora*), bivalve (*Gastrochaenolites*), phoronid (*Talpina*), and cirripedian (*Rogerella*) borings, among other ichnogenera. Sedimentation rate is a major limiting factor. Low sedimentation rates promote intense bioerosion on dead coral, mostly by siphunculids, polychaetes, and lithophagians. With high rates of sedimentation bioerosion is less intense and bivalves become the dominant forms, mostly in living coral (Bertling, 1997). Perry (2000) documented boring distribution in a Pleistocene fringing reef complex in Jamaica. This fossil reef contains *Entobia*, *Gastrochaenolites*, *Maeandropolydora*, and *Trypanites*. Diverse assemblages of borers, dominated by sponges and polychaetes, with bivalves being locally important, occur in back-reef/lagoon facies. Shallow fore-reef facies are dominated by borings produced by sponges, with polychaete borings being locally important and bivalve borings rare or absent.

11.1.3 SHELF AND DEEP-SEA CHALK

The term "chalk" refers to pelagic sediment mostly consisting of calcareous nanoplankton (Scholle *et al.*, 1983). Arguably, most ichnological studies in carbonates have focused on chalk (e.g. Bromley, 1967; Frey, 1970, 1972; Frey and Bromley, 1985; Bromley and Ekdale, 1984a, 1986; Ekdale and Bromley, 1984a, 1991). In addition, chalk deposits represent the birthplace of a number of ichnological concepts, such as tiering, ichnofabrics, and ichnoguilds (see Chapter 5). In chalk deposits observations are usually performed in cross-section due to the absence of available bedding planes. In addition, a number of techniques are used in order to visualize biogenic structures in cores (Bromley and Ekdale, 1984a). The combination of very slow rates of sedimentation and fully marine conditions leads to complete biogenic reworking of chalk deposits (Ekdale and Bromley, 1991).

Two main types of chalk deposits can be distinguished, shelf and deep-sea chalk. Shelf chalk forms between water depths of 50 and 300 m, while deep-sea chalk occurs at much greater depths, up to thousands of meters (Scholle *et al.*, 1983). Both are similar in terms of texture and composition because they share the same pelagic components regardless of water depth. However, minority components show some differences. Shelf chalk commonly contains fine detrital particles (e.g. quartz, feldspar), while those formed below the carbonate compensation depth (CCD) contain siliceous organisms, such as diatoms and radiolarians. In any case, the most significant controls on the infauna are linked to post-depositional processes (e.g. early cementation and erosion by currents; Ekdale and Bromley, 1984). In general, deep-sea chalk is compositionally and texturally more homogeneous.

Shelf-chalk ichnofaunas have been documented in Upper Cretaceous outcrops of Europe (England, Denmark) and United States (Alabama, Kansas) (Bromley, 1967; Kennedy, 1967, 1970, 1975; Frey, 1970, 1972; Frey and Bromley, 1985; Bromley and Ekdale, 1984a; Ekdale and Bromley, 1984, 1991) (Box 5.2). Crustacean burrow systems, such as *Thalassinoides* (Fig. 11.9), are dominant in shelf chalk (Ekdale and Bromley, 1984). Preferential preservation of these systems results from differential cementation or silicification of burrow fills, commonly accompanied by changes in colors, leading to the formation of elite trace fossils (Bromley and Ekdale, 1984a; Bromley, 1990, 1996) (see Section 5.2.2). Extensive development of omission surfaces and hardgrounds is conducive to the establishment of pre-omission, omission, and post-omission suites, which may be delineated based on the morphology and architecture

Figure 11.9 Trace fossils from chalk. Deep-tier *Thalassinoides* isp. and *Chondrites* isp. Upper Cretaceous, Austin Chalk, east of Austin, central Texas, United States. Scale bar is 1 cm.

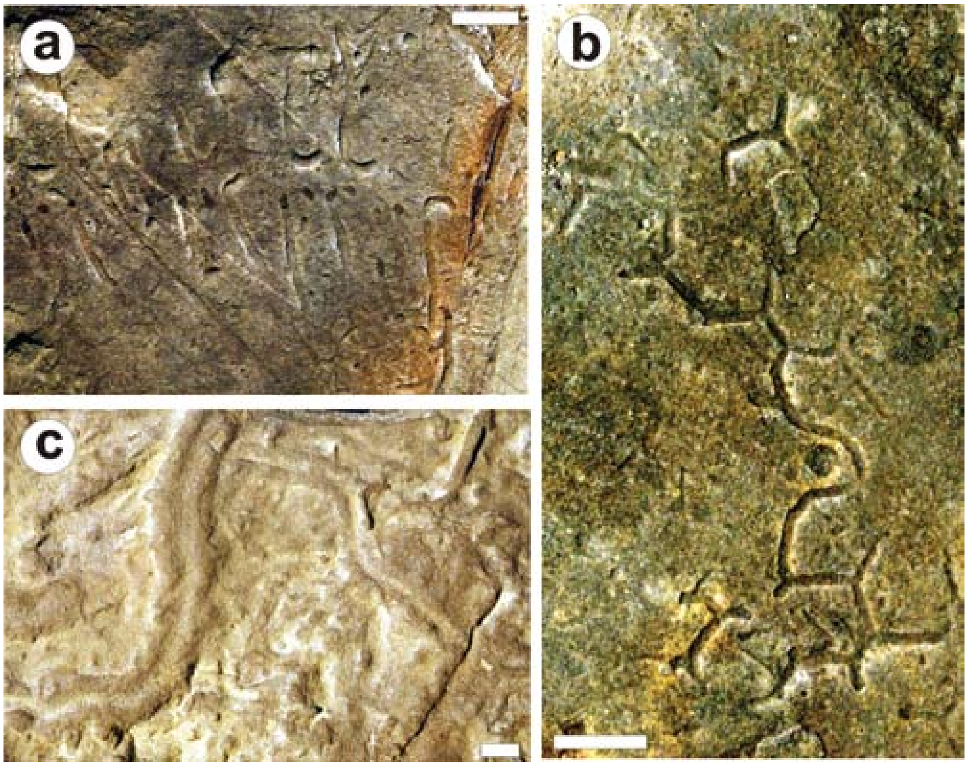

Figure 11.10 Trace fossils preserved at the base of carbonate turbidites. Eocene, Punta Carnero Formation, Margarita Island, Venezuela. (a) *Desmograpton* isp. (b) *Megagrapton submontanum*. (c) *Scolicia strozzi*. Scale bars are 1 cm.

of the associated *Thalassinoides* systems. Pre-omission burrows are commonly ideomorphic (e.g. *T. suevicus*). With progressive cementation and formation of calcareous nodules (omission and post-omission suites), burrows of irregular architecture having abundant constrictions (e.g. *T. paradoxicus*) tend to dominate (Bromley, 1967; Kennedy and Garrison, 1974). Other crustacean structures, such as *Ophiomorpha* and *Gyrolithes*, may occur as subordinate components (Bromley and Ekdale, 1984a). Feeding trace fossils (e.g. *Chondrites*, *Zoophycos*, *Planolites*, *Teichichnus*) are relatively common, but are less conspicuous because they are not usually affected by differential cementation (Bromley and Ekdale, 1984a). Another typical structure is the large burrow *Bathichnus paramoudrae*, which has been linked to rapid sedimentation (Nygaard, 1983). Bioerosion is commonly both in hardground surfaces and invertebrate shells (e.g. Bromley, 1970, 1979).

Deep-sea chalks are known almost exclusively by the study of deep-sea cores from the southwest Pacific, Mediterranean, Caribbean, and Philippine seas, as part of the Deep-Sea Drilling Project (e.g. Ekdale, 1977, 1978, 1980). The age of these deposits ranges from late Mesozoic to Holocene (Scholle *et al.*, 1983). Feeding trace fossils, such as *Planolites*, *Zoophycos*, and *Chondrites*, are dominant (Ekdale and Bromley, 1984a). Other differences with respect to their shallow counterparts are the absence of crustacean burrows and substrate-controlled suites, as well as the lower ichnodiversity. However, the latter feature may simply reflect the small width of cores (Ekdale and Bromley, 1984a).

11.1.4 CARBONATE TURBIDITES

The ichnology of carbonate turbidites is poorly understood and only a few studies have been undertaken. Eocene carbonate turbidites from Margarita Island (Venezuela) contain a moderately diverse ichnofauna dominated by graphoglyptids, such as *Paleodictyon*, *Helminthorhaphe*, *Desmograpton* (Fig. 11.10a), *Megagrapton* (Fig. 11.10b), *Protopaleodictyon*, and *Urohelminthoida* (Muñoz, 1986; Muñoz *et al.*, 1997). Other elements include *Scolicia* (Fig. 11.10c) and *Thalassinoides*. In contrast to siliciclastic turbidites of similar age, ichnodiversity and abundance seem to be lower. Jurassic carbonate turbidites of Morocco also contain graphoglyptids (*Paleodictyon*), but feeding structures, such as *Teichichnus*, *Zoophycos*, and *Chondrites*, are dominant (Ekdale and Warme, 1975). In addition, studies in Cretaceous–Paleocene carbonate turbidites in Italy suggest that diagenetic processes may favor preservation of full-relief structures, in comparison with the typical semirelief preservation which is dominant in siliciclastic turbidites (Powichrowski, 1989).

11.2 ROCKY SHORELINES

Rocky shorelines are extensive in modern environments (one third of the world's present coastlines), but have not been recognized in the fossil record to the same degree (Johnson, 1988, 2006). Bioerosion is extremely common in rocky shorelines, particularly in those formed by limestone (Fig. 11.11a–c) and represented by the *Trypanites* ichnofacies, the archetypal association in these settings. Although other substrates

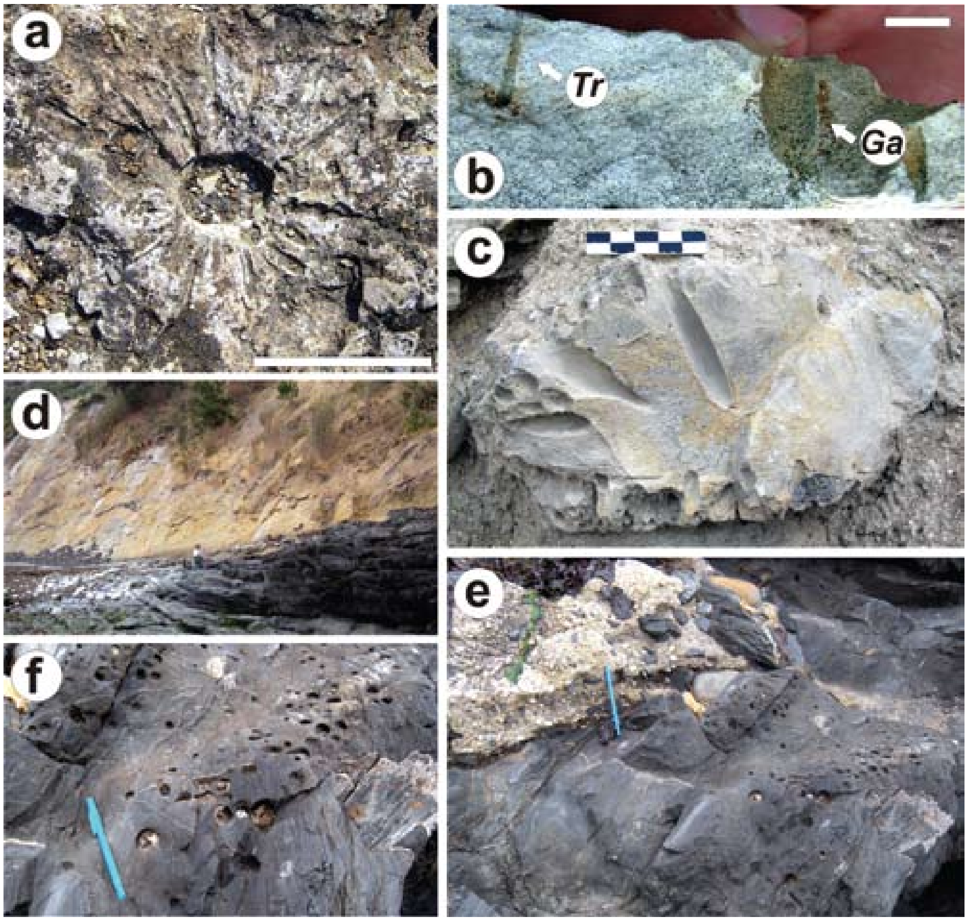

Figure 11.11 Trace fossils in rocky shorelines (a) *Entobia cracoviensis*. A large chambered sponge boring formed in a Late Cretaceous abrasion platform cut into Upper Jurassic limestone. Upper Cretaceous, Bonarka Quarry, Cracow, Poland. See Bromley *et al.* (2009a). Scale bar is 5 cm. (b) *Trypanites* isp. (*Tr*) and *Gastrochaenolites* isp. (*Ga*) in a rocky shoreline formed during a Middle Miocene transgression. Borings are emplaced in an Upper Jurassic limestone. Skotniki Quarry, Holy Cross Mountains, Poland. Scale bar is 1 cm. (c) Cliff conglomerate clast containing deep borings of *Gastrochaenolites* isp. Middle Miocene, Skotniki Quarry, Holy Cross Mountains, Poland. See Radwański (1969). (d) General view of Cretaceous shoreface sandstone (Quiriquina Formation) overlying the Upper Paleozoic metamorphic basement. Cocholgue, Chile. See Buatois and Encinas (2011). (e) Detailed view of the contact showing several specimens of *Gastrochaenolites* isp. penetrating the metamorphic basement. Pen is 16 cm. See Buatois and Encinas (2011). (f) Close-up of *Gastrochaenolites* isp. Pen is 16 cm. See Buatois and Encinas (2011).

Box 11.1 Ichnology of a Pliocene rocky shoreline in Rhodes, Greece

Pliocene rocky coasts of the Island of Rhodes have been closely scrutinized to elucidate patterns of distribution of bioerosion structures. A wide variety of habitats were identified along a transgressed rocky shoreline, including cliff-foot platforms, steep surfaces along cliff-lines, caves, and overhangs. Thirty one ichnospecies were recognized, belonging to the ichnotaxa *Caulostrepsis*, *Entobia*, *Gastrochaenolites*, *Gnathichnus*, *Oichnus*, *Radulichnus*, *Rogerella*, and *Trypanites*, among others. These borings can be ascribed to living tracemakers with different degrees of confidence. The bivalves *Lithophaga lithophaga*, *Jouannetia semicaudata*, *Gastrochaena dubia*, and *Petricola lapicida* are producers of different ichnospecies of *Gastrochaenolites*. The endolithic sponge *Aka* sp. and several species of clionid sponges are producers of different *Entobia* ichnospecies. Six ichnoguilds were recognized. Ichnoguild I is the most superficial and consists of the rasping traces *Radulichnus* and *Gnathichnus*, produced mechanically by algae-browsing mollusks and echinoderms. Ichnoguild II occurs immediately below ichnoguild I, and includes *Centrichnus* and *Renichnus*, produced by sessile mollusks etching the surface of the substrate chemically. Ichnoguild III is represented by shallow-tier suspension-feeder sponge borings illustrated by several *Entobia* ichnospecies. Ichnoguild IV consists of worm borings included in *Trypanites*, *Caulostrepsis*, and *Maeandropolydora*, which record various feeding strategies. Ichnoguild V records the activity of borer bivalves, and is represented by *Gastrochaenolites* and *Phrixichnus*. Finally, Ichnoguild VI is illustrated by the predator boring *Oichnus*. Two main associations are identified. The *Entobia* association occurs in the cliff surface, and records the activity of the deeper tiers. The *Gnathichnus* association is present on the surface of rapidly buried shell material, allowing for the preservation of very shallow-tier rasping borings.

Reference: Bromley and Asgaard (1993b).

may be bioeroded, diversity and abundance of structures is typically lower (Fig. 11.11d–f). Bathymetric gradients from supratidal to subtidal settings are commonly displayed by modern bioeroders (Lewis, 1964; Stearley and Ekdale, 1989), and similar trends have been found in the fossil record (e.g. Bromley and Asgaard (1993b) (Box 11.1).

The inclination of the rock surface plays a role in controlling colonization by borers (Johnson, 2006). Time-averaged

Box 11.2 Volcanic eruption, bioturbation, and ash-layer preservation in the South China Sea

Excellent ichnological work was done following the eruption of Mount Pinatubo (Philippines) in 1991. The volcanic ash produced during this eruption was transported westward to the South China Sea, strongly affecting the deep-sea fauna. The resultant ash layer is up to 10 cm thick, and covers an area of more than 400 000 km^2. Because volcanic ash is barren of organic matter, benthic food availability was restricted to newly produced organic flocs. In addition, deposition of ash layers, at least 3 cm thick, diminished the oxygen diffusion into the sediment below, leading to anoxia in the interstitial waters. Also, as ash consists of angular to subrounded grains exhibiting a granular behavior different from that of mud, unlined burrows tend to collapse. As a result, organisms exhibited a number of adaptations. While surface grazers disappeared, deep burrowers reopened their connection to the sea floor and were able to survive. Bioturbators interacted with the ash layer in three main ways. Some were able to dig through the ash layer, producing significant mixing. In other cases, animals reworked the ash layer from below, as illustrated by the echinoid tracemaker of *Scolicia*, which can completely mix layers up to 6 cm thick. Finally, other organisms mixed the layer from above. The preservation of the ash layer is highly variable across the South China Sea. In general, ash deposits thinner than 1 mm have not been observed as a continuous layer, while an approximately 2 mm layer is patchily bioturbated. In addition, a number of factors control preservation, and allow four main provinces to be distinguished: (1) In areas of high primary production along the Philippines margin, mixing of the layer is intense because the benthic fauna is adapted to variable grain sizes and rapid deposition. (2) In areas affected by turbidity currents and hyperpycnal flows typical of canyons in front of river margins, rapid deposition allows preservation of the ash layer. (3) In areas with low amounts of benthic food, the ash is preserved due to limited mixing. (4) In the central part of the South China Sea, the ash is thinner than 3 cm and the benthic food content is high, resulting in less preservation potential for the ash layer. This work opens new perspectives to understand how benthic organisms respond to catastrophic events in basins affected by explosive volcanism.

Reference: Wetzel (2009).

communities seem to be more common in low-angle to horizontal surfaces. High topographic relief areas tend to contain more rapidly emplaced suites that form during a short span coeval with rising sea level. As a result, boring overlap is less common on vertical to high-angle rock surfaces than in horizontal ones. Some rocky shorelines are exposed to wave action, while others occur in more protected areas (Johnson, 2006; Johnstone *et al*., 2006). Open rocky shorelines exposed to wave action may be extensively bioeroded, containing dense concentrations of organisms that bore or nestle to shelter from waves (Johnson, 2006). Sediments associated with storm-swept rocky shoreline ichnofaunas tend to be sparsely bioturbated and contain typical ichnotaxa of high-energy settings, such as *Macaronichnus*, *Ophiomorpha*, and *Skolithos*, illustrating a *Skolithos* ichnofacies (Johnstone *et al*., 2006). However, continuous deepening during transgression leads to replacement by elements of the *Cruziana* ichnofacies (e.g. *Asterosoma*, *Chondrites*), signaling a change to lower-energy conditions. Overall bioturbation is sparse in sediments associated with storm-swept rocky shorelines. Rocky shorelines formed in protected environments may enclose sediments which are slightly more bioturbated than their storm-swept equivalents, but ichnodiversity remains very low and suites are dominated by opportunistic ichnotaxa (*Ophiomorpha*, *Palaeophycus*). With transgression, sheltered shorelines become more exposed to open-ocean storms and fair-weather waves, and ichnodiversity remains significantly low. The degree of bioturbation decreases as a result of higher-energy conditions.

11.3 VOLCANIC TERRANES

Present knowledge on the ichnology of volcanic terranes is patchy at best. The absence of studies most likely results from the common scarcity of trace fossils in environments strongly affected by volcanism, particularly in proximal zones of volcanic arcs (Crimes, 1970b), and the lower number of paleoenvironmental analyses dealing with volcaniclastic successions in comparison with siliciclastic and carbonate rocks. However, modern studies in marine basins affected by volcanism are providing valuable data for better understanding of benthic fauna response to volcanic eruptions (Wetzel, 2009) (Box 11.2).

A number of ichnological studies were focused on Ordovician volcanic-arc related rocks of Argentina (Mángano *et al*., 1996c; Mángano and Buatois, 1996, 1997). Although trace fossils are relatively uncommon, dense assemblages occur locally, suggesting short-term colonization windows during pauses in volcaniclastic sedimentation (Fig. 11.12a). Slope apron successions include *Planolites montanus*, *Palaeophycus tubularis*, and *Helminthopsis abeli* in overbank deposits adjacent to a submarine channel. Shallow-marine successions include *Cruziana furcifera*, *Helminthopsis* isp., *Palaeophycus tubularis*, *Phycodes* isp., and *Planolites beverleyensis* in tempestites. Low-ichnodiversity levels probably result from overall environmental instability in volcanic-arc related settings. A large supply of volcaniclastic material in high-gradient areas promotes frequent sediment gravity flows that inhibit the establishment of a diverse resident fauna. These deposits may locally contain burrows that

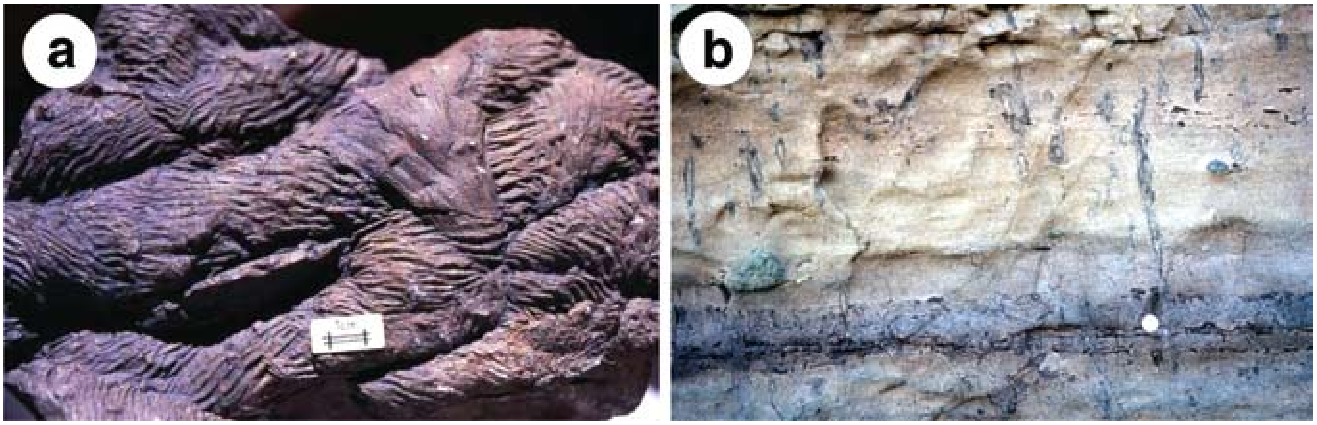

Figure 11.12 Trace fossils in volcaniclastic-flow deposits. (a) *Cruziana furcifera* cross-cut by *Phycodes* isp. preserved at the base of a shallow-marine volcaniclastic sandstone. Lower Ordovician, Loma del Kilómetro Member, Suri Formation, Punta Pétrea, Chaschuil, northwest Argentina. See Mángano *et al*. (1996c). (b) Deep *Rosselia socialis* penetrating from a colonization surface at the top of a shallow-marine volcaniclastic sandstone. Upper Permian, Kiama Sandstone Member, Broughton Formation, Pheasant Point, southern Sydney Basin, eastern Australia. Lens cover is 5.5 cm. See Shi and Weldon (2002).

penetrate from the top of the event layer reflecting opportunistic colonization (Fig. 11.12b).

Silurian carbonate turbidites emplaced in a slope apron adjacent to a volcanic arc contain trace-fossil assemblages that are similar in both overall features and taxonomic composition (Soja, 1991). This ichnofauna contains a few poorly specialized ichnotaxa (*Palaeophycus*, *Planolites*, *Chondrites*). Recurrent local catastrophes were regarded as the most important limiting factor affecting the benthic fauna. Similarly, Cretaceous deep-marine deposits of Turkey, rich in volcaniclastic grains make of sharp-edged glass shards, contain an unusually low diversity ichnofauna (Uchman *et al*., 2004a). It has been argued that those materials were unsuitable for the development of a bacterial film that is essential for the infaunal food chain, and that hydrochemical conditions and the release of poisonous substances due to active volcanism were detrimental to benthic life (Uchman *et al*., 2004a). On the other hand, Cretaceous volcaniclastic shallow-marine deposits in Antarctica emplaced in a most distal position with respect to the volcanic arc contain more diverse suites that resemble those from similar environments in siliciclastic settings (Scasso *et al*., 1991).

Part III A matter of time

12 Trace fossils in sequence stratigraphy

> For my part, following out Lyell's metaphor, I look at the natural geological record, as a history of a world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines.
>
> Charles Darwin
> *On the Origin of Species* (1859)

> Trace fossils are proving to be one of the most important groups of fossils in delineating stratigraphically important boundaries related to sequence stratigraphy.
>
> George Pemberton and James MacEachern
> "The sequence stratigraphic significance of trace fossils: examples from the Cretaceous Foreland Basin of Alberta, Canada" (1995)

The appearance of sequence stratigraphy in the late eighties resulted in a revolution in the study of sedimentary rocks. The shift from seismic stratigraphy (Vail *et al.*, 1977) to sequence stratigraphy brought the incorporation of outcrops and cores as sources of data in stratigraphic analysis (Posamentier *et al.*, 1988; Posamentier and Vail, 1988; Van Wagoner *et al.*, 1990). Coincident with this shift, ichnological studies began to emphasize the importance of trace fossils in sequence stratigraphy (e.g. Savrda, 1991b; MacEachern *et al.*, 1992; Pemberton *et al.*, 1992b). In little more than a decade, the field experienced a rapid increase in the number of studies devoted to exploring the applicability of ichnology in refining sequence-stratigraphic analysis (e.g. MacEachern *et al.*, 1992, 1999a, 2007c; Savrda *et al.*, 1993; Taylor and Gawthorpe, 1993; Pemberton and MacEachern, 1995; Ghibaudo *et al.*, 1996; Martin and Pollard, 1996; Buatois *et al.*, 1998d, 2002b; Pemberton *et al.*, 2001, 2004; Carmona *et al.*, 2006). At present, ichnological aspects are currently covered in sequence-stratigraphic textbooks (e.g. Catuneanu, 2006). The aim of this chapter is to provide a detailed review of the applications of ichnology in sequence stratigraphy. Although a large part of this chapter deals with the recognition of discontinuity surfaces in marine siliciclastic successions, we will also cover other topics which are commonly overlooked in the literature. These include characterization of parasequences, parasequence sets, and systems tracts, but also the potential of trace fossils to address sequence-stratigraphic issues in carbonates and continental deposits.

12.1 RECOGNITION OF DISCONTINUITY SURFACES

Recognition of discontinuity surfaces is key to sequence stratigraphy (e.g. Posamentier and Allen, 1993; Catuneanu, 2006), and trace fossils have proven to be particularly useful in this respect (MacEachern *et al.*, 1992; Pemberton *et al.*, 2001, 2004). Identification of these stratal surfaces highlights allogenic processes, which are external to the depositional system, as opposite to autogenic processes, which are internal to the depositional system and lead to the accumulation of environmentally related facies successions. By identifying trace-fossil suites in hard, firm, and xylic substrates of siliciclastic successions, allostratigraphic surfaces can be identified. The recognition of substrate-controlled ichnofacies, such as *Glossifungites, Trypanites*, and *Teredolites*, is critical in identifying stratigraphic discontinuities.

Of the above three ichnofacies, the *Glossifungites* ichnofacies has been the most intensively used in sequence stratigraphy (Fig. 12.1). The *Glossifungites* ichnofacies develops in firm (but unlithified) substrates. In siliciclastic sediments, dehydration is the result of burial and substrates become available for colonization by organisms if exhumed by subsequent erosion (MacEachern *et al.*, 1992) (Fig. 12.2a–b). For carbonates, occurrence of the *Glossifungites* ichnofacies is not necessarily indicative of erosive exhumation because early diagenetic processes may take place at the water–sediment interface (e.g. Bromley, 1975; Mángano and Buatois, 1991).

The elements of substrate-controlled ichnofacies typically cut across a pre-existing softground suite (Fig. 12.2c). Therefore, they reflect new conditions which commonly do not coincide with those controlling early deposition. Thus, the substrate-controlled association develops during a hiatus between the erosive event (which exhumed the substrate) and the deposition of the overlying unit. During such periods of time, the dehydrated and/or cemented bed is colonized by organisms (MacEachern *et al.*, 1992). The *Glossifungites* ichnofacies is generally easy to identify in cores, and is preserved in lithological interfaces (typically mudstone overlain by sandstone or conglomerate). In these cases, sharply defined, unlined wall burrows occur in fine-grained sediments and are passively filled by coarser material from the overlying bed. However, the *Glossifungites* ichnofacies may also occur in sandstone (e.g. Pemberton *et al.*, 2004).

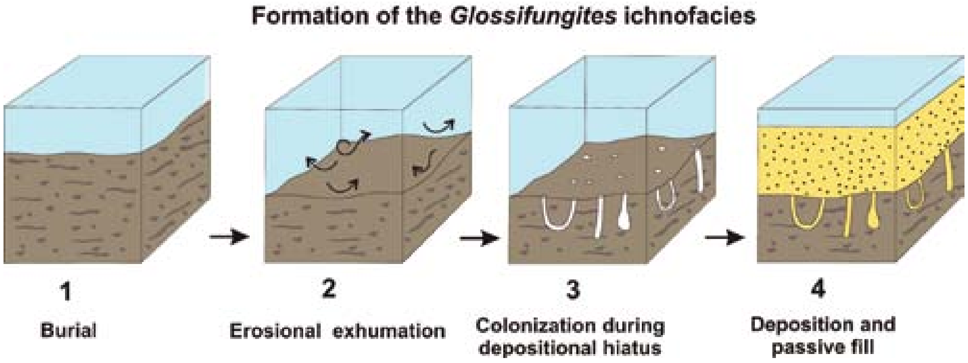

Figure 12.1 Origin of the *Glossifungites* ichnofacies. Modified from MacEachern *et al.* (1992).

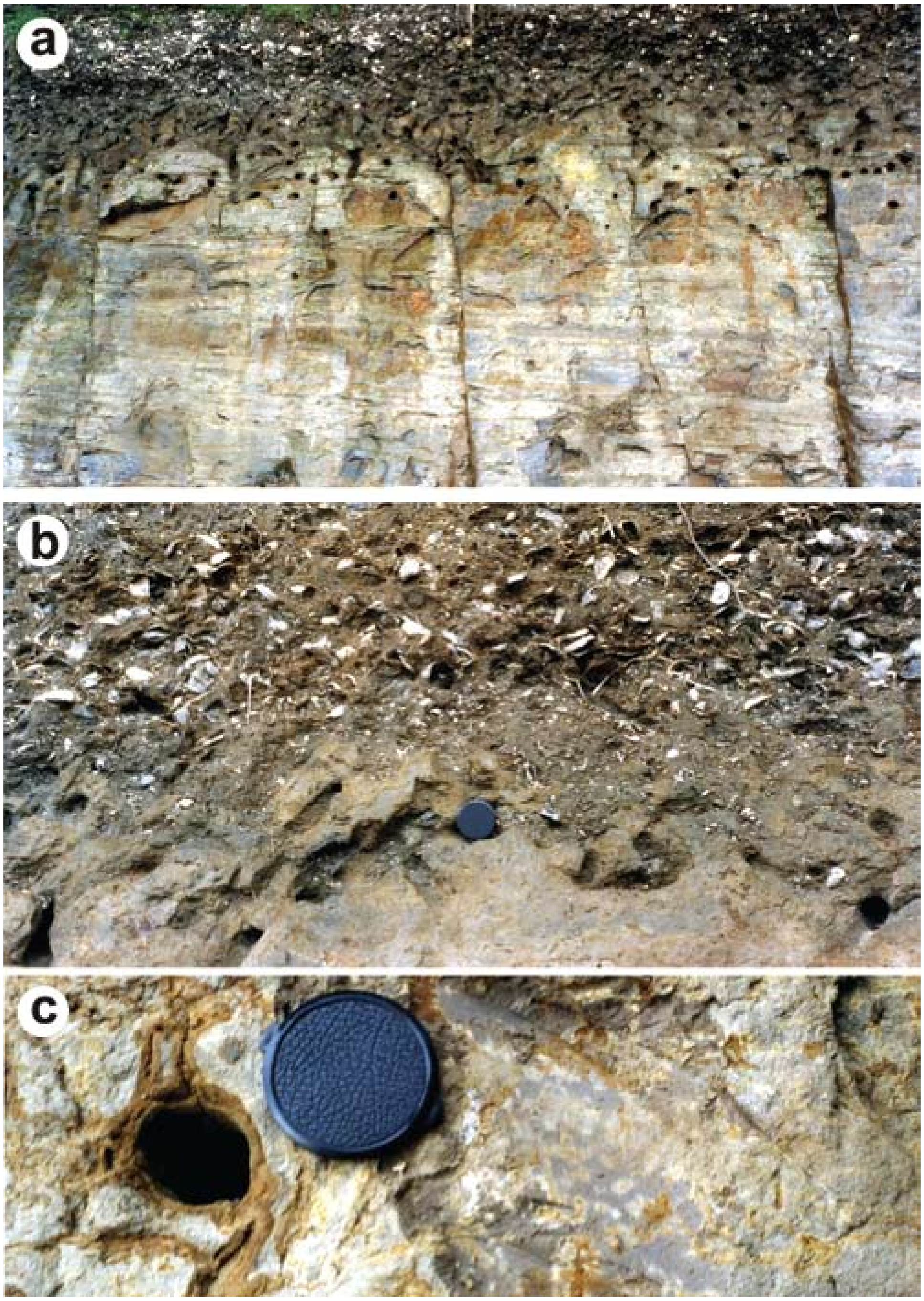

Figure 12.2 Formation of the *Glossifungites* ichnofacies in erosional discontinuities, Holocene, Willapa Bay, Washington, United States. (a) General view of transgressive-lag deposits overlying intertidal-channel deposits with inclined heterolithic stratification (note surfaces gently dipping towards the right). *Thalassinoides* penetrates into the heterolithic deposits from the erosive surface. Pen (lower right) is 16 cm. (b) Close-up showing firmground *Thalassinoides* passively filled with shell fragments from the overlying transgressive lag. Lens cap is 5.5 cm. (c) Firmground burrows overprinted to a poorly defined softground background trace-fossil suite. Lens cap is 5.5 cm. See Gingras *et al.* (2001) for additional information.

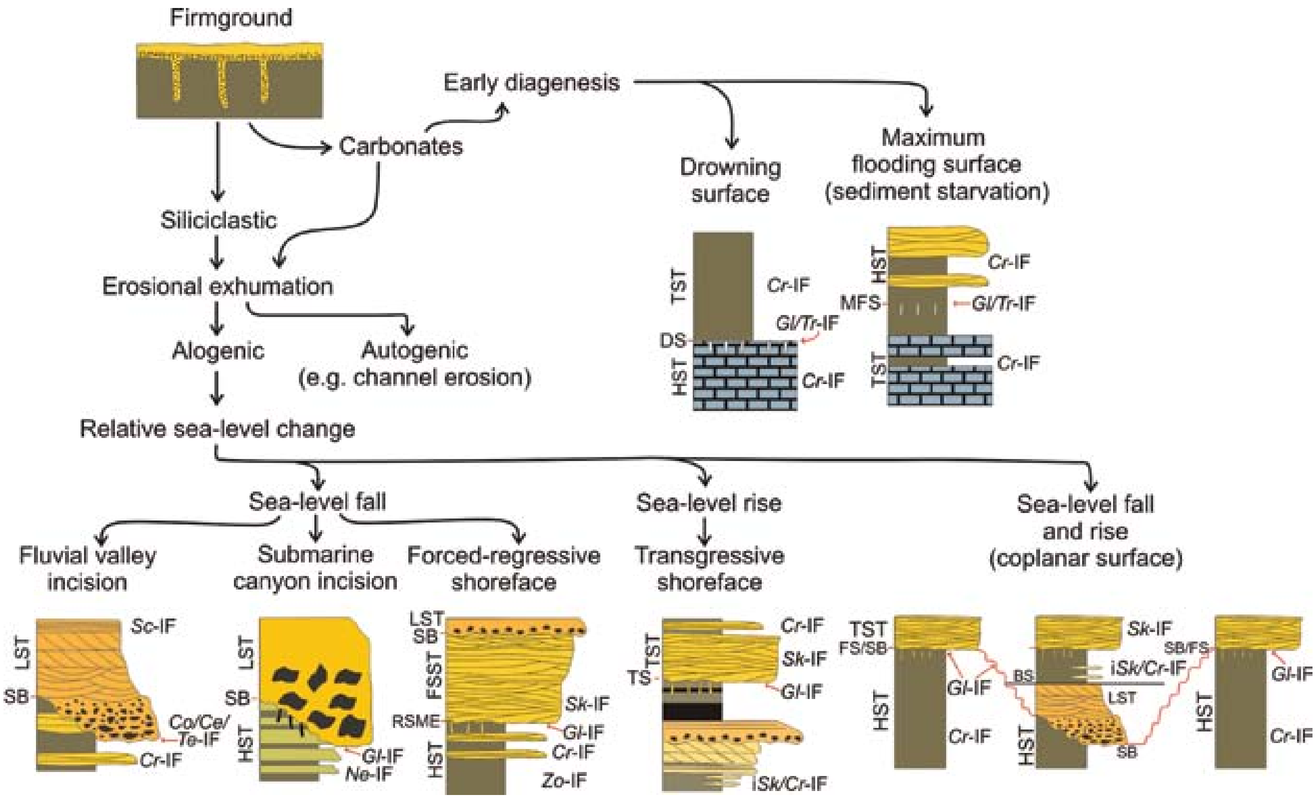

Figure 12.3 Sequence-stratigraphic significance of the *Glossifungites* ichnofacies and associated softground ichnofacies. LST = lowstand systems tract, TST = transgressive systems tract, HST = highstand systems tract, SB = sequence boundary, FS/SB = flooding surface/sequence boundary, TS = transgressive surface, DS = drowning surface, BS = bayline surface, MFS = maximum flooding surface, *Sk*-IF = *Skolithos* ichnofacies, *Cr*-IF = *Cruziana* ichnofacies, i*Cr*/*Sk*-IF = mixed impoverished *Cruziana*/*Skolithos* ichnofacies, *Zo*-IF = *Zoophycos* ichnofacies, *Ne*-IF = *Nereites* ichnofacies, *Gl*-IF = *Glossifungites* ichnofacies, *Gl*/*Tr*-IF = *Glossifungites* or *Trypanites* ichnofacies, *Sc*-IF = *Scoyenia* ichnofacies, *Co*/*Ce*/*Te*-IF = *Coprinisphaera, Celliforma*, or *Termitichnus* ichnofacies.

Whereas identifying substrate-controlled ichnofacies results in the recognition of an erosional discontinuity, an accurate interpretation of such surfaces requires the detailed analysis of the soft substrate trace-fossil assemblages occurring in the underlying and overlying units (Fig. 12.3) (MacEachern *et al.*, 1992; Pemberton *et al.*, 2004). Recognition of vertical changes in softground ichnofaunas allows interpretation of the type or types of sea-level fluctuations involved. Stratigraphic discontinuities can be divided into two major groups, erosional and non-erosional discontinuities. Most ichnological studies on sequence stratigraphy focus on the former group.

12.2 EROSIONAL DISCONTINUITIES

There are several available schemes for subdividing sedimentary packages into systems tracts and placing the sequence boundary (see Catuneanu, 2006). Here, we adopt a model that considers four systems tracts (lowstand, transgressive, highstand, and falling stage) and places the sequence boundary at the base of the lowstand systems tract (Plint and Nummedal, 2000). Erosional discontinuities are subdivided into regressive surfaces of marine erosion, lowstand surfaces of erosion, transgressive surfaces of erosion, and co-planar surfaces of lowstand erosion and transgressive erosion, also known as flooding surfaces/sequence boundaries or FS/SB (Pemberton *et al.*, 1992b; 2004; MacEachern *et al.*, 1992).

12.2.1 REGRESSIVE SURFACES OF MARINE EROSION

The regressive surface of marine erosion is formed due to wave scouring during relative sea-level fall associated with forced regression (Plint and Nummedal, 2000). Forced regressions represent the rapid seaward migration of shoreline and nearshore deposits in response to a relative sea-level fall (Plint, 1988; Posamentier *et al.*, 1992). Forced-regression strata are included in the falling stage systems tract (Plint and Nummedal, 2000). While normal regressions are generally characterized by a gradual progradation of the shoreline during stillstands or highstands (Fig. 12.4a), forced regressions are abrupt and triggered by a drop in sea-level (Fig. 12.4b). In contrast to shorefaces formed during normal regressions, those incised during the falling stage are fairly thin due to diminished accommodation space during sea-level fall (MacEachern *et al.*, 1999a). Shoreface progradation during forced regression occurs irrespective of sediment supply (Catuneanu, 2006).

During forced regressions, wave scouring leads to the exhumation of compacted and dewatered sediments, making a firm

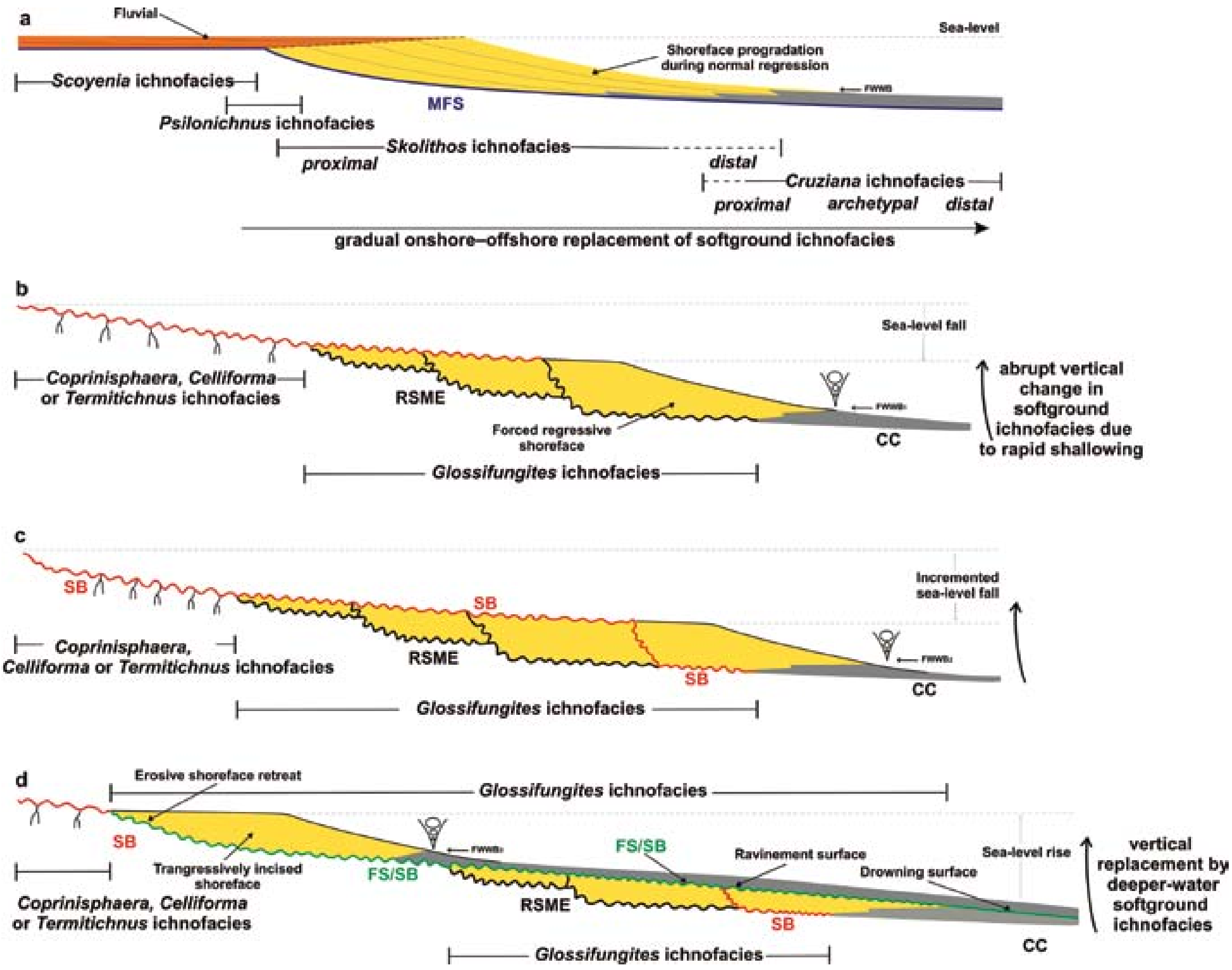

Figure 12.4 Distinction between normal-regressive, and sharp-based (forced-regressive, lowstand, and transgressively incised) shorefaces. (a) Normal-regressive shoreface (highstand systems tract). Vertical softground ichnofacies replacement is gradual due to progressive shallowing. (b) Forced-regressive shoreface (falling stage systems tract). Vertical softground ichnofacies replacement is abrupt due to rapid shallowing. The base of the forced-regressive shoreface is delineated by the *Glossifungites* ichnofacies. (c) Lowstand shoreface (lowstand systems tract). Vertical softground ichnofacies replacement is abrupt due to rapid shallowing. The base of the lowstand shoreface is delineated by the *Glossifungites* ichnofacies. Cannibalization of the underlying forced-regressive shoreface is significant. (d) Transgressively incised shoreface (transgressive systems tract). Vertical softground ichnofacies reflects deepening due to transgression. The base of the transgressively incised shoreface is delineated by the *Glossifungites* ichnofacies. Firmground colonization is typically more extensive than in forced-regressive and lowstand shorefaces because of prolonged colonization windows during depositional hiatus. MFS = maximum flooding surface. SB = sequence boundary. RSME = regressive surface of marine erosion. FWWB = fairweather wave base. CC = correlative conformity. FS/SB = flooding surface/sequence boundary. Modified from MacEachern *et al*. (2007c).

substrate available for the *Glossifungites* producers. Accordingly, the *Glossifungites* ichnofacies locally delineates the basal erosional surface of forced-regression packages (MacEachern *et al*., 1992; Monaco, 1995; Pemberton and MacEachern, 1995; Buatois *et al*., 2002b). Colonization windows may be rather narrow, due to a short hiatus followed by rapid deposition. In contrast to shorefaces formed during normal regressions, those incised during forced regressions are fairly thin due to diminished accommodation space during sea-level fall (MacEachern *et al*., 1999a).

Prograding shoreface successions form during normal regressions separated by periods of relative sea-level rise, and exhibit a gradual change in softground trace-fossil associations reflecting progressive shallowing (Pemberton *et al*., 1992b; Pemberton and MacEachern, 1995). Conversely, falling-stage shorefaces are characterized by the abrupt occurrence of proximal ichnofaunas that sharply contrast with those of the underlying, more distal sediments (Pemberton and MacEachern, 1995). Typically, pervasively bioturbated offshore-transition to offshore deposits, which contain a distal to archetypal *Cruziana* ichnofacies, are sharply replaced by erosive-based, coarser-grained shoreface deposits containing the *Skolithos* or the proximal *Cruziana* ichnofacies.

Mid-shelf and shelf-edge deltas can also form as a result of forced regression, and are included in the falling stage systems tract (Porębski and Steel, 2006). Empirical data on the ichnology of these systems are not available yet. However, it would be reasonable to expect that due to forced progradation of the delta elements of the distal *Cruziana* to *Zoophycos* ichnofacies are replaced by more proximal and depauperate ichnofaunas, as a response of combined shallowing and fluvial discharge.

12.2.2 LOWSTAND SURFACES OF EROSION

The lowstand surface of erosion is produced as a result of relative sea-level fall. During sea-level fall, fluvially transported sediment by-passes the alluvial and coastal plain, eroding into the underlying older deposits. Sediment by-pass is associated either with incision of fluvial valleys, or formation of unincised fluvial channels (Posamentier, 2001). In any case, these processes result in the establishment of a subaerial unconformity that is regarded as a sequence boundary. Although erosion results in firmground development, no substrate-controlled ichnofacies occur at the base of incised fluvial valleys or unincised fluvial systems because of freshwater or terrestrial conditions (MacEachern *et al.*, 1992). However, because typically subaerial unconformities correspond to the largest stratigraphic hiatuses, paleosol development may be extensive and rooted horizons together with the *Coprinisphaera*, *Celliforma*, or *Termitichnus* ichnofacies may occur in interfluve areas (Buatois and Mángano, 2004a; Catuneanu, 2006).

In addition, subaerial unconformities can be detected by looking not at the surfaces themselves, but at the changes of ichnofaunas throughout the interval analyzed. The typical example is the vertical replacement of elements of the *Skolithos* or *Cruziana* ichnofacies in highstand systems tract deposits by the *Scoyenia* ichnofacies in continental lowstand systems tract deposits. It should be noted, however, that in the absence of a sharp change in sedimentary facies and associated erosion, this change in ichnofaunas may simply result from normal progradation of the highstand systems tract and no sequence boundary is implied.

The subaerial unconformity may extend basinwards into an erosional surface produced subaqueously during maximum lowstand. This surface is excavated prior to burial due to lowstand progradation, resulting in the incision of sharp-based lowstand shorefaces (Fig. 12.4c). In terms of their ichnological signatures, substrate-controlled ichnofacies, particularly the firmground *Glossifungites* ichnofacies, may be present at the base of lowstand surfaces (MacEachern *et al.*, 1992, 2007c; Pemberton *et al.*, 2004). However, because of rapid deposition after formation of the erosive surface the colonization window may close relatively fast, preventing extensive excavation of the substrate.

Lowstand shorefaces are difficult to distinguish from forced-regressive shorefaces. Both record rapid progradation and overlie erosional surfaces cut by wave erosion (MacEachern *et al.*, 2007c). Another similarity with lowstand shorefaces is the abrupt occurrence of proximal ichnofaunas over more distal ichnofaunas (Pemberton and MacEachern, 1995; Buatois *et al.*, 2002b). However, falling-stage shorefaces are thinner than their lowstand counterparts because of reduced accommodation space during falling sea level (Mellere and Steel, 1995; Catuneanu, 2006; MacEachern *et al.*, 2007c). As recently discussed by MacEachern *et al.* (2007c), one of the main differences between falling-stage and lowstand shorefaces resides in the lower preservation potential of the former. Because continuing sea-level fall leads to the subaerial exposure of falling-stage shorefaces, cannibalization is quite intense. In addition, the correlative conformity of the regressive surface of erosion is unlikely to be preserved due to subsequent incision of the lowstand shoreface emplaced in a further seaward position. In basinal positions, lowstand shorefaces tend to be gradationally based and the sequence boundary passes into its correlative conformity. Because the lowstand shoreface lies in the most seaward position prior to the subsequent sea-level rise, the preservation potential of the sequence boundary, and the correlative conformity is high (MacEachern *et al.*, 2007c). Shelf-edge deltas also form during lowstand (Porębski and Steel, 2006), but the ichnology of these systems is still poorly understood.

Sea-level fall also plays a major role in slope and basin settings either by shifting depocenters towards the shelf edge or by producing incisions of submarine canyons (Posamentier and Allen, 1999; Posamentier and Kolla, 2003). In the case of incised submarine canyons, extensive firmground surfaces are formed during incision due to erosional exhumation of previously deposited sediment (MacEachern *et al.*, 1992). Surfaces associated to incised submarine canyons are typically delineated by the *Glossifungites* ichnofacies (e.g. Hayward, 1976; Anderson *et al.*, 2006) (Figs. 12.5a–b, and 12.6). Additional information is provided by the related softground ichnofaunas. Highstand systems tract deposits underlying the incision surface commonly contain elements of the *Zoophycos* ichnofacies that characterizes outer shelf to slope environments. Although a dominance of low-diversity suites of suspension feeders were originally considered as typical of canyon-fill deposits (Crimes, 1977), subsequent studies documented more variability of biogenic structures (Pickerill, 1981). This is consistent with the relatively wide variability of submarine canyon-fill sediments. In general, those ichnofaunas present immediately above the unconformity may contain elements of the *Zoophycos* or *Skolithos* ichnofacies (Fig. 12.5c) depending of the energy levels involved in canyon filling. Alternatively, canyon deposits may be virtually unbioturbated as a result of rapid sedimentation (Pemberton *et al.*, 2004).

12.2.3 TRANSGRESSIVE SURFACES OF EROSION

Transgressive surfaces of erosion, also known as ravinement surfaces, are formed due to scouring by tides and waves during the landward shift of the shoreline (Cattaneo and Steel, 2003; Catuneanu, 2006). Commonly they mark the boundary between the lowstand systems tract and the transgressive systems tracts (Posamentier and Allen, 1999). However, they may also delineate parasequence boundaries formed under high-energy conditions (Pemberton *et al.*, 1992b), representing within-trend facies contacts (Catuneanu, 2006). Typically, the ravinement surface is delineated by the firmground *Glossifungites* ichnofacies (MacEachern *et al.*, 1992) (Figs. 12.4d, 12.7a–c, and 12.8a–c). In fact, the landward shift of the shoreline generates extensive erosion leading to widespread exhumation of the underlying marine, and marginal-marine deposits under brackish to fully marine conditions. Furthermore, because during transgressions

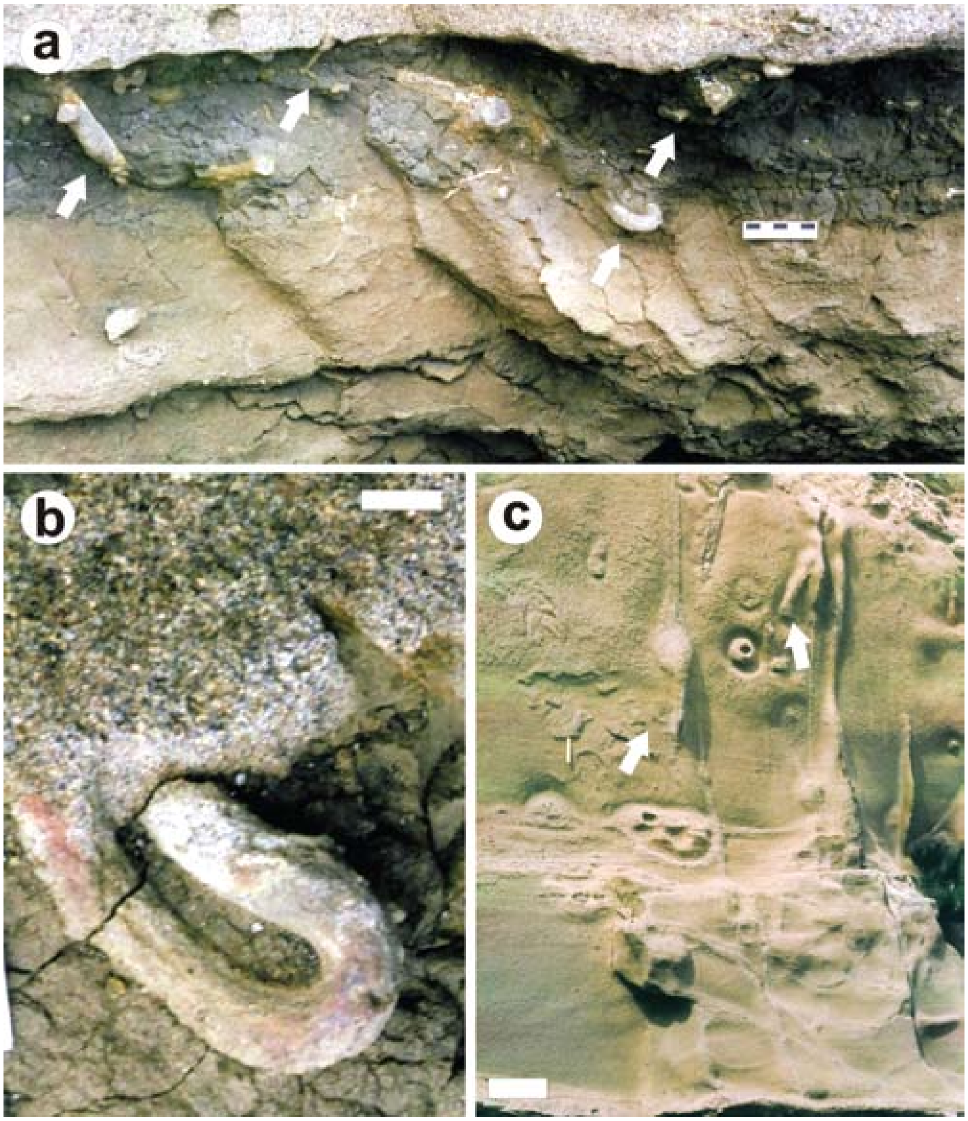

Figure 12.5 Ichnofaunas of lowstand surfaces of erosion in incised submarine canyons, Lower Miocene, Nihotopu and Tirikohua formations, Bartrum Bay, New Zealand. (a) General view of the erosive contact between slope deposits of the Nihotopu Formation below and canyon-fill deposits of the Tirikohua Formation above. Elements of the firmground *Glossifungites* ichnofacies (arrows) penetrate into the slope deposits, and are passively infill by submarine-canyon very coarse- to coarse-grained sand. Scale bar is 5 cm. (b) Close-up of a firmground *Rhizocorallium* specimen with scratch marks. Scale bar is 1 cm. (c) Vertical specimens of *Ophiomorpha* (arrows) forming the high-energy softground suite of canyon-fill deposits. Scale bar is 5 cm. See Hayward (1976).

sediment is trapped in the most proximal positions, sedimentation rate is very low in nearshore to shelf areas, providing relatively continuous colonization windows. As a consequence, conditions for colonization by the *Glossifungites* producers are ideal during transgressions. Although the *Glossifungites* ichnofacies is the most common substrate-controlled ichnofacies in transgressive surfaces of erosion, the *Trypanites* and *Teredolites* ichnofacies may occur if hardgrounds and woodgrounds are formed, respectively. In particular, the ichnogenus *Teredolites* may occur in large densities in transgressive lags (Savrda, 1991a; Savrda *et al*., 1993). Continuous scouring during ravinement tends to concentrate logs bored with *Teredolites* that accumulate after erosion of forested coastal plains during flooding (Box 12.1).

During transgressive retreat followed by a stillstand, sharp-based, incised shorefaces can be formed (Downing and Walker, 1988; Pemberton and MacEachern, 1995; MacEachern *et al*., 1998). Under these conditions a wave-ravinement surface, produced by wave scouring during transgression, is formed. Discerning between transgressively incised shorefaces, and forced-regression and lowstand shorefaces is difficult because tracemakers are subject to identical environmental parameters in both settings (Pemberton and MacEachern, 1995). MacEachern *et al*. (1999a) noted that transgressively incised, and forced-regressive shorefaces may be distinguished on the basis of detailed analysis of the erosional extent of the basal discontinuity (Fig. 12.4d). The basal discontinuity of transgressively incised shorefaces remains erosional even seaward of fair-weather wave base during subsequent progradation because the surface was cut prior to stillstand progradation while sea level was considerably lower. In contrast, the basal discontinuity of forced-regressive shorefaces becomes non-erosional where overlying facies are deposited below fair-weather wave base.

Transgressive surfaces of erosion are also associated with abandonment of deltaic systems (Fig. 12.7b). In proximal positions, alluvial and delta-plain deposits containing freshwater to brackish-water ichnofaunas are sharply replaced by more

Figure 12.6 Firmground *Thalassinoides* of the *Glossifungites* ichnofacies delineating the base of an incised submarine canyon, Lower Cretaceous, Brewster Sands, Vulcan Formation, Gorgonichnthys field, Northwest Shelf Australia. Core width is 10 cm.

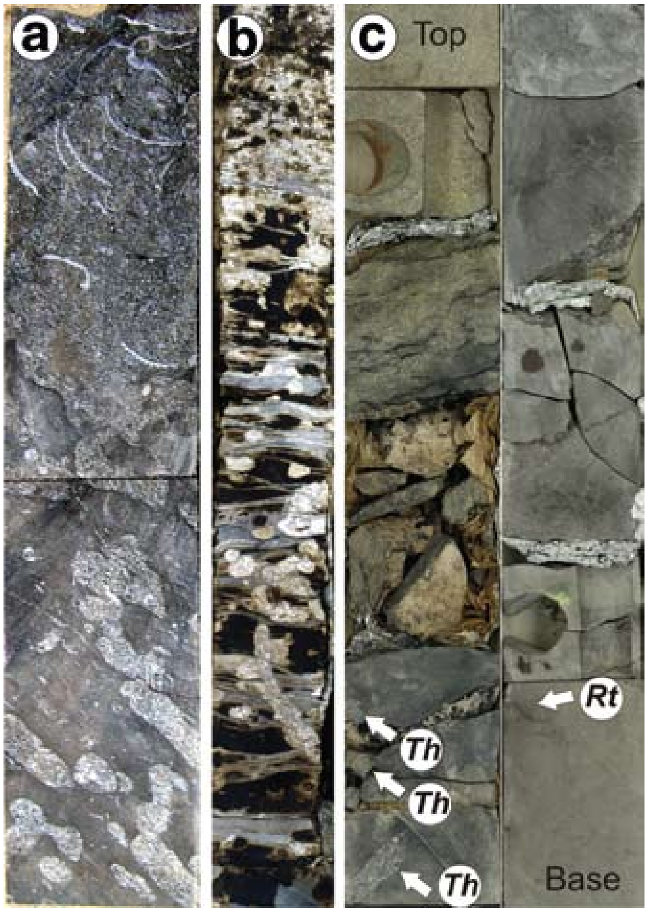

Figure 12.7 *Glossifungites* ichnofacies in transgressive surfaces of erosion. (a) High density of firmground *Thalassinoides* and *Rhizocorallium* in a ravinement surface. Burrows are filled with coarse- and very coarse-grained sand and shell fragments from the overlying transgressive deposit. Oligocene, Los Jabillos Formation, Orocual Field, Eastern Venezuela Basin. Core width is 6.5 cm. (b) High density of *Thalassinoides* in a ravinement surface associated with delta abandonment. Burrow systems penetrate into underlying interdistributary-bay deposits, and are filled with coarse- and very coarse-grained sand and shell fragments from the overlying transgressive deposits. Lower to Middle Miocene, Oficina Formation, Oritupano Field, Eastern Venezuela Basin. Core width is 9 cm. (c) Firmground *Thalassinoides* (*Th*) penetrating from transgressive deposits above into a paleosol below. Note root trace fossils (Rt) in paleosol. Lower Miocene, Naricual Formation, El Furrial Field, Eastern Venezuela Basin. Core width is 9 cm.

diverse ichnofaunas as a result of deepening. Ravinement surfaces cut into floodplain, interdistributary-bay, and abandoned-channel fine-grained clastic deposits are commonly delineated by the *Glossifungites* ichnofacies, while coals are most likely penetrated by elements of the *Teredolites* ichnofacies (e.g. Dam, 1990; Buatois *et al*., 2002a). In subaerial to paralic settings, the *Glossifungites* may truncate paleosols (e.g. Driese and Foreman, 1991) (Fig. 12.7c). Towards distal positions, transgressive surfaces of erosion demarcated by the *Glossifungites* ichnofacies may display extremely high densities and relatively high diversity of firmground burrows (e.g. Buatois, 1995; Buatois *et al*., 2002a).

During shoreline transgression, tidal currents may scour the underlying sediments resulting in the formation of a tidal-ravinement surface. This surface is typical of estuarine settings and specifically occurs between the finer-grained deposits of the estuary basin and the sandy deposits of the estuary-mouth complex (Allen and Posamentier, 1993) (Fig. 12.10). Another transgressive surface in estuarine settings, specifically in those that are wave-dominated, is the wave ravinement surface (Zaitlin *et al*., 1994). This surface separates the overlying transgressive shoreface from the underlying estuary-mouth-deposits (Fig. 12.10). The tidal- and wave-ravinement surfaces do not represent boundaries between different systems tracts but occur within the transgressive systems tract. The firmground *Glossifungites* ichnofacies is extremely common in both tidal- and wave-ravinement surfaces (MacEachern and Pemberton, 1994).

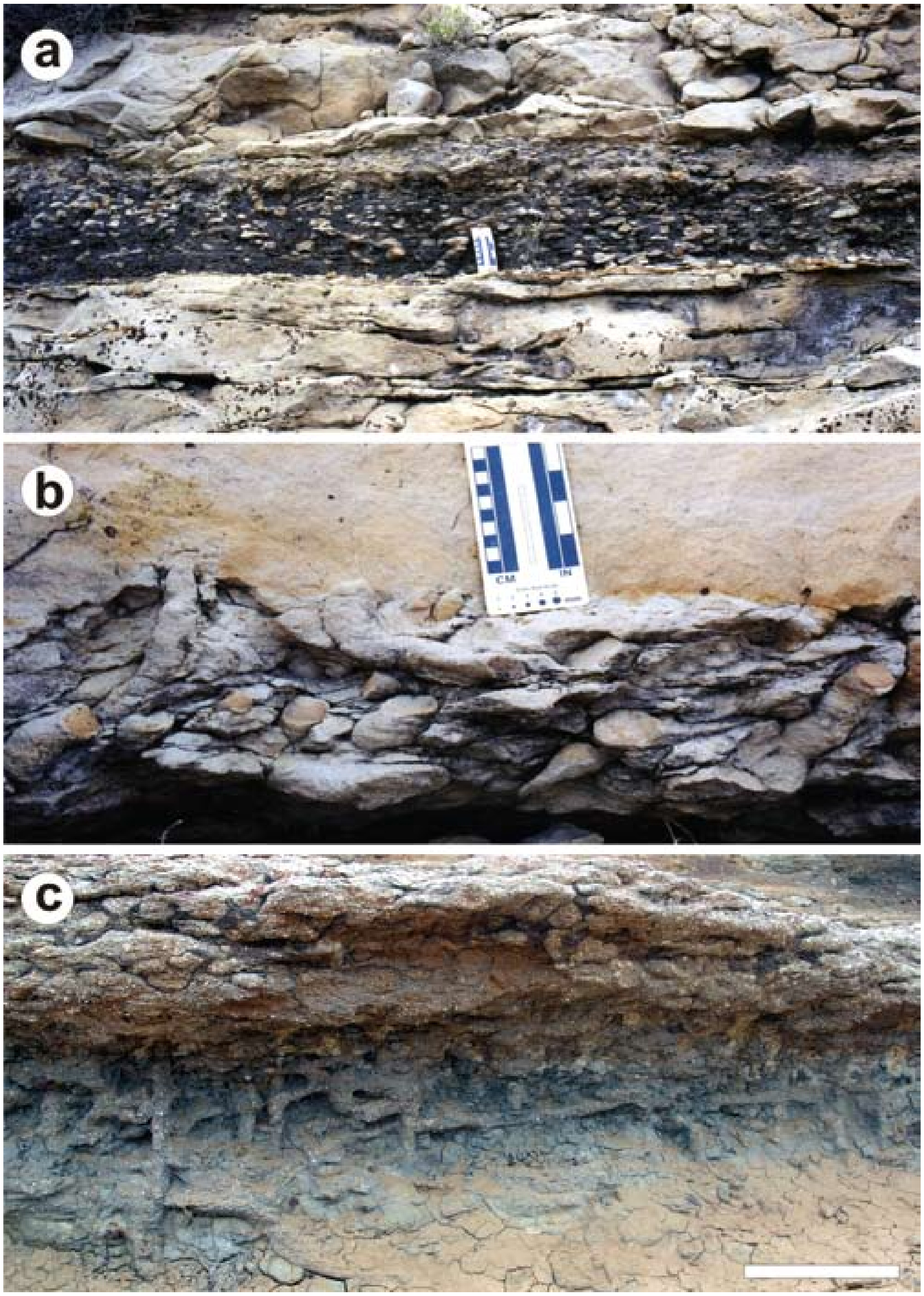

Figure 12.8 Ravinement surfaces delineated by firmground *Thalassinoides* suites of the *Glossifungites* ichnofacies. (a) The surface separates estuarine basin deposits below from sandy-channel deposits above. Upper Cretaceous, Desert Member, Blackhawk Formation, Book Cliffs, Utah, United States. (b) Close-up of firmground burrows shown in (a). (c) Transgressive deposits with thick shell lag overlying delta-plain deposits. Middle to Upper Miocene, Urumaco Formation, Urumaco River, northwestern Venezuela. Scale bar is 30 cm.

12.2.4 CO-PLANAR SURFACES OF LOWSTAND EROSION AND TRANSGRESSIVE EROSION

Co-planar surfaces of lowstand erosion and transgressive erosion occur when the fluvially cut, subaerial unconformity is modified during subsequent transgression, and no fluvial deposits are preserved above the surface (Pemberton *et al*., 1992b). Co-planar surfaces represent sequence boundaries that are overlain not by lowstand systems tract deposits, but by transgressive systems tract deposits. The most common occurrence of co-planar surfaces is associated with incised estuarine valleys (Figs. 12.9, 12.10, and 12.11a–d). In incised valleys, fluvial deposits tend to accumulate along the valley axis during a late phase of sea-level fall, and are part of the lowstand systems tract. During the subsequent transgression, the downstream portion of incised valleys is converted into estuaries (Zaitlin *et al*., 1994). Estuarine deposits showing varying degrees of tidal influence tend to accumulate along the valley axis, but also onlap the interfluves where they mantled a co-planar surface of lowstand and transgressive erosion.

Co-planar surfaces are commonly delineated by a whole array of substrate-controlled ichnofacies, with the *Glossifungites* ichnofacies being the most common of all (MacEachern and Pemberton, 1994). MacEachern *et al*. (1992) suggested that the

Box 12.1 *Teredolites* and sea-level changes

Studies in the Lower Paleocene Clayton Formation of Alabama have demonstrated the utility of the wood bivalve boring *Teredolites* in delineating transgressive systems tracts (TST) (Fig. 12.9). The Clayton Formation contains a thin (approximately 1.5 m) TST interval bounded at the top by a condensed section. *Teredolites* is present in high densities in logs forming a transgressive lag at the base of the TST interval. This accumulation results from an influx pulse of wood fragments from flooded forested coastal plains into marginal-marine and shallow-marine areas, and concentration of logs due to continuous scouring during ravinement. A second concentration of drifted bored logs occurs in the condensed section, marking the maximum flooding surface formed under conditions of sediment starvation. In addition, four preservational styles in *Teredolites* log-grounds have been recognized: well-preserved log-grounds, relict log-grounds, ghost log-grounds, and reworked *Teredolites*. All four preservational styles are present in the transgressive lag, albeit with different abundances and commonly showing patchy distribution. Only ghost log-grounds are present in the condensed section. Biochemical degradation is highest in the ghost log-grounds as a result of reduced sedimentation rates. Similar patterns in *Teredolites* distribution to those detected originally in the Clayton Formation have subsequently been recognized in other regions of the United States Gulf coastal plain and elsewhere.

References: Savrda (1991a); Savrda *et al*. (1993).

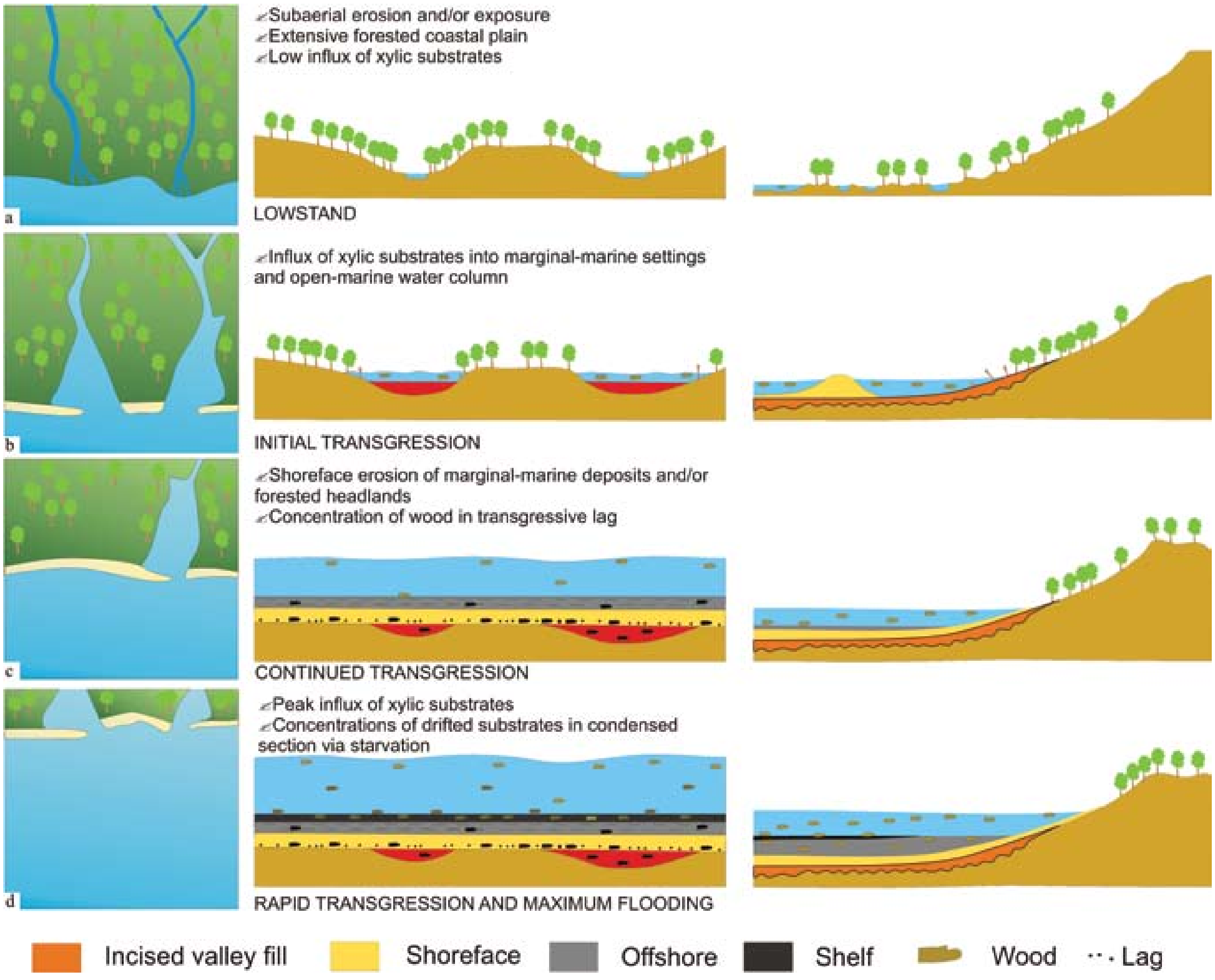

Figure 12.9 Relationships between *Teredolites* and sea-level changes. (a) During lowstand, influx of xylic substrates is low. (b) During the initial transgression, influx of xylic substrates increases due to continuous scouring during transgressive ravinement across forested coastal plains, and logs become abundant in the water column. (c) Dense concentrations of wood fragments with *Teredolites* accumulate forming transgressive lags. (d) Condensed sections form during maximum flooding. These are characterized by ghost log-grounds that have suffered intense biodegradation (modified from Savrda *et al*., 1993).

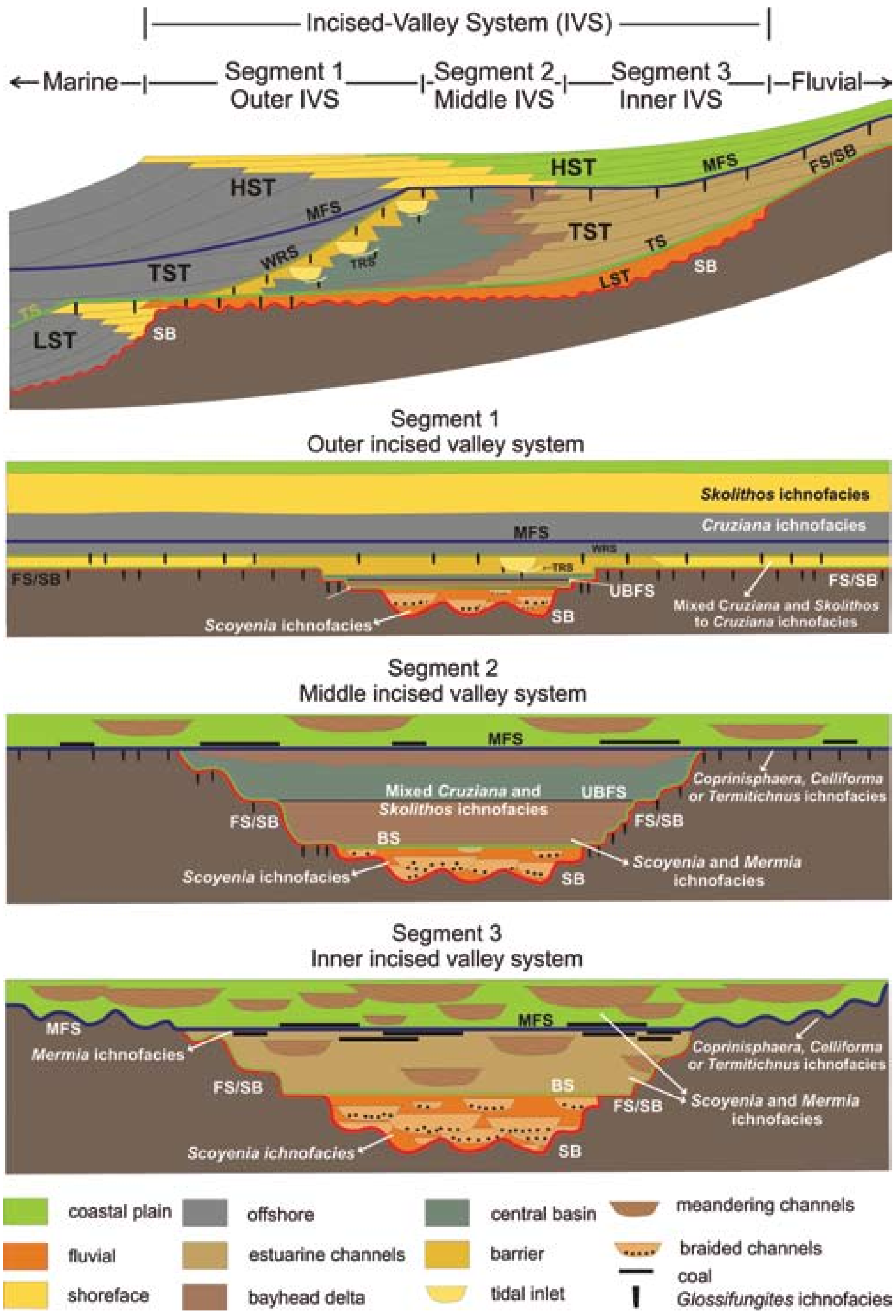

Figure 12.10 Ichnology of incised-valley systems. Modified from MacEachern and Pemberton (1994) and Buatois *et al.* (1998d). Valley segments based on Zaitlin *et al.* (1994). Segment 1 extends from the most seaward extent of valley incision, near the lowstand mouth of the incised valley, to the point where the shoreline stabilizes at the beginning of highstand progradation. Segment 2 lies between the inner end of segment 1 (i.e. the initial highstand shoreline) and the estuarine limit (i.e. the landward limit of recorded tidal influence) at the time of maximum flooding. Segment 3 is located in the innermost region of the valley, lying landward of the transgressive marine–estuarine limit, but it is still influenced by changes in base level associated with relative sea-level change. The *Glossifungites* ichnofacies occurs at multiple levels, delineating flooding surfaces/ sequence boundaries, tidal-ravinement surfaces, and wave-ravinement surfaces. Note that this ichnofacies is not present if the sequence boundary is coincident with the base of lowstand fluvial deposit. LST = lowstand systems tract. TST = transgressive systems tract, HST = highstand systems tract, SB = sequence boundary, FS/SB = flooding surface/sequence boundary, TS = transgressive surface, BS = bayline surface, UBFS = upper-bay flooding surface, TRS = tidal-ravinement surface, WRS = wave-ravinement surface, MFS = maximum flooding surface.

distribution of the *Glossifungites* ichnofacies along the base of the valley may be useful to delineate the maximum landward limit of marine influence in the incised valley during initial deposition. This distribution results from the fact that the *Glossifungites* producers cannot colonize under freshwater conditions. Accordingly, the ichnofacies is not developed at the base of the lowstand systems tract (Savrda, 1991b). Carmona *et al.* (2006, 2007) noted that careful evaluation of the ichnological content, truncation of trace fossils, and the relationship between firmground biogenic structures commonly indicates a complex history for co-planar surfaces, suggesting successive events of ravinement erosion and benthic colonization during the transgression.

Bored substrates are also common along co-planar surfaces, particularly where rocky shorelines and cliffs are transgressed. The *Trypanites* ichnofacies occurs in such settings (Gibert and Martinell, 1992, 1993, 1996; Martinell and Domènech, 1995). Uchman *et al.* (2002) noted that as transgression progresses different suites of bioeroders are emplaced in the discontinuity

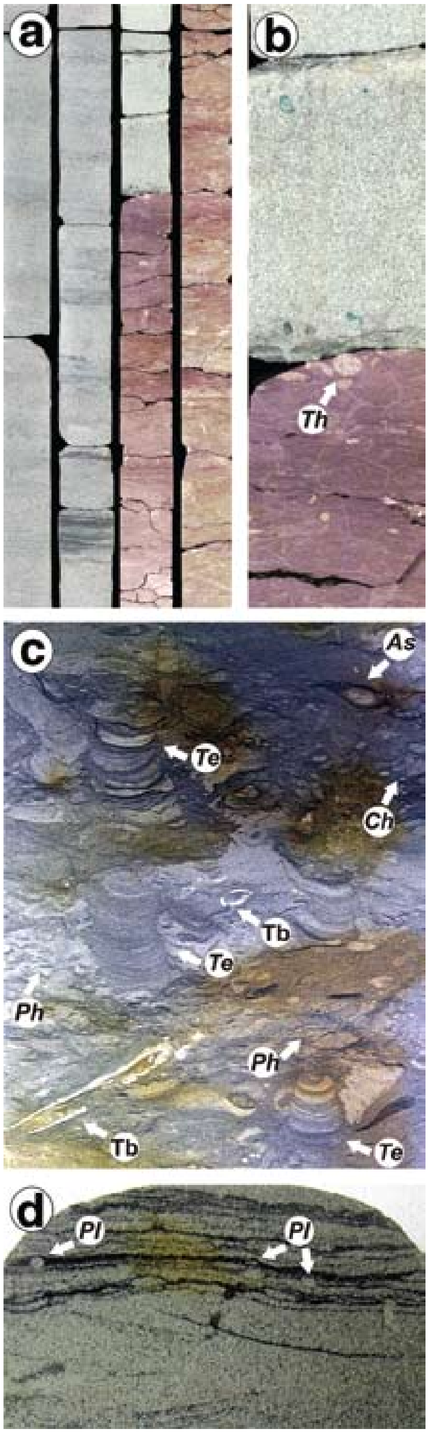

Figure 12.11 *Glossifungites* ichnofacies in a valley-incision surface, Upper Cretaceous, Magallanes Formation, Austral Basin, Patagonia, Argentina. (a) Sparsely bioturbated incised valley-fill deposits with a depauperate *Cruziana* ichnofacies sharply replace lower-offshore deposits with an archetypal to distal *Cruziana* ichnofacies. Core is read from base at lower right to top at upper left. (b) Close-up showing firmground *Thalassinoides* (*Th*) of the *Glossifungites* ichnofacies at the incision surface. (c) Close-up of intensely bioturbated lower-offshore deposits. Evenly distributed *Phycosiphon* (*Ph*) cross-cut by *Asterosoma* (*As*), *Chondrites* (*Ch*) and deep *Teichichnus* (*Te*). Note thick wall in "Terebellina (Tb)". (d) Close-up of sparsely bioturbated incised valley-fill deposits. Small *Planolites* (*Pl*) occurs in mud drapes. Core widths are 10 cm.

as a result of a decrease in light and energy that parallels an increase in water depth. In their example, the polychaete boring *Caulostrepsis* was emplaced with water depths of less than 2 m and subsequently overprinted by the bivalve boring *Gastrochaenolites* when the water depth reaches approximately 10 m. Finally, the sponge boring *Entobia* cross-cuts the other ichnofossils in water depths of a few tens of meters. Therefore, assemblages in these co-planar surfaces represent the work of several overprinted communities.

12.3 NON-EROSIONAL DISCONTINUITIES

Other surfaces of importance in sequence stratigraphy are not erosive in nature and, therefore, lack substrate-controlled ichnofacies if they are formed in siliciclastic sediments. Non-erosional discontinuities developed in carbonates are much more complex and will be addressed below. Three main situations can be recognized: low-energy drowning surfaces, low-energy flooding surfaces and maximum flooding surfaces.

Low-energy drowning surfaces separate deeper-water deposits resting on shallower-water strata (Posamentier and Allen, 1999). These surfaces are characterized by a vertical change in softground trace-fossils assemblages reflecting that deepening trend (e.g. Taylor and Gawthorpe, 1993). Examples include foreshore or upper-shoreface sandstone with a *Skolithos* ichnofacies that is sharply replaced by offshore or offshore-transition mudstone having a proximal to archetypal *Cruziana* ichnofacies. This same surface is represented seaward by offshore mudstone with a *Cruziana* ichnofacies replaced by shelf deposits containing a distal *Cruziana* ichnofacies or a *Zoophycos* ichnofacies.

Low-energy flooding surfaces separate subaerially exposed sediments from overlying subaqueous deposits as a result of a rise in base level (Posamentier and Allen, 1999). Flooding surfaces represent a special category of drowning surfaces and, in actuality, they are the landward extension of the drowning surface. These surfaces can be recognized by a vertical change in softground trace-fossil assemblages that reflect inundation of the substrate (e.g. Taylor and Gawthorpe, 1993). A typical situation is the vertical passage from alluvial or coastal-plain deposits containing the *Scoyenia* ichnofacies or paleosol trace-fossil assemblages to nearshore deposits hosting marine or brackish-water ichnofacies.

Maximum flooding surfaces refer to the surface of deposition at the time the shoreline is at its maximum landward position and, therefore, separates the transgressive from the highstand systems tract (Posamentier and Allen, 1999). Because during maximum transgression coastal depocenters are located at their maximum landward position, slow sedimentation occurs in the offshore and shelf. As a result, maximum flooding is characterized by a condensed section representing thin deposits that accumulate during long periods of time (Loutit *et al.*, 1988). The ichnological signatures of maximum flooding surfaces have not been explored in detail. However, it is well known that these surfaces are commonly associated with oxygen-poor conditions.

Therefore, condensed sections commonly are unbioturbated or display suites that are typical of dysaerobic sediments (Savrda, 1992; Pemberton *et al*., 1992b). Where transgressions are associated with flooding of forested coastal plains, maximum flooding surfaces may be characterized by concentrations of logs with *Teredolites* that accumulate under sediment starvation (Savrda, 1991a; Savrda *et al*., 1993, 2005) (Box 12.1).

12.4 CHARACTERIZATION OF PARASEQUENCES

In addition, recognizing changes in ichnofaunal content across a succession may help to identify parasequences. A parasequence is a shallowing-upward succession bounded by marine flooding or drowning surfaces (Van Wagoner *et al*., 1990). The concept is particularly useful for the study of shallow-marine successions and, less commonly, lake systems, but its application to the study of alluvial and deep-marine strata is not recommended (Posamentier and Allen, 1999). The use of ichnology to delineate parasequences is based on the fact that trace-fossil associations are excellent indicators of environmental conditions that generally change according to a bathymetric gradient. In parasequences of clastic shallow-marine settings, two situations must be considered depending on the predominant depositional process: wave-dominated coasts and tide-dominated coasts. A third type of parasequence is generated in deltaic systems. Little is known about the architecture, grain-size vertical trends, and trace-fossil distribution in parasequences formed in mixed tide- and wave-dominated systems. However, preliminary information from modern environments (see Section 7.3) suggests that tidal beaches may show parasequences that are very similar to those of wave-dominated shallow-marine settings, while parasequences in wave-dominated tidal flats may display much more similarity to those of tide-dominated shorelines, particularly if inner mud-flat zones are developed.

12.4.1 WAVE-DOMINATED PARASEQUENCES

A wave-dominated parasequence coarsens and thickens upward, recording shoreline progradation (Van Wagoner *et al*., 1990). In terms of associated environmental factors, each parasequence reflects a progressive upward increase in hydrodynamic energy, degree of oxygenation, sand content, amount of organic particles in suspension, and mobility of the substrate that control the vertical distribution of trace fossils (Pemberton *et al*., 1992c; Mángano *et al*., 2002a, 2005a). Parasequences in wave-dominated strandplain environments pass gradually, from base to top, from a distal *Cruziana* ichnofacies in the lower offshore, an archetypal *Cruziana* ichnofacies in the upper offshore to offshore transition, a proximal *Cruziana* ichnofacies that is partially combined with a *Skolithos* ichnofacies in the lower shoreface, a *Skolithos* ichnofacies from the middle shoreface to the foreshore, and a *Psilonichnus* ichnofacies across the backshore (MacEachern and Pemberton, 1992; MacEachern *et al*., 1999a; Mángano *et al*., 2002a, 2005a). It should be noted, however, that this ideal parasequence is the exception rather than the rule because not all subenvironments are represented in each parasequence. This environmental zonation is based on the characteristics of the resident ichnofauna, and the displacement of the *Skolithos* ichnofacies towards more distal parts in response to storm events (Pemberton and MacEachern, 1997) renders it complicated.

12.4.2 TIDE-DOMINATED PARASEQUENCES

Less attention has been focused on tide-dominated parasequences, and several problems have arisen as a result of arbitrarily extrapolating the wave-dominated model to environments where tide is the driving process. A tide-dominated parasequence fines and thins upward, recording tidal-flat progradation (Van Wagoner *et al*., 1990). The energy peak is in the deeper-subtidal zone rather than in intertidal areas. Therefore, each parasequence reflects an upward decrease in hydrodynamic energy, degree of oxygenation, sand content, amount of organic particles in suspension, and substrate mobility. Vertical ichnofacies replacement in a tide-dominated parasequence is just the opposite to that of a wave-dominated parasequence (Mángano *et al*., 2002a, 2005a; Mángano and Buatois, 2004a). A typical tide-dominated parasequence begins with non-bioturbated sandstone accumulating in subtidal-sandbar and dune complexes which upwards may contain colonization surfaces with low-diversity assemblages of the *Skolithos* ichnofacies. Lower-intertidal sand-flat deposits containing a mixture of elements from the *Skolithos* and *Cruziana* ichnofacies occur above. The *Cruziana* ichnofacies gets increasingly important to the point of becoming predominant in mixed intertidal flat, despite the fact that ichnodiversity is not necessarily high. The upper part of the parasequence generally involves mudstone deposits containing root trace fossils and elements of the *Psilonichnus* ichnofacies. Ichnofacies zonation depends largely on tidal regime (Mángano and Buatois, 2004a). In high-energy systems, lower-intertidal sectors tend to be dominated by elements of the *Skolithos* ichnofacies, which turn out to be similar to subtidal deposits from the ichnological viewpoint. In contrast, under lower-energy conditions, lower-intertidal zones are dominated by the *Cruziana* ichnofacies.

12.4.3 DELTAIC PARASEQUENCES

Deltaic parasequences are highly variable, depending on the dominant process operating (waves, tides, and fluvial). Parasequences can be particularly delineated in the prodelta to delta front. Recognition of parasequences in the delta plain remains a contentious issue (Posamentier and Allen, 1999). In addition, shallowing-upward successions apparently limited by flooding surfaces may be produced by deltaic-lobe switching rather than by true allogenic processes, such as sea-level change (e.g. Törnqvist *et al*., 1996). Little is known about trace-fossil distribution in parasequences formed in tide-dominated deltas and our discussion is, therefore, focused on parasequences from wave- and river-dominated deltas.

Parasequences from wave-dominated deltas are similar to those formed in wave-dominated, non-deltaic shorelines because wave energy tends to buffer fluvial effects (MacEachern *et al*., 2005). As in strandplain parasequences, a wave-dominated parasequence coarsens and thickens upward, recording delta progradation (Van Wagoner *et al*., 1990). Parasequences formed in these settings pass gradually, from base to top, from a distal *Cruziana* ichnofacies in the distal prodelta, an archetypal *Cruziana* ichnofacies in the proximal prodelta to distal delta front and a proximal *Cruziana* ichnofacies or *Skolithos* ichnofacies in the proximal delta front. However, subtle differences can be detected. The *Cruziana* ichnofacies may be slightly impoverished with respect to its more fully marine bathymetric equivalents of strandplain parasequences. In addition, high concentration of silt and clay in the water column reduces the amount of suspension feeders, producing an anomalous *Skolithos* ichnofacies.

Parasequences formed in river-dominated deltas also coarsen and thicken upward. In contrast to those from wave-dominated settings, river-induced stresses are more profound (MacEachern *et al*., 2005). Parasequences from river-dominated deltas pass gradually, from base to top, from a distal *Cruziana* ichnofacies in the distal prodelta, a depauperate *Cruziana* ichnofacies in the proximal prodelta to distal delta front and sparse indistinct bioturbation, if any, in the proximal delta front. River discharge often results in dilution of marine salinity, resulting in impoverishment of the *Cruziana* ichnofacies. In addition, water turbidity is very high, resulting in the suppression of the *Skolithos* ichnofacies.

12.5 DELINEATION OF PARASEQUENCE SETS AND SYSTEMS TRACTS

Integrating ichnological evidence, and sedimentological and stratigraphic data, sedimentary successions at the parasequence-set scale can be characterized in order to detect transgressive and regressive trends, assisting in systems-tract recognition. In this respect, two situations will be addressed: progradational and retrogradational patterns. The former is illustrated by either prograding deltas or strandplains and the latter by transgressive estuarine valley fill.

12.5.1 PROGRADATIONAL PATTERNS

Because deltas are, by definition, progradational, deltaic parasequences tend to stack forming progradational parasequence sets. Ichnofaunas are generally indicative of vertical replacement of forms which are typical of alternating normal or nearly normal salinity and brackish-water environments across the prodelta and delta front by forms adapted to brackish-water across the delta plain. As discussed above, whether deltas are river-, tide-, or wave-dominated results in great variations in ichnofossil content. The top of the parasequence set may even exhibit biogenic structures resulting from freshwater fauna living in water bodies across deltaic plains or in distributary streams.

12.5.2 RETROGRADATIONAL PATTERNS

In contrast to deltaic and strandplain successions, however, identification of parasequences in incised valleys is not straightforward (Posamentier and Allen, 1999). In any case, successions recording an estuarine valley fill typically show a clear retrogradational trend that illustrates transgressive stratigraphy (Fig. 12.10). The estuarine valley incision surface is carved during a sea-level fall but the valley fill corresponds mostly to the subsequent transgressive phase (Zaitlin *et al*., 1994). Lowstand-fluvial deposits may even be preserved along the valley axis above the basal incision surface. These deposits commonly exhibit limited bioturbation, resulting from the activity of freshwater biotas or, more commonly, are devoid of biogenic structures.

According to Dalrymple *et al*. (1992), the onset of estuarine deposition is indicated by the lowest occurrence of sandstone with clay drapes of tidal origin, which therefore can be used to detect the boundary between the lowstand systems tract and the transgressive systems tract. The surface separating these two systems tracts within incised valleys is referred to as the bayline surface (Thomas and Anderson, 1994) (Fig. 12.10). Substrate-controlled ichnofacies delineate the valley incision surface where basal fluvial-lowstand deposits do not separate the sequence boundary from the initial flooding surface (Savrda, 1991b). Estuarine valley fill deposits overlying the bayline surface along the valley axis or the incision surface towards the valley margins contain an impoverished ichnofauna characterized by a mixture of the *Skolithos* and *Cruziana* ichnofacies (Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994) (Fig. 12.10). This depauperate ichnofauna records the activity of an opportunistic community developed under stressful conditions in a brackish-water estuarine setting.

Another surface present within incised valleys is the upper-bay flooding surface, which separates sandy upper-estuary deposits from overlying finer-grained facies of the estuary basin (Thomas and Anderson, 1994). The passage from upper-estuary into lower-energy estuary-basin deposits is usually paralleled by a slight increase in ichnodiversity. Upward into the sequence, estuary-basin deposits are separated from the estuary-mouth complex by the tidal-ravinement surface. Due to tidal scouring, this surface commonly hosts a *Glossifungites* ichnofacies (MacEachern and Pemberton, 1994) (Fig. 12.10). Because the estuary mouth commonly experiences near-marine salinity conditions, trace-fossil assemblages may be fairly diverse in this outer region of the incised valley (e.g. Buatois and Mángano, 2003c). Overlying the estuary-mouth complex and underlying the transgressive shoreface, the wave-ravinement surface occurs. Above this surface, ichnofaunas are typically fully marine.

A slight variation to this pattern may occur in the innermost zone of macrotidal estuarine systems that are characterized by arthropod-dominated, diverse assemblages (Buatois *et al*., 1997b). These ichnofaunas belong to mixed *Scoyenia* and *Mermia* ichnofacies, and tend to occur in the basal transgressive deposits immediately above the co-planar surface (Fig. 12.10). In this specific setting and at this particular stage of estuarine valley evolution, freshwater conditions coexist with tidal influence (Buatois *et al.*, 1998d). As transgression proceeds, backstepping brackish-water deposits accumulate. The ichnological signature of such a change in depositional conditions is reflected in the upward replacement of the mixed *Scoyenia* and *Mermia* ichnofacies by the mixed *Skolithos* and impoverished *Cruziana* ichnofacies.

Overall, and in contrast with deltaic successions that typically display a vertical decrease in ichnodiversity due to an increased influence of fluvial processes, estuarine valley-fill successions show vertical passage of brackish-water ichnofaunas exhibiting increasing marine influence into more diverse associations which are indicative of normal salinity (MacEachern and Pemberton, 1994; Buatois *et al.*, 1998d, 2002b). In compound valley systems, which record more that one cycle of relative sea-level change, the ichnological record is more complex and more diverse climax and depauperate opportunistic trace-fossil assemblages tend to alternate as a result of reincision.

12.6 CARBONATE SEQUENCE STRATIGRAPHY

Comparatively little is known with respect to the sequence-stratigraphic significance of trace fossil in carbonates. Carbonate sequence stratigraphy shows significant departures with respect to its siliciclastic equivalent (Bosence and Wilson, 2003; Schlager, 2005; Catuneanu, 2006). Most of these differences stem from the fact that carbonates are produced within the basin itself in the so-called "carbonate factory". Carbonate production is directly proportional to the area of flooded platform top. Accordingly, sediment availability in carbonate systems shows an opposite trend to that of siliciclastic systems. While in siliciclastic systems there is an increased in sediment supply during lowstands and sediment starvation characterizes transgressions, in carbonate systems carbonate factories achieve their maximum production during transgressions, but sea-level fall generates their shutdown. However, if the rise of sea level is very fast and the water depth exceeds the photic limit, carbonate production is terminated and a drowning unconformity is formed. During highstand, the volume of carbonate sediment exceeding accommodation space is shed to the deep water (highstand shedding; see Bosence and Wilson, 2003).

A major departure with respect to siliciclastic substrate-controlled ichnofacies results from the fact that firmgrounds and hardgrounds can be formed in carbonates without erosional exhumation, simply as a result of early diagenetic changes in the substrate (Bromley, 1975). Consequently, the *Glossifungites* and *Trypanites* ichnofacies can develop during periods of reduced depositional rates or breaks in sedimentation. While substrate-controlled ichnofacies in siliciclastic settings are not typically associated with low-energy transgressive surfaces, the opposite is true in carbonate systems. Drowning unconformities may contain firmground and hardground suites. Surfaces containing deep and widespread borings of the *Trypanites* ichnofacies may occur due to the shutdown of the carbonate factory during rapid drowning. In addition, condensation may occur along maximum flooding surfaces in carbonate ramps, leading to the development of substrate-controlled ichnofacies.

If sufficient time is involved, composite ichnofabrics showing progressive changes in substrate consistency are formed (Bromley, 1975; Frey and Bromley, 1985; Ekdale and Bromley, 1991; Lewis and Ekdale, 1992). Omission surfaces and hardgrounds are commonly associated. Omission surfaces are characterized by pre-omission, omission, and post-omission trace-fossil suites (Bromley, 1975, 1996). Pre- and post-omission suites contain softground assemblages, while the omission suite is characterized by the firmground *Glossifungites* ichnofacies. Because no cementation is involved in the formation of omission surfaces, no hardground suites developed. Pre- and post-omission suites in hardgrounds also host softground suites. However, and in contrast to omission surfaces in firmgrounds, the omission suite in hardgrounds is subdivided into pre- and post-lithification suites (Bromley, 1975, 1996). The former hosts the *Glossifungites* ichnofacies, while the latter contains the *Trypanites* ichnofacies. The *Trypanites* suite typically cross-cuts the *Glossifungites* suite, resulting in palimpsest surfaces (e.g. Mángano and Buatois, 1991; Bertling, 1999). In some cases, these surfaces contain bored shells that also reveal breaks in sedimentation (e.g. Martinius and Molenaar, 1991).

In addition to these cases, substrate-controlled ichnofacies may also occur in erosional surfaces, and are commonly associated with rocky shorelines consisting of truncated limestone. Transgressive surfaces of erosion formed by wave ravinement of carbonate substrates contain the *Glossifungites* ichnofacies, commonly exhibiting high-density suites of firmground burrows (e.g. Rodríguez-Tovar *et al.*, 2007). Well-known examples are also associated with co-planar surfaces. During lowstands, carbonates dissolve and karstic surfaces develop under subaerial conditions. Calcareous paleosols may form, and display an ichnofauna dominated by nests of halictid bees, representing the *Celliforma* ichnofacies (Melchor *et al.*, 2002). During the subsequent transgression, karstic surfaces are colonized, and the *Trypanites* ichnofacies is the typical ichnofacies present (e.g. Pemberton *et al.*, 1980; Hanken *et al.*, 1996; Wilson *et al.*, 1998). Some of these surfaces may evidence a complex history of colonization, particularly in reef systems (Fig. 12.12a–d). Shallow borings emplaced in the reef can be removed due to erosion during sea-level fall and only the deepest borings (*Gastrochaenolites*) are preserved. A second generation of borings occurs on the same surface after the subsequent transgression (Wilson *et al.*, 1998).

Studies dealing with the ichnological characterization of carbonate parasequences are uncommon, but examples are known from tropical carbonates (Pemberton and Jones, 1988; Jones and Pemberton, 1989; Curran, 1992, 1994, 2007). Parasequences documented in modern and Quaternary Bahamian-type carbonates consists, from base to top, of: (1) shallow-subtidal coral reef, coral rubblestone, and calcarenite with borings of the *Trypanites* ichnofacies (e.g. *Gastrochaenolites*), and burrows

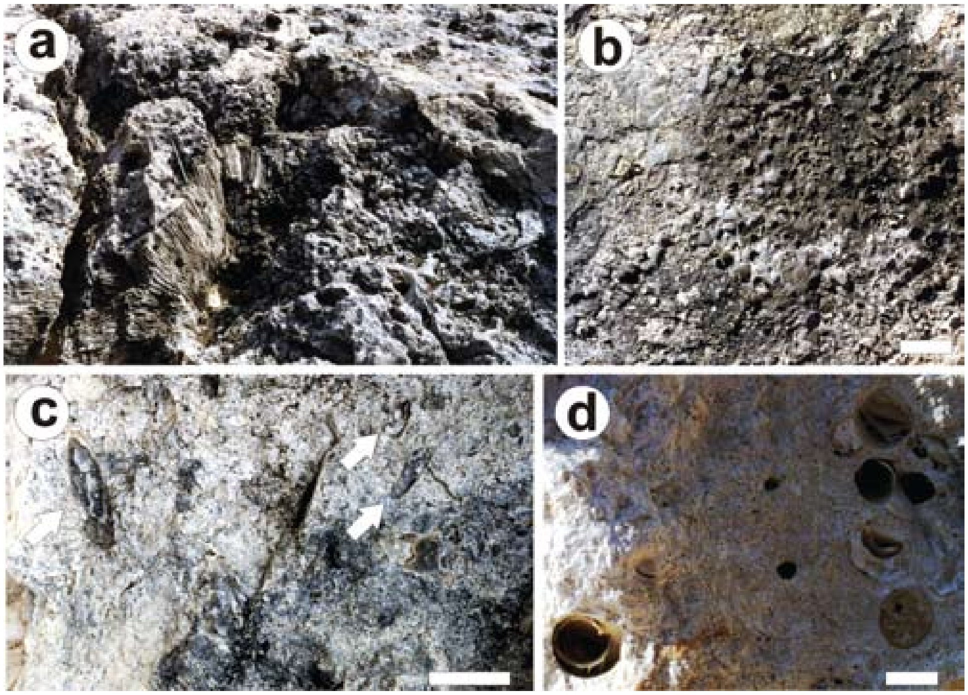

Figure 12.12 Substrate-controlled ichnofacies delineating a co-planar surface in carbonates. Pleistocene, Cockburn Town Member, Grotto Beach Formation, San Salvador Island, Bahamas. (a) Erosional surface sculpted in a coral reef. Note the presence of the encrusting coral *Diploria strigosa*. Pencil (center left) is 16 cm. (b) Close-up of the erosional surface showing high density of the bivalve boring *Gastrochaenolites torpedo*. Some of these borings are truncated, and only their bases are preserved. These borings represent colonization prior to erosion due to sea-level fall. Scale bar is 5 cm. (c) *Gastrochaenolites torpedo* (arrows) emplaced in the encrusting coral *Acropora palmata*. Scale bar is 3 cm. (d) *Gastrochaenolites torpedo* formed prior to the sea-level fall and filled with material derived from a terra rossa paleosol developed during the lowstand. Scale bar is 1 cm. See Wilson *et al*. (1998).

of the *Skolithos* ichnofacies (e.g. *Skolithos*, *Ophiomorpha*), (2) lagoonal intertidal oolitic limestone with the mixed *Skolithos*–*Cruziana* ichnofacies, (3) beach-backshore calcarenite containing the *Psilonichnus* ichnofacies, and (4) coastal eolian-dune calcarenite, and paleosols with insect and arachnid trace fossils (see Section 11.1.1).

12.7 CONTINENTAL SEQUENCE STRATIGRAPHY

In comparison with their marine counterparts, continental ichnology has been less explored with respect to its utility in sequence stratigraphy, and trace fossils are undoubtedly still underutilized in this field. Application of ichnology in continental sequence stratigraphy cannot be simply based on the extrapolation of marine sequence stratigraphy and a modified conceptual framework should be adopted (Buatois and Mángano, 2004a, 2007, 2009a). While substrate-controlled ichnofacies reflect erosive exhumation of the sediment in marine environments, this is rather unusual in continental settings. In continental successions, substrate-controlled ichnofacies are commonly related to firmgrounds that rapidly developed under subaerial exposure by autogenic processes, without implying a significant hiatus (e.g. Fürsich and Mayr, 1981; Zonneveld *et al*., 2006).

12.7.1 LAKE BASINS

Further problems result from the application of sequence-stratigraphic concepts in continental environments, particularly in the case of lacustrine systems. As noted by Bohacs *et al*. (2000), lacustrine systems differ from oceans in several ways, including the smaller volumes of sediment and water included in lakes, the direct link between lake level and sediment supply, and the fact that shoreline migration may be due not only to progradation but also to withdrawal of water. Bohacs *et al*. (2000) recognized three different types of lake basins, overfilled, balanced-fill, and underfilled, providing a conceptual and practical framework to evaluate the potential of trace fossils in lacustrine sequence stratigraphy (Buatois and Mángano, 2004a, 2007, 2009a) (Fig. 12.13). This framework has been also used to place changes in species diversity in modern and ancient lakes (Gierlowski-Kordesch and Park, 2004).

OVERFILLED LAKES

Overfilled-lake basins are formed when rate of sediment/water input exceeds potential accommodation (Bohacs *et al*., 2000). According to these authors, overfilled lakes are commonly hydrologically open, contain fluvio-lacustrine siliciclastic deposits and display parasequences driven mainly by shoreline progradation and delta-channel avulsion. Overfilled-lake basins contain well-developed softground trace fossils that are useful to delineate parasequences and parasequence sets (e.g. Buatois and Mángano, 1995c; Melchor *et al*., 2003; Melchor, 2004). Fluvial discharge into overfilled lakes commonly contributes to the formation of underflow currents that oxygenate lake bottoms. These density currents allow epifaunal and infaunal communities to become established (Buatois and Mángano, 1998).

In addition to being well oxygenated, overfilled lakes are typically freshwater and no stress due to hypersalinity occurs, leading to the development of a relatively diverse benthos. Shallowing-upward successions due to delta and shoreline

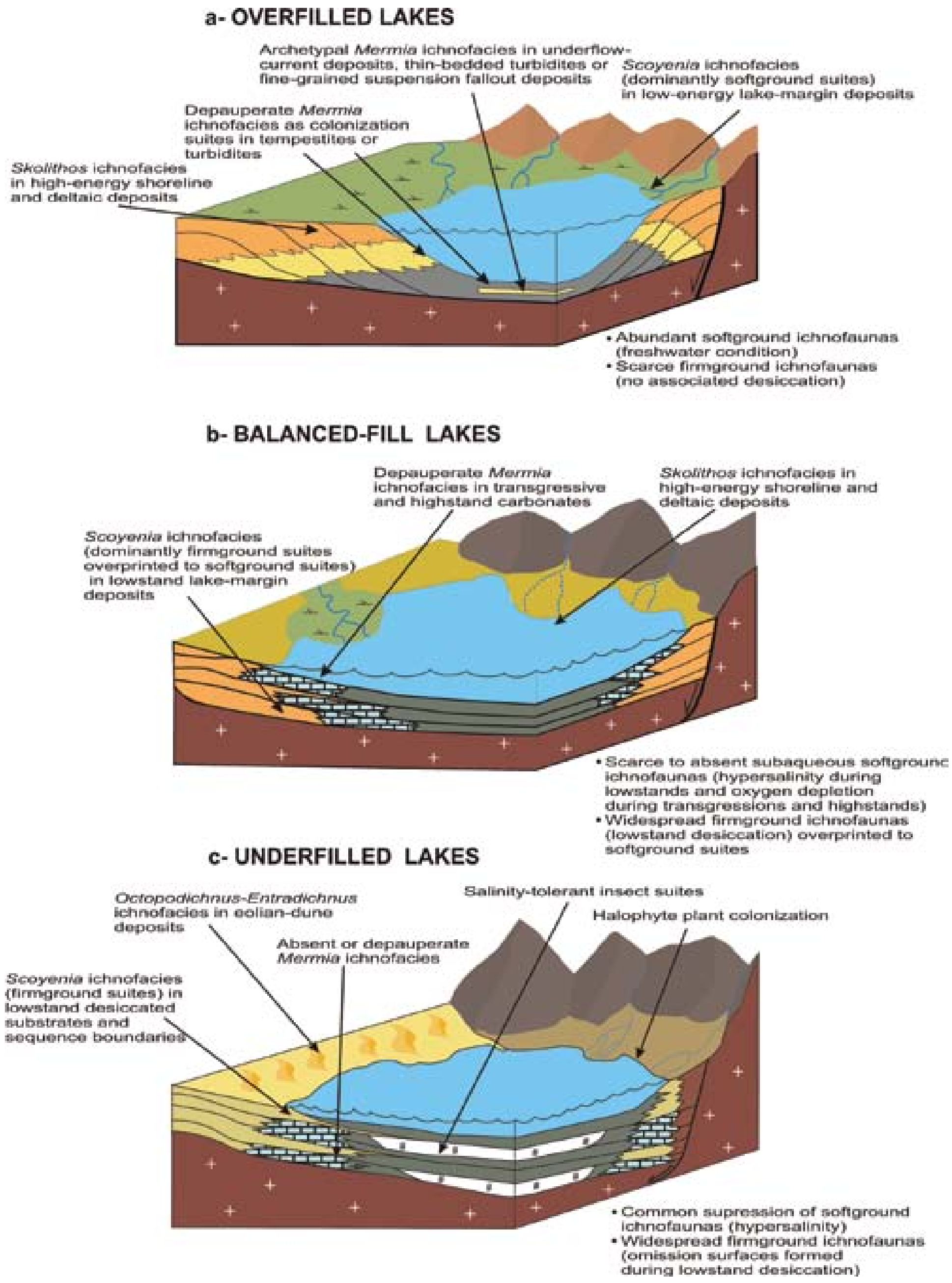

Figure 12.13 Trace-fossil assemblages, environmental controls, and lacustrine sequence stratigraphy. (a) Overfilled lakes. (b) Balanced-fill lakes. (c) Underfilled lakes. Modified from Buatois and Mángano (2004a, 2009a) with stratal patterns illustrated after Bohacs *et al.* (2000).

progradation are the rule (Fig. 12.14). Distal facies commonly consist of underflow-current and background-fallout deposits hosting the *Mermia* ichnofacies. Intermediate facies may contain wave-dominated delta-front and nearshore deposits, including storm-emplaced hummocky cross-stratified sandstone and fair-weather wave- and combined-flow ripple cross-laminated sandstone. Grazing trails of the *Mermia* ichnofacies may form colonization suites at the top of storm beds in such settings. However, assemblages are commonly impoverished with respect to those of the more distal facies (Buatois and Mángano, 1998). Under conditions of moderate to high energy due to continuous wave action, the *Skolithos* ichnofacies tends to occur. More energetic, proximal facies, encompassing trough and tabular cross-bedded distributary-channel sandstone, are commonly unbioturbated. Locally, these deposits may contain escape trace fossils, and vertical domiciles of suspension feeders, representing the *Skolithos* ichnofacies (e.g. Melchor *et al.*, 2003).

In the case of deep overfilled lakes, extensive basin-floor turbidite systems are formed. Middle to distal regions of turbidite-lobe successions are characterized by the *Mermia* ichnofacies which may comprise both pre- and post-depositional suites in thin-bedded turbidite sandstone (e.g. Buatois *et al.*, 1996b; Buatois and Mángano, 1998). Thick-bedded turbidites are typically unbioturbated. Paleoenvironmental zonations in aggradational and progradational turbidite lobes can be established by integrating ichnological and sedimentological evidence (e.g.

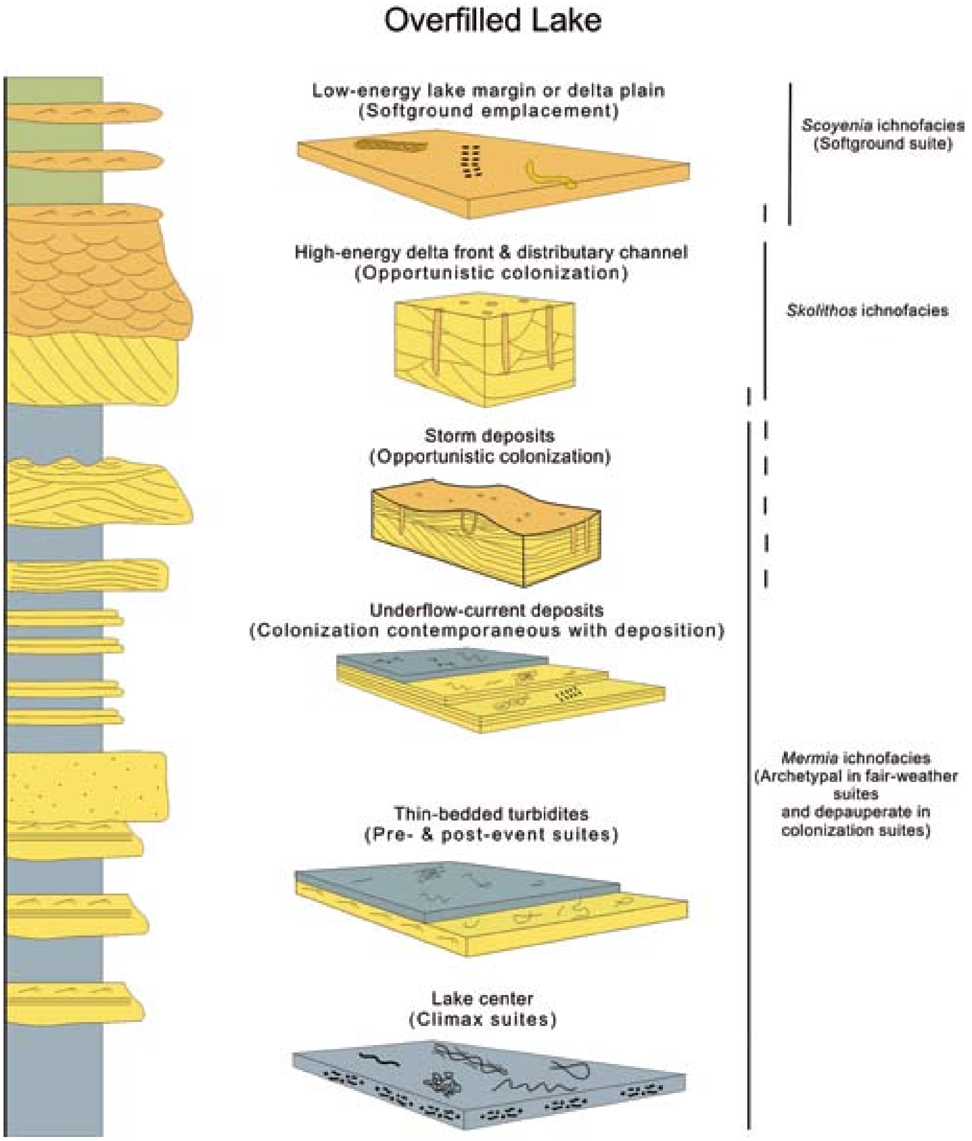

Figure 12.14 Trace-fossil distribution in overfilled lake basins. Note the overwhelming dominance of softground suites and the progressive replacement of ichnofacies due to shallowing (after Buatois and Mángano, 2009a).

Buatois and Mángano, 1995c; Buatois *et al.*, 1996b). Organic matter in overfilled lakes is essentially derived from land plants, representing the prime source of nutrients and, therefore, favoring the development of a deposit-feeding benthic fauna in permanently subaqueous, low-energy zones. Because such large lakes usually do not experience desiccation, firmground suites are rare, and only the softground suite of the *Scoyenia* ichnofacies is present.

BALANCED-FILL LAKES

Balanced-fill lake basins are characterized by rates of sediment/water supply in balance with potential accommodation (Bohacs *et al.*, 2000). Carbonate and siliciclastic facies accumulate in lakes that periodically shift from hydrologically open to closed and vice versa. In contrast to overfilled lakes, successions record not only progradational parasequences, but also aggradation of chemical sediments due to desiccation. Abundant firmground trace-fossil suites occur in balanced-fill lakes, but softground assemblages are usually depauperate (Fig. 12.15). During lowstands, shallow balanced-fill lakes are characterized by relatively thin aggradational parasequences due to desiccation (Bohacs *et al.*, 2000). Due to pervasive desiccation, lowstand deposits tend to host abundant and widespread ichnofaunas of the *Scoyenia* ichnofacies. In particular, the firmground suite of this ichnofacies, containing striated trace fossils, such as *Scoyenia* and *Spongeliomorpha*, is common (e.g. Bromley and Asgaard, 1979; Gierlowski-Kordesch, 1991; Metz, 1995; Clemensen *et al.*, 1998). Biogenic structures are usually preserved during subsequent flooding by rapid influx of sand.

During lowstands relatively thick aggradational parasequence sets form in lake-floor turbidite systems if the balanced-fill lakes are of sufficient depth (Bohacs *et al.*, 2000). Under

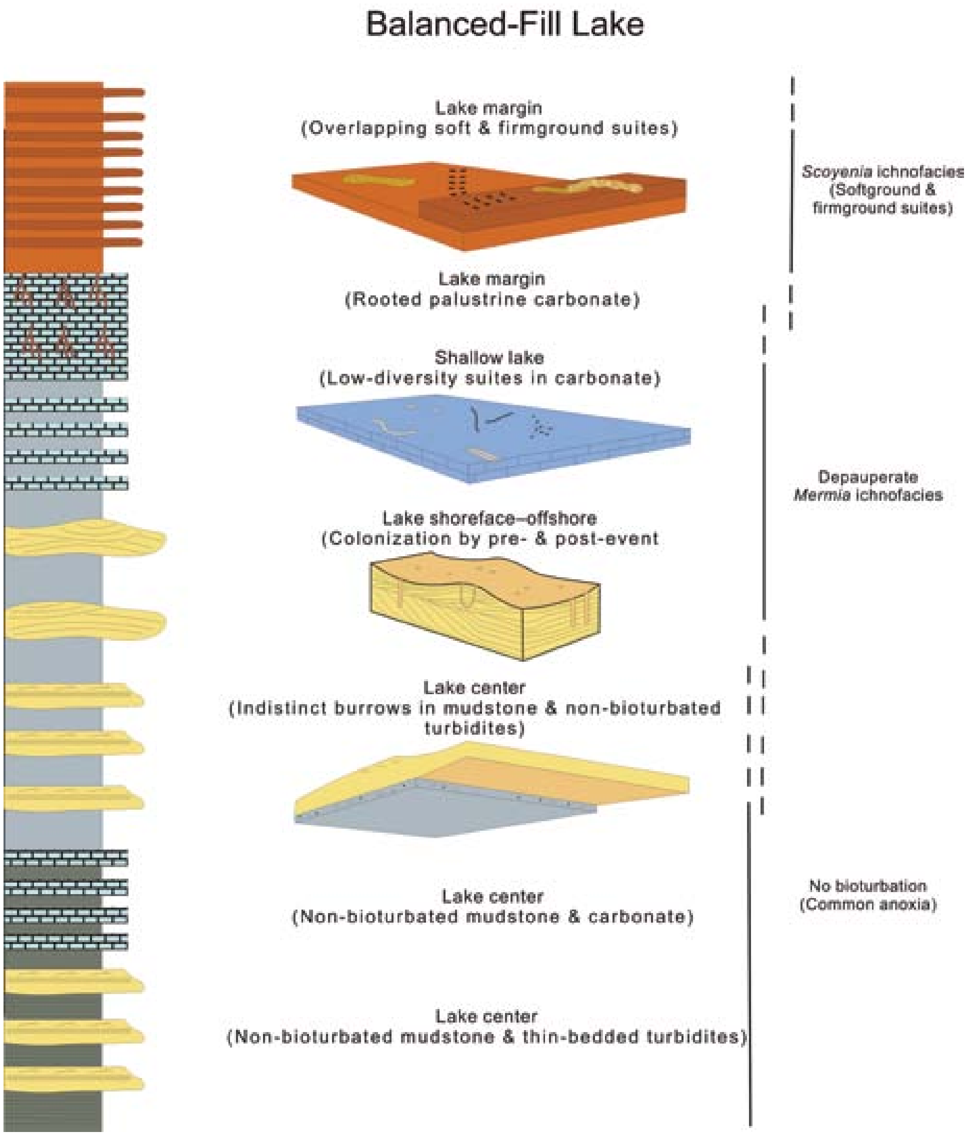

Figure 12.15 Trace-fossil distribution in balanced-fill lake basins. Note the paucity of subaqueous suites and the common superimposition of softground and firmground suites in lake-margin deposits (after Buatois and Mángano, 2009a).

these conditions, no firmground suites occur in the lowstand package. Lake hydrology is closed during lowstands and salinity usually increases (Bohacs *et al*., 2000), imposing a stress factor on the lake biota and, therefore, softground ichnofaunas are of low diversity if not absent at all. Ichnofaunas in thin-bedded turbidites of balanced-fill lakes are less abundant and diverse than those in turbidites of overfilled lakes (Buatois *et al*., 1996b; Buatois and Mángano, 2007; Uchman *et al*., 2007).

Parasequences formed during transgressions are relatively thick and display retrogradational stacking patterns, while highstand parasequences are variable in thickness and are either aggradational or progradational (Bohacs *et al*., 2000). Freshwater conditions are common during transgression, but dysaerobic conditions may prevail, imparting a stress factor on lacustrine communities. Although trace fossils may occur locally in transgressive and highstand carbonates, ichnodiversity is low and trace fossils are produced by epifaunal rather than infaunal organisms, suggesting brief periods of oxygenated bottom waters, but permanently anoxic interstitial waters (e.g. Buatois *et al*., 2000). The depauperate *Mermia* ichnofacies is characteristic of these deposits. Further complications result from the low preservation potential of trace fossils in carbonates due to diagenetic alteration. Scarcity or even absence of biogenic structures due to oxygen depletion may also be the rule in transgressive and highstand siliciclastic deposits of balanced-fill lakes (e.g. Olsen, 1989; Mángano *et al*., 1994, 2000; Metz, 1995). During highstand progradation of deltaic systems, elements of the *Skolithos* ichnofacies may occur in delta mouth-bar deposits (Bromley and Asgaard, 1979; Mángano *et al*., 1994, 2000).

UNDERFILLED LAKES

Underfilled-lake basins occur when rates of accommodation exceed rate of supply of sediment/water (Bohacs et al., 2000). In

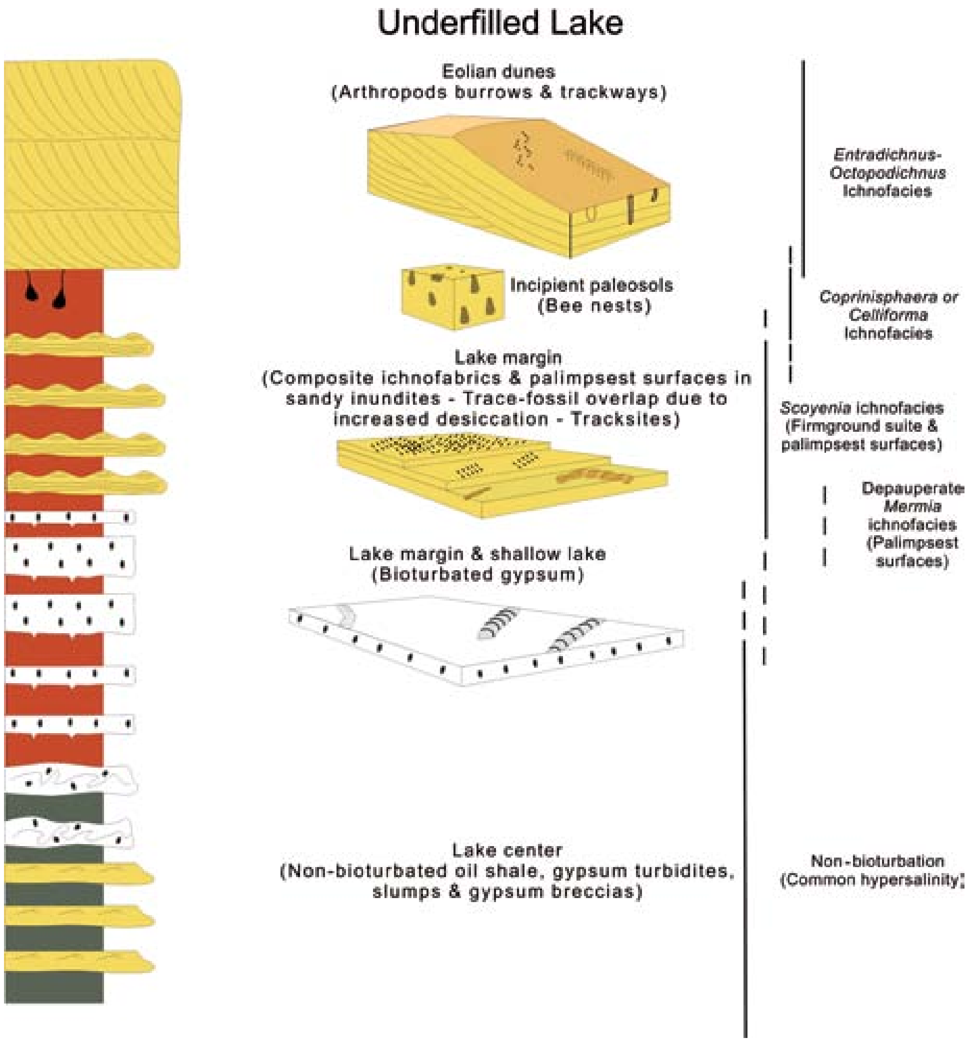

Figure 12.16 Trace-fossil distribution in underfilled lake basins. Note the typical absence of bioturbation in most of the subaqueous deposits as a result of hypersalinity. Instead of progressive replacement of ichnofacies throughout the stratigraphic column, a complex overlap of suites characterizes the lake-margin interval reflecting omission surfaces formed in response to desiccation (after Buatois and Mángano, 2009a).

hydrologically closed lakes, deposition of evaporites dominates and parasequences record vertical aggradation. The *Scoyenia* ichnofacies is widespread in underfilled lake basins, but the *Mermia* ichnofacies is commonly absent (Fig. 12.16). Lowstand deposition is characterized by evaporite accumulation in remnant pools developed in the zones of maximum subsidence (Bohacs *et al.*, 2000). Evaporite pools are very stressful environments and almost invariably lack biogenic structures. In the remaining zones, sediments that accumulated during the previous highstand experience extreme desiccation during lowstand (Bohacs *et al.*, 2000).

The *Scoyenia* ichnofacies is associated with lowstand desiccated substrates in underfilled lakes (e.g. Metz, 1996, 2000; Scott *et al.*, 2007b). The density of arthropod trackways, as well as various trace fossils produced by insects, may be high, forming tracked omission surfaces (e.g. Zhang *et al.*, 1998; Minter *et al.*, 2007b; Scott *et al.*, 2007b; Bohacs *et al.*, 2007). Extensive surfaces with high densities of tetrapod trackways or tracksites occur also (e.g. Farlow and Galton, 2003; Szajna and Hartline, 2003). Some of these omission surfaces may represent sequence boundaries expressed by co-planar surfaces of lowstand and subsequent flooding (Scott *et al.*, 2009) (Box 12.2). Lake-level fluctuations, particularly in gently dipping lacustrine coastal plains, are conducive to complex cross-cutting relationships due to trace-fossil suite overprinting, particularly where the surfaces involve more than one transgressive-regressive cycle (Scott *et al.*, 2009). During pluvial periods, underfilled lakes experience rapid expansion and flash floods reach the basin, leading to deposition of event sandstones. Trace-fossil preservation is mostly linked to rapid influx of sand via sheet floods entering into the lake (Zhang *et al.*, 1998).

Hypersalinity usually prevents the establishment of a subaqueous *Mermia* ichnofacies during transgression and highstand. However, elements of the *Mermia* ichnofacies may occur, albeit in reduced numbers, in very shallow-water thin deposits immediately above flooding surfaces at the base of parasequences. This assemblage is abruptly replaced upward by the *Scoyenia* ichnofacies reflecting lake regression (Metz 1996, 2000). Additionally, dwelling traces possibly produced by aquatic chironomid larvae may be present (Rodríguez-Aranda and Calvo, 1998; Uchman and Álvaro, 2000).

Box 12.2 Ichnological complexity of co-planar surfaces in underfilled lakes

A set of interfingering Upper Pleistocene and Holocene exhumed surfaces in the underfilled saline Lake Bogoria of Kenya reveals a complex story of changes in lake level and environmental controls on biogenic structures through time. Ongoing exhumation of the surface near the present shoreline has reactivated the sediments as a substrate for animal and plant colonization. The modern environmental setting at Lake Bogoria is very similar to that of the preserved exhumed surfaces, favoring comparisons on both sides of the fossilization barrier. These exhumed surfaces are amalgamated in places forming a co-planar surface that includes up to five suites of animal and plant traces, which are commonly overprinted forming palimpsest surfaces. Suite 1 includes the traces of chironomid larvae formed in subaqueous lacustrine environments. Suite 2 consists of flamingo traces formed at the shoreline. This suite is comparable to the *Grallator* ichnofacies. Suite 3 comprises trails (incipient *Gordia* isp. and *Helminthoidichnites* isp.) and burrows systems (incipient *Labyrintichnus* and *Vagorichnus* isp.). These were emplaced in relatively fresh, saturated to extremely shallow subaqueous substrates. This suite compares well with the *Mermia* ichnofacies. Suite 4 consists of simple vertical (*Skolithos* ispp.), simple horizontal (*Planolites* isp.) and branched (incipient *Vagorichnus* isp. and *Spongeliomorpha* isp.) burrows, trackways (e.g. incipient *Diplichnites*, *Diplopodichnus*, and *Siskemia*), rhizoliths, and various vertebrate footprints including mainly birds and mammals. This suite is present at the lake margin and is associated with substrates of various degrees of consolidation, commonly near fresh and brackish water sources, including hot-springs and rivers. The striated burrows (i.e. *Spongeliomorpha* isp.) occur in drying, firmer, and slightly indurated substrates. This suite illustrates the *Scoyenia* ichnofacies, including both pre- and post-desiccation elements. Suite 5 contains termite (?*Termitichnus* isp.) and ant nests, simple burrows (*Planolites* isp., *Palaeophycus* isp.), meniscate trace fossils (?*Beaconites* isp., *Taenidium* isp.), and rhizoliths. This suite records colonization in subaerially exposed substrates associated with low water tables, and favors comparison with paleosol assemblages described elsewhere. Suite overprinting of the exhumed surface reflects lake-level fluctuations. For example, in some areas the terrestrial suite 5 overprints the lake-margin suite 4 and the subaqueously emplaced suite 2 as a result of shoreline regression. Because the surface is active today, overprinting of the subaerial, shoreline, and subaqueous portions of the surfaces by animal and plant traces, representing the five suites recognized, is occurring in response to the various sets of environmental factors that control the lateral distribution of biogenic structures. The example from Lake Bogoria clearly illustrates the complexity of the ichnology of lacustrine co-planar surfaces and sheds new light onto the nature of continental ichnofacies.

References: Scott *et al*. (2009).

Transgressive systems tracts recorded by thin transgressive parasequences usually reflect drastic ichnofaunal changes, from terrestrial assemblages (*Coprinisphaera* or *Celliforma* ichnofacies) to transitional terrestrial–subaqueous assemblages (*Scoyenia* ichnofacies) and salinity-tolerant subaqueous monospecific assemblages of *Beaconites filiformis* attributed to chironomids (Uchman and Álvaro, 2000). Rapid changes in depositional conditions reflecting desiccation during vertical aggradation led to the formation of composite ichnofabrics reflecting successive bioturbation events.

12.7.2 ALLUVIAL PLAINS

In alluvial settings, the sparse distribution of trace fossils primarily reflects changes in depositional systems which, in turn, may be linked to systems tracts (Buatois and Mángano, 2004, 2007). Widespread erosion, and high energy and sedimentation rates lead to channel amalgamation, and extensive reworking of fluvial deposits, preventing formation and/or preservation of biogenic structures in fluvial channels. As previously discussed, interfluve areas are commonly characterized by rooted paleosols, and terrestrial insect ichnofossils may occur, particularly in late Mesozoic and Cenozoic strata (Genise *et al*., 2000, 2004b; Genise, 2004). In particular, any of the various paleosol ichnofacies may delineate sequence boundaries.

Due to higher accommodation during the late lowstand, increasingly isolated fluvial channels encased in overbank deposits tend to occur, promoting preservation of biogenic structures. Eventually transgressive lacustrine and marsh deposits accumulate when rate of accommodation exceeds sediment supply (Legarreta *et al*., 1993; Posamentier and Allen, 1999). These changes may be paralleled by the progressive replacement of vertical dwelling burrows, and escape trace fossils of the *Skolithos* ichnofacies in active channels by low-diversity assemblages of meniscate trace fossils in abandoned channels. Both the softground and firmground suites of the *Scoyenia* ichnofacies, and even the subaqueous *Mermia* ichnofacies in overbank deposits and ponds may occur as a result of increased accommodation (Buatois and Mángano, 2004a, 2007). If, during transgression the alluvial plain becomes affected by marine processes (e.g. tides), depauperate examples of the brackish-water *Skolithos* and *Cruziana* ichnofacies may occur. This situation is not uncommon because tidal influence and brackish-water conditions may extend for tens of kilometers inland (Shanley *et al*., 1992). This trend in ichnofacies replacement is reversed under increased sediment supply, and decreased fluvial accommodation leading to deltaic progradation, and increased establishment of channel bodies during the subsequent highstand.

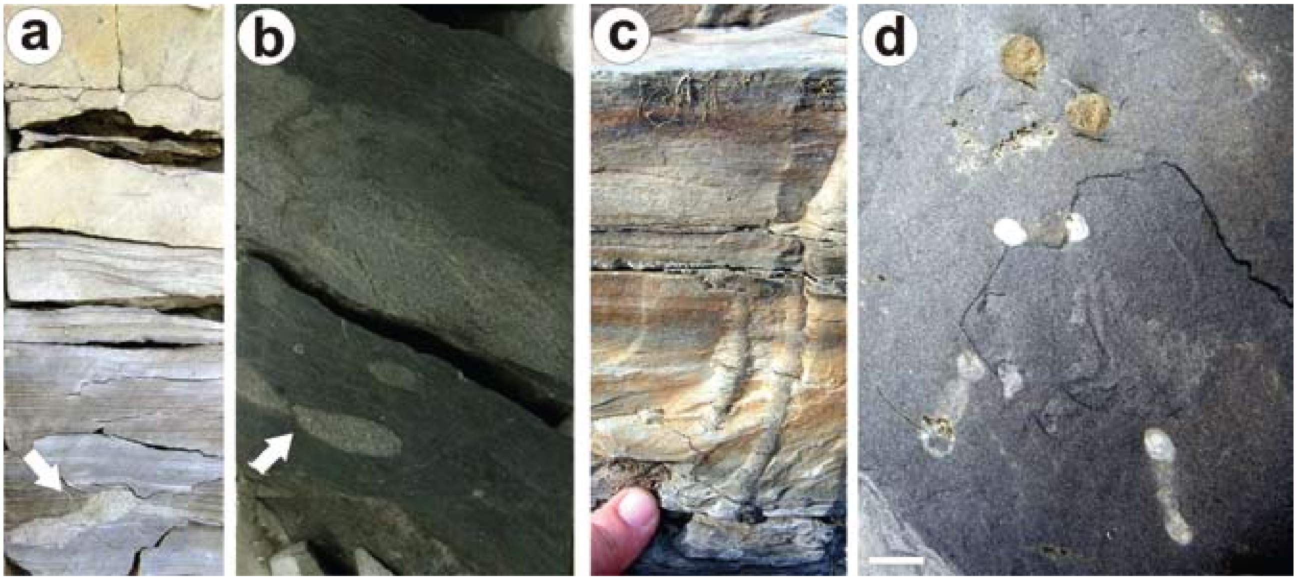

Figure 12.17 Autogenic examples of the *Glossifungites* ichnofacies. (a) Erosionally based distributary-channel deposits upon fine-grained interdistributary-bay deposits. The *Glossifungites* ichnofacies, represented by *Rhizocorallium* (arrow), occurs at the base of the channel delineating an autogenic firmground. Lower Miocene, Tácata Field, Eastern Venezuela Basin. See Buatois *et al.* (2008). Core width is 9 cm. (b) Thin-bedded turbidites. The erosive base is delineated by an autogenic *Glossifungites* ichnofacies, illustrated by *Rhizocorallium* (arrow), representing an autogenic firmground. Lower Miocene, La Blanquilla Basin, Offshore Venezuela. Core width is 6.5 cm. (c) Cross-section view of a firmground *Diplocraterion* penetrating from the base of a turbidite sandstone. Lower Oligocene, Sub-Cergowa Beds, Szczawa–Centrum, Outer Carpathians, Poland. See Uchman and Cieszkowski (2008b). (d) Bedding-plane view of several specimens of firmground *Diplocraterion* filled with coarser-grained sediment. Lower Oligocene, Sub-Cergowa Beds, Szczawa-Centrum, Outer Carpathians, Poland. See Uchman and Cieszkowski (2008c). Scale bar is 1 cm.

12.8 EVALUATION OF THE MODELS

Even its critics recognized that sequence stratigraphy represents a revolution in sedimentary geology (Miall, 1995). Undoubtedly, the success of ichnology as a tool in sequence stratigraphy records an expansion of the discipline, which has greatly enhanced its value to solve problems in sedimentary geology and basin analysis, particularly in the petroleum industry. However, a series of misconceptions surrounds the application of ichnology in this field. The widely accepted belief that the *Glossifungites* ichnofacies indicates sequence boundaries is somewhat surprising despite the fact that its true significance has been reiterated in several papers (e.g. MacEachern *et al.*, 1999a). As discussed above, in siliciclastic successions the *Glossifungites* ichnofacies delineates not only sequence boundaries, but also other surfaces, such as transgressive surfaces of erosion.

In addition, while erosional exhumation due to relative sea-level changes is commonly invoked to explain occurrences of substrate-controlled ichnofacies in siliciclastic rocks, some surfaces may be autogenic (e.g. McIlroy, 2007b; Buatois *et al.*, 2008; Yang *et al.*, 2009). As noted by MacEachern *et al.* (2007b), regional correlation of the surface is essential to recognize its allogenic nature. Allogenic surfaces tend to be regionally mappable and separate genetically unrelated facies successions.

Examples of autogenic surfaces in marginal- and shallow-marine settings are known to be produced due to erosion along the base of estuarine, distributary (Fig. 12.17a) and tidal channels, as well as cut-bank margins of tidal channels and creeks (e.g. Gingras *et al.*, 2000; MacEachern *et al.*, 2007c; Buatois *et al.*, 2008). Autogenic tidal scouring is a common process in a wide variety of subenvironments within tide-dominated deltas, further complicating recognition of firmgrounds produced by relative sea-level changes (Willis, 2005). Widely distributed examples of the *Glossifungites* ichnofacies have been noted to be associated with autogenic erosion in tidal channels of tide-dominated deltas (McIlroy, 2007). The *Glossifungites* ichnofacies also occurs as result of intense erosion in the zone of maximum wave energy of wave-dominated tidal flats (Yang *et al.*, 2009). More rarely, firmground surfaces can form even without erosion, during pauses in lateral accretion of tidal point bars (Bechtel *et al.*, 1994).

In the deep-marine realm, different types of currents, including bottom, oceanic and turbidity currents (Fig. 12.17b–d), may significantly scour the sea bottom, exposing previously buried firmground sediment to colonization (Ozalas *et al.*, 1994; Savrda *et al.*, 2001; Wetzel *et al.*, 2008). Particularly relevant is the increased recognition that deep *Diplocraterion* of the *Glossifungites* ichnofacies occur commonly at the base of turbidite channels penetrating into muddy sediment and indicating significant erosion and bypass of coarser-grained sediment (Gibert *et al.*, 2001a, b; Hubbard and Shultz, 2008; Gerard and Bromley, 2008; Uchman and Cieszkowski, 2008c). Gerard and Bromley (2008) noted the more subtle presence of these firmground burrows not only at the base of channels but also within graded mudstone. Occurrence of firmground burrows penetrating from by-pass surfaces suggests the potential presence of thick sands in more axial and/or downcurrent positions of the channel.

13 Trace fossils in biostratigraphy

> Invertebrate trace fossils can be used for the stratigraphic correlation of otherwise nonfossiliferous clastic sequences, provided that they share particular "fingerprints" and thus reflect behavioral diversification within taxonomically coherent groups of (commonly unknown) tracemakers.
>
> Dolf Seilacher
> *Trace Fossil Analysis* (2007)

In contrast to body fossils, trace fossils are often characterized by long temporal ranges and narrow facies ranges (see Section 1.2.8). As a consequence, trace fossils are highly useful in paleoenvironmental analysis and less so in biostratigraphic studies. Although most ichnogenera display long temporal ranges, it is also true that some biogenic structures can preserve specific fingerprints of their producers. If the producers record significant evolution, then the trace fossils may also yield biostratigraphic implications (Seilacher, 2007b). There are some ichnofossils that reflect particular kinds of animals in which body morphology and behavior underwent closely related evolutionary transformations through time (Seilacher, 2000). The more complex (in terms of fine morphological detail) a structure is, the more direct its biological relationship, distinctive its behavioral program, and hence, larger its biostratigraphic significance. Historically invertebrate trace fossils have been applied in biostratigraphy in two main areas: the positioning of the Proterozoic–Cambrian boundary (e.g. Seilacher, 1956; Banks, 1970; Alpert, 1977; Crimes *et al.*, 1977; Narbonne *et al.*, 1987; Crimes, 1992, 1994; Jensen, 2003) and the establishment of relative ages in lower Paleozoic clastic successions based on *Cruziana* and related trilobite trace fossils (e.g. Seilacher, 1970, 1992a, 1994; Crimes, 1975). In recent years, attempts have been made to incorporate other ichnotaxa, such as *Arthrophycus* and related trace fossils (e.g. Seilacher, 2000; Mángano *et al.*, 2005b). In the field of vertebrate ichnology, tetrapod trackways have a long tradition in biostratigraphy, particularly in upper Paleozoic–Mesozoic strata (e.g. Haubold and Katsung, 1978; Lucas, 2007). In this chapter we will address the utility of both invertebrate and vertebrate trace fossils in biostratigraphy.

13.1 THE PROTEROZOIC–CAMBRIAN BOUNDARY

Arguably, the most intensely researched area in ichnostratigraphy is the Proterozoic–Cambrian boundary (Fig. 13.1). In fact, the Proterozoic–Cambrian boundary Global Standard Stratotype-section and Point (GSSP) has been established at the base of the *Treptichnus pedum* zone at Fortune Head, Newfoundland (Narbonne *et al.*, 1987; Brasier *et al.*, 1994; Landing, 1994). Subsequently, the *Treptichnus pedum* zone was extended approximately 4 m below the boundary at the GSSP (Gehling *et al.*, 2001). Trace-fossil data are, therefore, essential to establish the position of the most important boundary in the stratigraphic record.

Alpert (1977) established one of the first syntheses by defining three main groups of trace fossils. Group 1 contains ichnotaxa restricted to the Proterozoic (e.g. *Harlaniella*, *Intrites*). Since the trace-fossil origin of these structures has now been abandoned (see Section 14.1.2), group 1 is no longer valid. Group 2 includes all those ichnotaxa that occur for the first time in the Proterozoic, but range into the Phanerozoic (e.g. *Helminthopsis, Helminthoidichnites*). Finally, group 3 contains ichnotaxa that first occur in Lower Cambrian rocks (e.g. *Diplocraterion*, *Arenicolites*). Within this group, there are some ichnotaxa with a stratigraphic range restricted to the Lower Cambrian, such as *Syringomorpha nilssoni* (Fig. 13.2a), *Psammichnites gigas* (Fig. 13.2b), and *Didymaulichnus miettensis* (Fig. 13.2c).

Further research by Crimes (1987, 1994), Narbonne *et al.* (1987), Walter *et al.* (1989), MacNaughton and Narbonne (1999), and Jensen (2003) led to the definition of a series of biostratigraphic zones encompassing the Proterozoic–Cambrian boundary. In particular, Jensen (2003) presented a tentative biostratigraphic scheme that includes six zones: three in the Neoproterozoic and three in the Lower Cambrian. The lowermost Neoproterozoic zone supposedly consists of simple horizontal trace fossils assigned to *Planolites*, but its validity is still questionable (Jensen *et al.*, 2006) and is not considered here.

Accordingly, a scheme of two Ediacaran zones and three Lower Cambrian zones is adopted (Fig. 13.3). The lower Ediacaran zone consists of poorly specialized grazing trails, such as *Helminthoidichnites*, *Helminthopsis*, and *Archaeonassa*. Dickinsonid and *Kimberella* trace fossils occur also in this zone (see Section 14.1.2). Dickinsonid resting traces have been attributed to the recently proposed ichnogenus *Musculopodus* (Getty and Hagadorn, 2008), but they differ from the type specimens of this ichnotaxon and, therefore, they best represent a new, still unnamed ichnogenus. *Kimberella* rasping trace fossils have

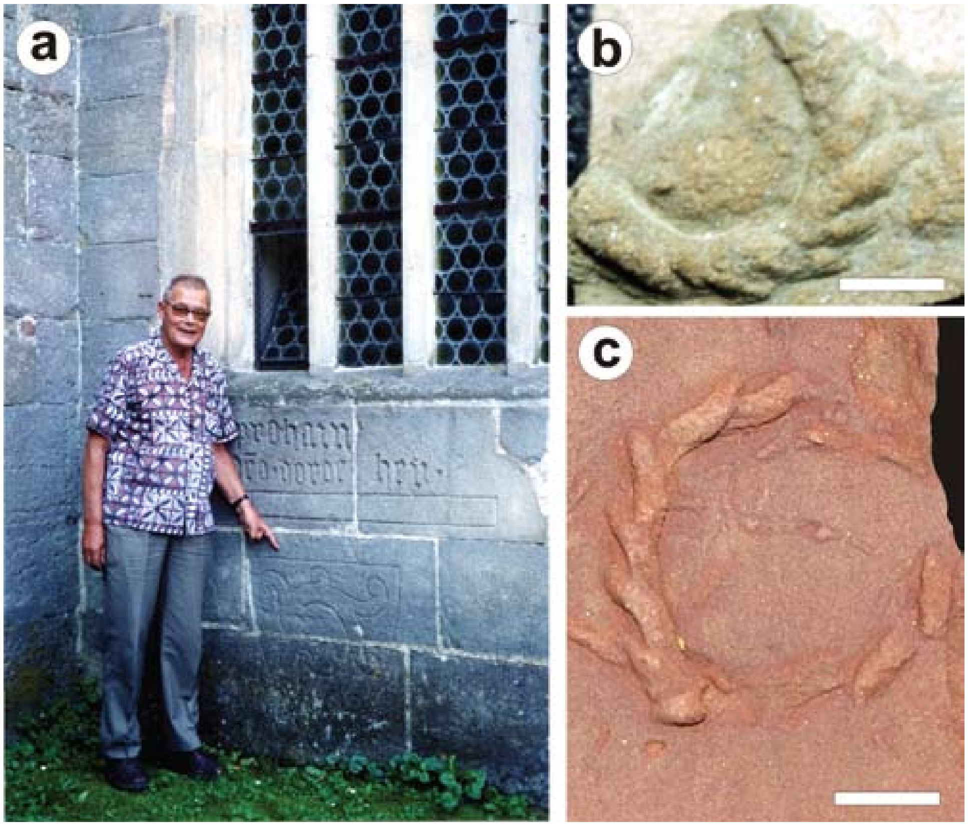

Figure 13.1 *Treptichnus pedum*, whose first appearance indicates the Proterozoic–Cambrian boundary. (a) Dolf Seilacher pointing towards the image of a *pedum* (i.e. crook) carved on a wall of a Tubingen church, where he lived while a university student after the Second World War. Photo taken in the summer of 2003. (b) *Treptichnus* (*Phycodes*) *pedum*. Lower Cambrian, Nobulus Shale, Salt Range, Pakistan. Seilacher introduced this ichnospecies in a classic paper on the ichnology of the Salt Range Cambrian in 1955. (c) *Treptichnus* (*Phycodes*) *pedum*. Lower Cambrian, Klipbak Formations, Brandkop Subgroup, Gannabos Farm, South Africa. Scale bars are 1 cm.

been included in *Radulichnus* (Seilacher *et al.*, 2005). This lower Ediacaran zone is represented in the Ediacara Member of South Australia (Gehling *et al.*, 2005) and the Ust Pinega Formation of the White Sea, Russia (Fedonkin, 1985). The age of this interval is approximately 560–550 Ma (Martin *et al.*, 2000; Jensen *et al.*, 2006). The upper Ediacaran zone includes the oldest branching burrow systems (*Treptichnus* and *Streptichnus*), as well as three-lobate trace fossils similar to *Curvolithus*. This zone is represented in the Urusis Formation of the Nama Group in Namibia (Jensen *et al.*, 2000). Radiometric dating in Namibia indicates that this zone is approximately bracketed between 550 and 542 Ma (Grotzinger *et al.*, 1995; Jensen *et al.*, 2006).

The lowermost Lower Cambrian zone is referred to as the *Treptichnus pedum* zone, and is of Fortunian age. Its base, the Proterozoic–Cambrian boundary, is marked by the first appearance of *T. pedum*. The zone also contains *Gyrolithes polonicus* and *Bergaueria*. This zone has been identified in many sections worldwide, including the Chapel Island Formation of Avalon Peninsula, Newfoundland (Narbonne *et al.*, 1987; Droser *et al.*, 2002), the upper interval of the Ingta Formation in the Mackenzie Mountains, Canada (MacNaughton and Narbonne, 1999), and the Nomtsas Formation of Namibia (Crimes and Germs, 1982; Geyer and Uchman, 1995), among many other areas. The *Rusophycus avalonensis* zone contains the oldest bilobate, trilobite-like resting traces (*R. avalonensis*) together with a bilobate epichnial trail that has been historically referred to as *Taphrelminthopsis circularis*, although it should be removed from this ichnogenus (Jensen *et al.*, 2006). This zone has been identified in the Chapel Island Formation of Avalon Peninsula (Narbonne *et al.*, 1987), and the Backbone Ranges Formation and lower interval of the Vampire Formation in the Mackenzie Mountains (MacNaughton and Narbonne, 1999). The *Cruziana tenella* (= *problematica*) zone contains the oldest bilobate, trilobite-like locomotion traces (*Cruziana problematica*) together with large back-filled traces (*Psammichnites gigas*). This zone occurs in the middle to upper interval of the Vampire Formation in the Mackenzie Mountains (MacNaughton and Narbonne, 1999).

To a large extent, this biostratigraphic scheme is based on shallow-marine ichnofaunas, which were considerably more diverse than their deep-marine counterparts by the Ediacaran–Cambrian (Buatois and Mángano, 2004). The ichnogenus *Oldhamia* has a widespread distribution, particularly in Lower Cambrian deep-marine deposits and its potential in biostratigraphy has been noted (e.g. Seilacher, 1974, 2007b; Lindholm and Casey, 1990; Seilacher *et al.*, 2005; MacNaughton, 2007). *Oldhamia curvata*, *O. radiata* (Fig. 13–2d), and *O. flabellata* are known from Lower Cambrian rocks, and *O. antiqua* has been recorded in Lower Cambrian to, more rarely, lower Middle Cambrian rocks (Seilacher *et al.*, 2005). Unfortunately, *Oldhamia* typically occurs in intensely tectonized rocks that are devoid of body fossils, and extensive empirical support to proposed evolutionary lineages (Lindholm and Casey, 1990; MacNaughton, 2007) is not available yet.

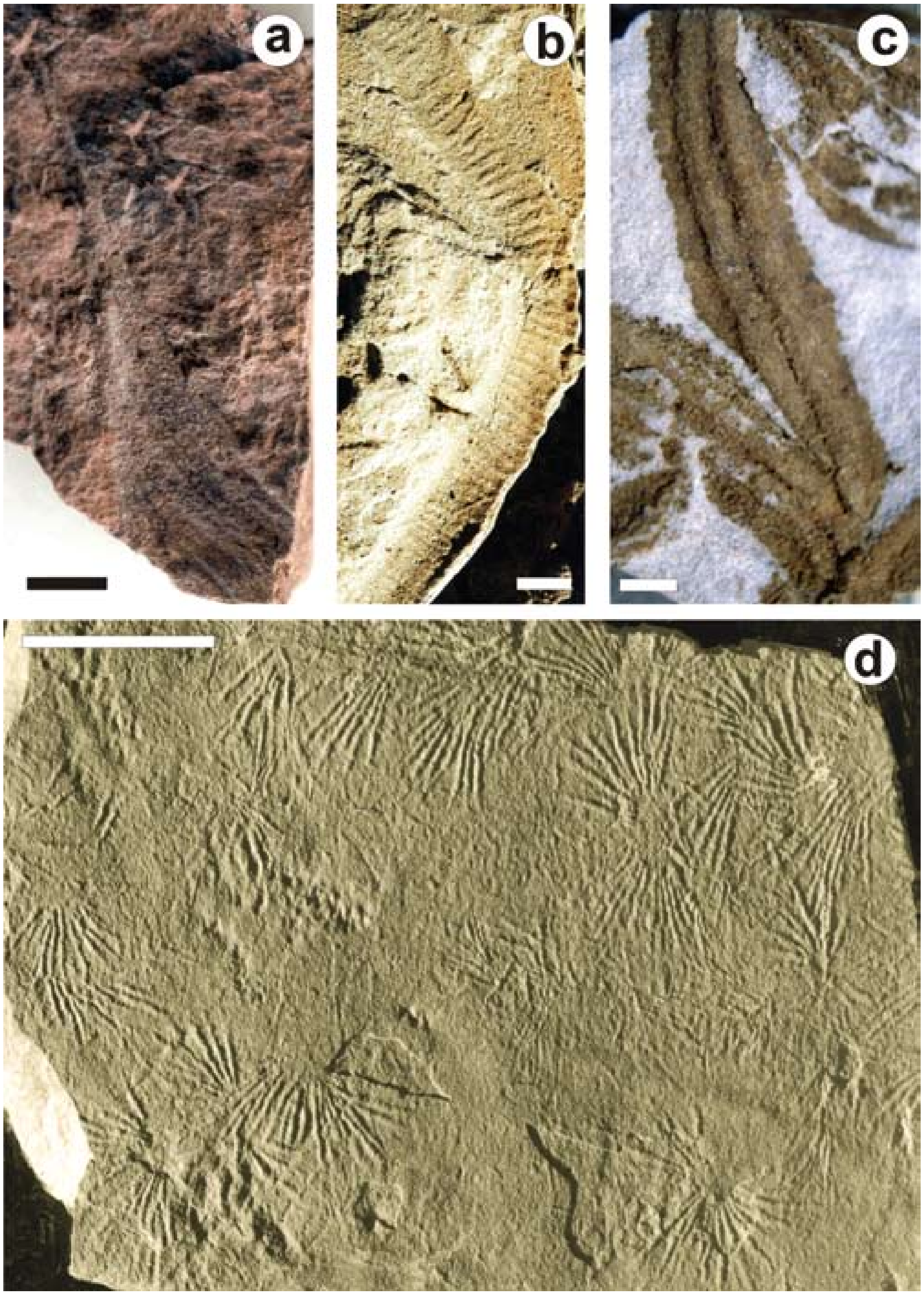

Figure 13.2 Typical Lower Cambrian trace fossils. (a) *Syringomorpha nilssoni*. Campanario Formation, Alfarcito Hills, northwest Argentina. See Mángano and Buatois (2004a). (b) *Psammichnites gigas* (= *Plagiogmus arcuatus*). Parachilna Formation, Ediacara Hills, Australia. See Gehling (2002). (c) *Didymaulichnus miettensis*. Meishucun Formation, Meishucun, Yunnan Province, China. See Crimes and Jiang (1986). (d) *Oldhamia antiqua*. Grand Pitch Formation, Maine, United States. See Seilacher *et al*. (2005). Scale bars are 1 cm.

13.2 *CRUZIANA* STRATIGRAPHY

The so-called *Cruziana* stratigraphy was first developed in the seventies and early eighties based on rocks containing trilobite trace fossils from Wales and Spain, particularly of Furongian (Late Cambrian)–Early Ordovician age (e.g. Crimes, 1969, 1970a, b, 1975; Seilacher, 1970; Moreno *et al*., 1976; Baldwin, 1977; Crimes and Marcos, 1976; Pickerill *et al*., 1984b). However, it was Seilacher (1970, 1990b, 1992a) who further developed the time range and geographic extension of the model. Additional studies have considerably extended this ichnostratigraphic scheme by documenting *Cruziana* and related ichnotaxa from the Lower Cambrian (Series 2) of Western Canada (Magwood and Pemberton, 1990; Seilacher, 1994), Sweden (Jensen, 1990, 1997), Lower to Middle Cambrian of Argentina (Mángano and Buatois, 2003b), and Egypt (Seilacher, 1990b), and Jordan (Seilacher, 1990b); Middle Cambrian (Series 3) of Spain (Legg, 1985), and Poland (Orłowski, 1992); Middle Cambrian to Lower Ordovician of Norway (Knaust, 2004b); Furongian–Lower Ordovician of Argentina (Mángano *et al*., 1996b; 2001b, 2002c,

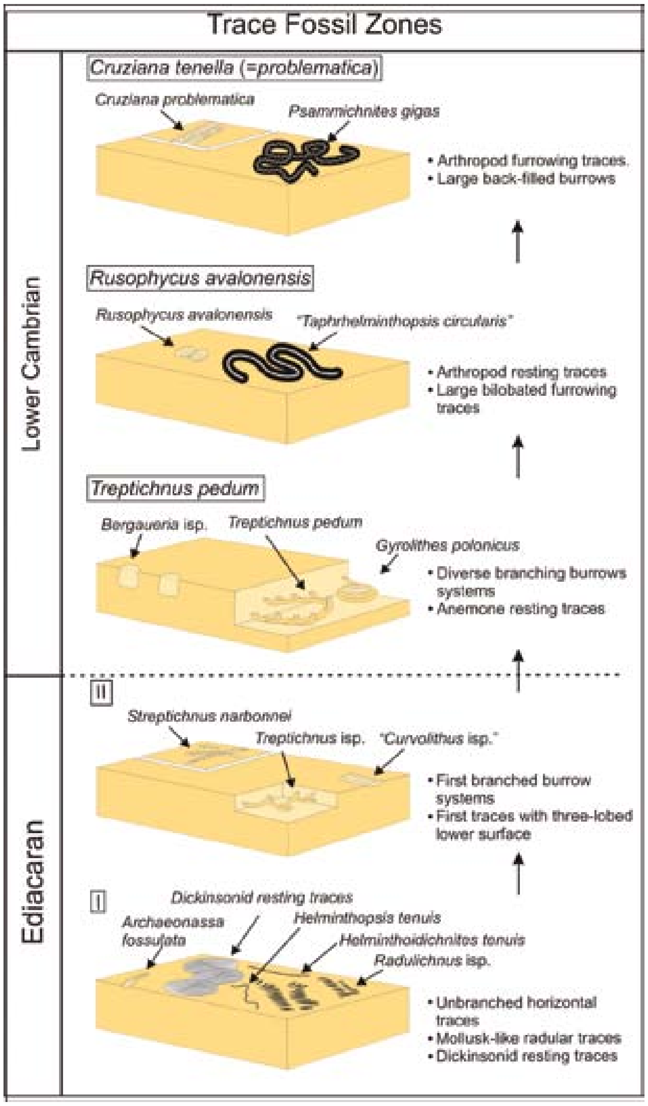

Figure 13.3 Trace-fossil zones spanning the Ediacaran–Cambrian boundary (modified from Jensen, 2003). As noted by Jensen *et al*. (2006), evidence for a lowermost Ediacaran zone characterized by *Planolites* is questionable and, therefore, it has been omitted here.

2005a; Mángano and Buatois, 2003a), Libya (Seilacher *et al*., 2002), Poland (Radwański and Roniewicz, 1963, 1972; Orłowski *et al*., 1971; Żylińska, 1999), and Eastern Canada (Seilacher and Crimes, 1969; Bergström, 1976; Pickerill and Fillion, 1983; Fillion and Pickerill, 1990); Lower Ordovician of Saudi Arabia (El Khayal and Romano, 1988), and Australia (Draper, 1980; Webby, 1983); Upper Ordovician of United States (Osgood, 1970), and Eastern Canada (Stanley and Pickerill, 1998); and Upper Ordovician–Lower Silurian (Llandovery) of Argentina (Seilacher *et al*., 2004; Seilacher, 2005), Libya (Seilacher, 1996, 2005; Seilacher *et al*., 2004), Benin (Seilacher and Alidou, 1988), and Chad (Seilacher *et al*., 2004).

The *Cruziana* stratigraphy is based on ribbon-like bilobate structures (*Cruziana sensu stricto*) and coffee bean-shaped structures (*Rusophycus*) identified at ichnospecies level. Although trilobites were the most likely producers of these structures in lower Paleozoic marine settings, other arthropods may have been involved. Other arthropod trace fossils (e.g. *Dimorphichnus*) have been proposed as having biostratigraphy utility (Seilacher, 1990b). However, their use is still limited. *Cruziana* and *Rusophycos* ichnospecies are based on fine morphological features, particularly the so-called "claw formula" (i.e. the fingerprint left by claws or setae present in the distal part of the walking appendages). However, as leg morphology may be convergent in different groups of trilobites, other features reflecting burrowing behavior (e.g. presence of cephalic impressions, coxal marks, exopodal brushings, pleural or genal spine impressions) are also included in defining a particular ichnotaxon. If leg morphology displays high rates of evolutionary change, then it is possible to establish narrow stratigraphic ranges for the different ichnospecies of *Cruziana* and *Rusophycus*. The most likely correlation is between a particular ichnospecies of *Cruziana* and a number of trilobite species probably phylogenetically related (i.e. belonging to the same family). Fortey and Seilacher (1997) showed the co-occurrence of *C. semiplicata* and *Maladiodella*. However, *C. semiplicata* is common ichnospecies in the Furongian to Tremadocian of northwest Argentina. where *Maladiodella* has not been recorded. The same discrepancy has been noted in the Furongian of the Holy Cross Mountains in Poland (Żylińska, 1999). It is clear that *C. semiplicata* can be produced by other olenids.

Cruziana stratigraphy has been essentially developed for Gondwana, where more than 30 ichnospecies of *Cruziana* (and *Rusophycus*) with biostratigraphic significance have been identified (Seilacher, 1970, 1992a). The stratigraphic ranges of these ichnospecies comprise between one and three series, but the majority of these ichnotaxa are restricted to only one or two series (Fig. 13.4). The most extensive dataset comes from the Furongian to Middle Ordovician interval, although recent improvements have been produced for the Lower Silurian (Llandovery) (Seilacher, 1996) (Figs. 13.5a–j and 13.6a–h). In the stratigraphic scheme proposed by Seilacher (1970, 1992a), *Cruziana* ichnospecies are in turn clustered into groups. This author recognized 11 groups throughout the Paleozoic (e.g. *dispar* group, *semiplicata* group, *rugosa* group). Groups are defined based fundamentally on the claw formula as recorded by scratch-mark morphology and grouping. However, if claw marks are too small, the presence of well-developed exopodal marks and lobes can be used (e.g. *semiplicata* group). Some of these groups display wide geographic distribution validating their use in biostratigraphy. However, many are known only from their type localities. Some of these groups may have just one appearance in the stratigraphic record (e.g. *semiplicata* group), but others may characterize more than one stratigraphic interval. For example, the *omanica* group is mostly Furongian–Tremadocian, but reappears in the Caradocian (represented by *C. petraea*) and the Lower Silurian (Llandovery) (*C. acacensis*). According to Seilacher (1970, 1992a), the Lower Cambrian (Series 2) is represented by the *fasciculata* group, while the *dispar* group spans the Lower to Middle Cambrian (Series 2 to 3). However, *C. fasciculata* has been recently recorded in Upper Cambrian rocks (Mángano

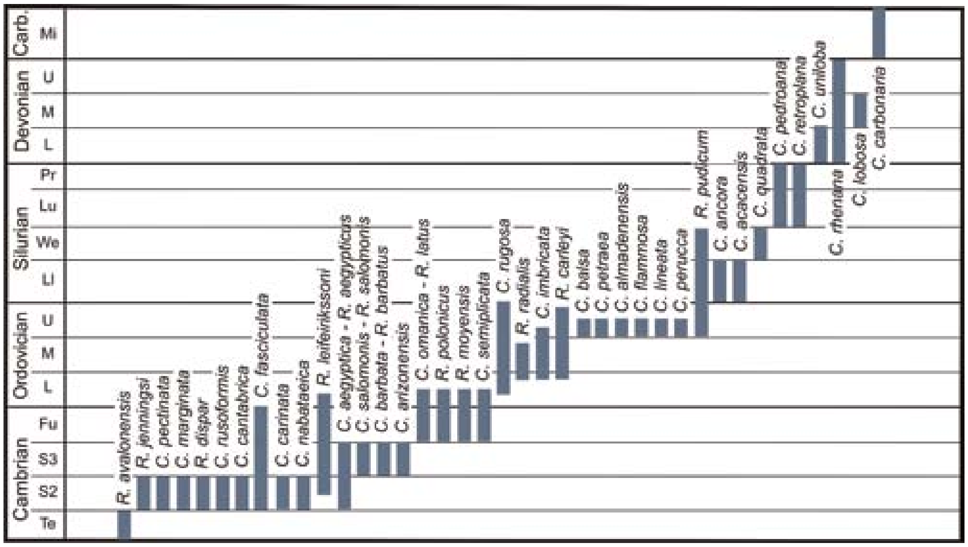

Figure 13.4 *Cruziana* and *Rusophycus* stratigraphy. Some of the stratigraphic ranges should be regarded as tentative due to limited occurrences. *Cruziana rugosa* comprises three ichnosubspecies, *C. rugosa rugosa*, *C. rugosa goldfussi*, and *C. rugosa furcifera*. Modified from Seilacher (1992a).

and Buatois, 2003a). The *semiplicata* group characterizes the Lower Cambrian to Tremadocian. The *rugosa* group is typically Arenigian–Llanvirnian, while the *imbricata* group seems to be restricted to the Arenigian. The Caradocian contains the *almadenensis* group, although one of its ichnospecies (*C. pedroana*) is Upper Silurian (Ludlow–Pridoli). The Ashgillian is characterized by the distinctive *carleyi* group, while the *pudica* group spans the Caradocian–Lower Carboniferous. The *quadrata* group is Lower Silurian–Devonian. The *costata* group seems to be restricted to the Carboniferous, but the true affinities of *C. costata* are doubtful. To illustrate *Cruziana* stratigraphy, we will address the *dispar*, *semiplicata*, and *rugosa* groups in more detail.

The *dispar* group consists of forms with several, but unequal, sharp scratch marks, revealing typically two but up to three secondary claws in front of the large primary one (Seilacher, 1970, 1992a). The group includes *Rusophycus dispar* (Fig. 13.5a), a typical Lower Cambrian (Series 2) ichnospecies known from Sweden and Poland, and *C. salomonis* (Fig. 13.5c), a Middle Cambrian (Series 3) ichnospecies from Jordan (Mángano *et al.*, 2007). *Cruziana barbata–Rusophycus barbatus* (Fig. 13.5d), known from the Middle Cambrian of Spain, Poland, Turkey, and China, are also in the *dispar* group.

The *semiplicata* group is not based on a claw formula because endopodal scratch marks are commonly too small; prominent exopodal "brushings" defining external lobes flanked by marginal thin ridges represent the diagnostic features (Crimes, 1969, 1970a; Seilacher, 1970, 1992a). *Cruziana semiplicata* (Fig. 13.5k), a common ichnospecies in Furongian–Tremadocian rocks, is the most typical ichnotaxa of the group, having been recorded in Argentina, Eastern Canada, Wales, Spain, Poland, and Oman (Seilacher, 1970, 1992a). *Cruziana semiplicata*, characterized by lateral exopodal brushings and typically trifid endopodal marks, is most likely paleobiologically related to olenids (Crimes, 1970a, b; Orłowski *et al.*, 1970; Fortey and Seilacher, 1997; Żylińska, 1999), although Bergström (1973, 1976) proposed selenopleuraceans as possible tracemakers. Other ichnospecies included in this group are *C. aegyptica, R. aegypticus*, *C. arizonensis* (Fig. 13.5e), *C. torworthi*, *R. leifeirikssoni* (Fig. 13.5f), *R. moyensis* (Fig. 13.5i), and *R. polonicus* (Fig. 13.5h). *Cruziana aegyptica*, and *R. aegypticus* occur in Middle Cambrian rocks of Jordan (Mángano *et al.*, 2007), probably extending into the Lower Cambrian in its type locality in Egypt (Seilacher, 1990b), while *C. arizonensis* is Middle Cambrian (Seilacher, 1992a). The stratigraphic range of *C. torworthi*, *R. moyensis*, and *R. polonicus* is roughly coincident with that of *C. semiplicata*. *Rusophycus leifeirikssoni* was originally recorded from Furongian–Tremadocian rocks of Eastern Canada (Bergström, 1976; Fillion and Pickerill, 1990), but is also known from older units (Lower to Middle Cambrian) in Argentina (Mángano and Buatois, 2003b).

Together with the *semiplicata* group, the *rugosa* group displays well-constrained stratigraphic distribution, and a distinctive and easy to identify morphology. The *rugosa* group is characterized by typically seven to ten, but up to twelve subequal claws; exopodial markings are absent (Seilacher, 1970, 1992a). The group includes *C. rugosa rugosa*, *C. rugosa goldfussi*, and *C. rugosa furcifera* (Fig. 13.5k), which occur in Arenigian–Llanvirnian rocks and, therefore, are useful to place the Tremadocian–Arenigian boundary. However, an overlap between some of the ichnotaxa of the *rugosa* group and *C. semiplicata* has been noted in the upper Tremadocian in some regions (Baldwin, 1975, 1977; Mángano and Buatois, 2003a). In addition, Seilacher (1992a) indicated that the *rugosa* group could extend into the Caradocian in quartzite facies in Bolivia. Recent biostratigraphic work by Egenhoff *et al.* (2007) confirmed the Caradocian age of the *rugosa*-bearing strata. Although the presence of *C. rugosa furcifera*, *C. rugosa goldfussi*, and *C. rugosa rugosa* in Lower Cambrian (Series 2) rocks of Eastern Canada has been reported (Magwood and Pemberton, 1990), specimens were subsequently assigned to a new ichnospecies, *C. pectinata*, upon reanalysis (Seilacher, 1994). The distinctive multiple and sharp scratch marks of the *rugosa* group generated a debate concerning their origin, with some authors suggesting production by multi-clawed endopodites (Seilacher, 1970, 1992a; Baldwin, 1977; Mángano and Buatois, 2003a)

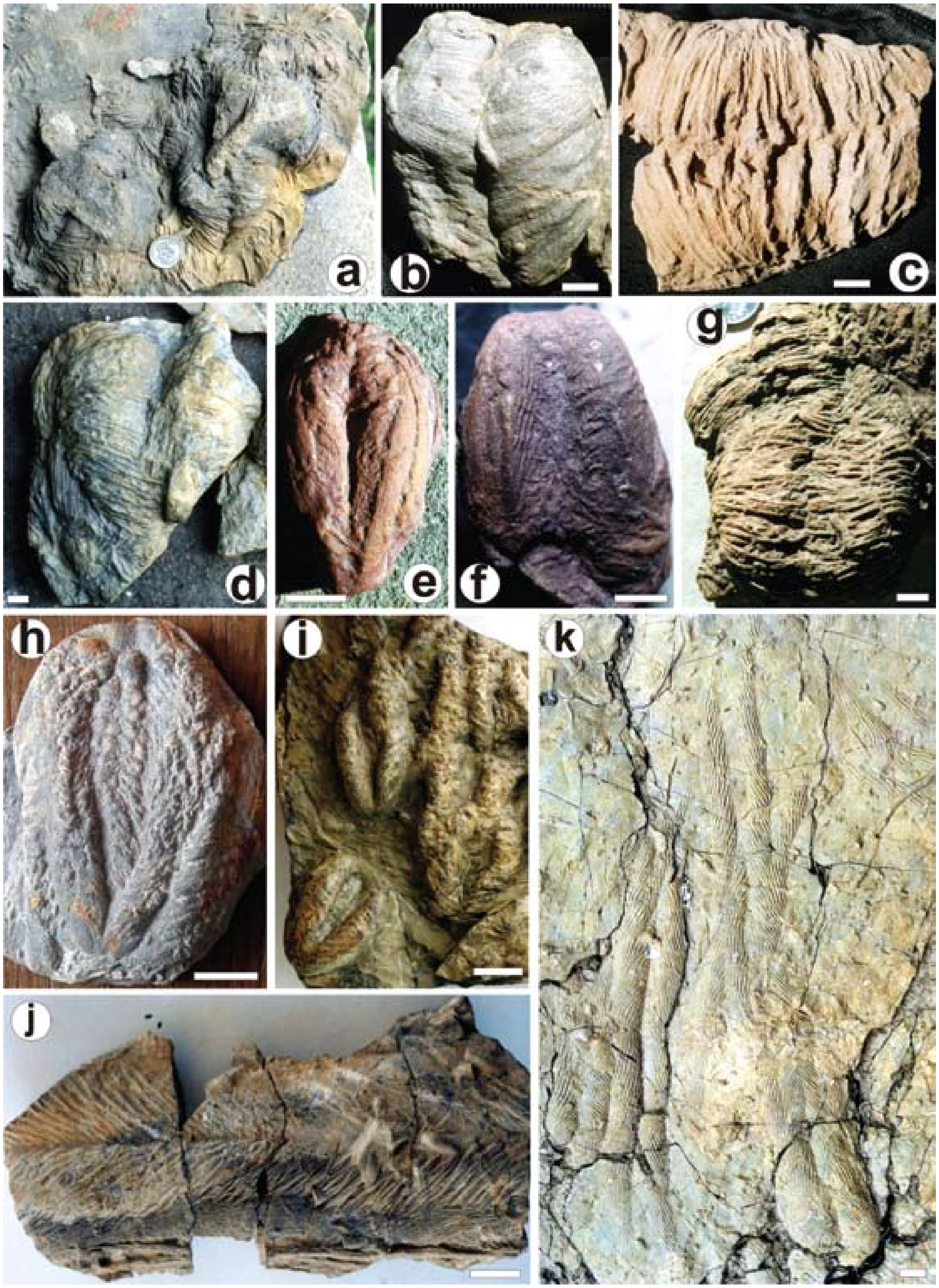

Figure 13.5 Cambrian to Lower Ordovician *Cruziana* and *Rusophycus*. (a) *Rusophycus dispar* forming clusters. Lower Cambrian, Mickwitzia Sandstone, Västergötland, Sweden. Coin is 1.9 cm. See Jensen (1997). (b) *Cruziana fasciculata* displaying sets of at least five endopodal fine scratch marks. Lower Cambrian, Herrería Sandstone, Boñar, Spain. See Seilacher (1970). (c) *Cruziana salomonis* showing scratch marks produced by strong proverse front legs (left) and weaker retroverse rear legs (right). Middle Cambrian, Burj Formation, Zerka Main, Jordan. See Seilacher (1990b) and Mángano *et al*. (2007). (d) *Cruziana barbata* with prominent front leg markings. Middle Cambrian, Obersfar Quartzite, Boñar, Spain. See Seilacher (1970). (e) *Rusophycus arizonensis (= Cruziana-arizonensis)*. Endopodal scratch marks are bordered and partially covered by exopodal scratch marks. Middle Cambrian, Tapeats Sandstone, Kaibab Trail, Grand Canyon, Arizona, United States. See Seilacher (1970). (f) *Rusophycus leifeirikssoni*. Posterior view showing axial groove and two lobes covered by coarse endopodal marks and thin exopodal marks. Lower to Middle Cambrian, Campanario Formation, Angosto del Morro de Chucalezna, Quebrada de Humahuaca, northwest Argentina. See Mángano and Buatois (2003b). (g) *Rusophycus latus* showing prominent endopodal scratch marks. Lower Ordovician, Scopes Range Beds, west of Bilpa, New South Wales, Australia. See Webby (1983). (h) *Rusophycus polonicus* with well-preserved coxal impressions between endopodal lobes. Upper Cambrian, Wiśniówka Sandstone Formation, Wielka Wiśniówka, Holy Cross Mountains, Poland. See Orłowski *et al*. (1970). (i) *Rusophycus moyensis* displaying central area and lobes covered by well-developed endopodal scratch marks. Upper Cambrian to Tremadocian, Alfarcito Member, Santa Rosita Formation, Angosto del Morro de Chucalezna, Quebrada de Humahuaca, northwest Argentina. See Mángano *et al*. (2002c). (j) *Cruziana semiplicata* displaying marginal furrows, exopodal external lobes with delicate scratch marks oriented subparallel to the axis, and endopodal lobes with scratch marks at an acute angle with respect to axis. Tremadocian, Guayoc Chico Group, Angosto del Moreno, northwest Argentina. See Mángano and Buatois (2003a). (k) *Cruziana rugosa furcifera* showing sharp, regular scratch marks forming a highly variable V-angle. Arenigian-Llanvirnian, Mojotoro Formation, Quebrada del Gallinato, northwest Argentina. See Mángano *et al*. (2001b). All scale bars are 1 cm.

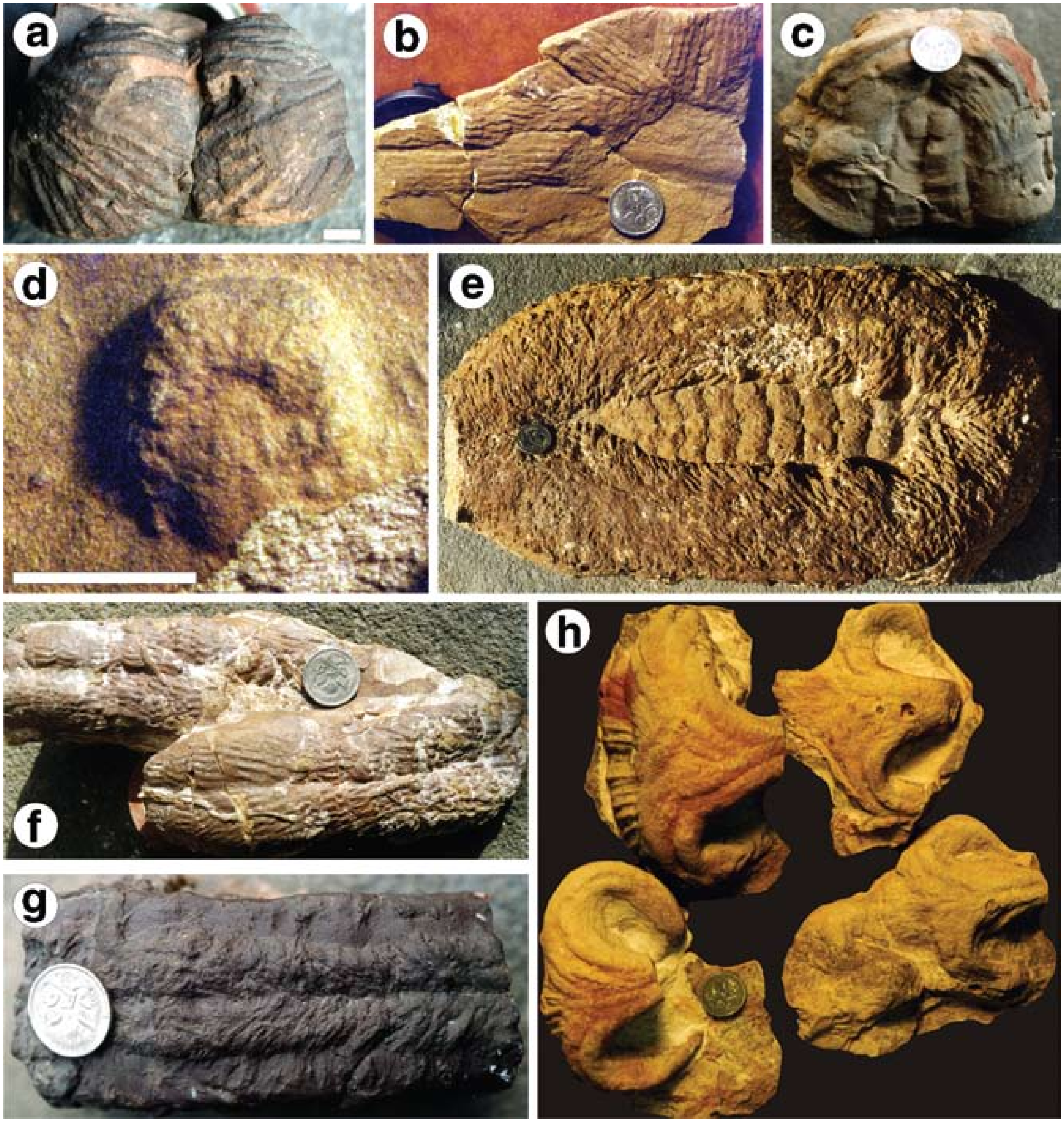

Figure 13.6 Upper Ordovician to Lower Silurian *Cruziana* and *Rusophycus*. (a) *Cruziana petraea* with rounded and subequal scratch marks. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. See Seilacher (1970). (b) *Cruziana flammosa* with flame-like front leg scratch marks. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. See Seilacher (1970). (c) *Rusophycus almadenensis* (= *Cruziana-almadenensis*) displaying radiating palm-tree scratch pattern. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. See Seilacher (1970). (d) *Rusophycus perucca* (= *Cruziana perucca*) showing typical deep wig-like structures as a result of front leg action. Upper Ordovician, Conularia Sandstone, northwest of Mudawwara, Jordan. See Seilacher (1970). (e) *Rusophycus radialis* (= *Cruziana radialis*) characterized by large size, radial scratch pattern, and well-developed coxal impressions. Upper Ordovician, Mithaka Formation, Toko Range, Queensland, Australia. See Draper (1980). (f) *Cruziana acacencis sandalina* displaying typical Turk sandal-shape Lower Silurian, Acacus Sandstone, Sebhā Ghāt, Libya. See Seilacher (1996). (g) *Cruziana quadrata* displaying its diagnostic rectangular cross section and oblique multiple scratch marks on endopodal lobes. Lower Silurian, Acacus Sandstone, Wadi Tanezzuft, Libya. See Seilacher (1970). (h) *Cruziana ancora ibex* showing anchor-shaped extension. Lower Silurian, Fada Oasis, Chad. See Seilacher (1970). All scale bars are 1 cm. All coins are 1.9 cm.

Box 13.1 *Cruziana* stratigraphy in the lower Paleozoic of northern Africa

The potential of *Cruziana* stratigraphy is particularly evident in the case of unfossiliferous sandstones. Ordovician–Silurian outcrops of the Kufra Basin in remote areas of the Sahara, southeast Libya, have been particularly appropriate for applying this tool. Nearshore prograding sandstone wedges advanced from south to north interfingering with anoxic shelf black shale. The black shale has been dated based on graptolites, but correlation with the sandstone wedges is complicated due to the absence of body fossils in these coarser-grained tongues. However, the presence of several *Cruziana* ichnospecies in the sandstone facies allows dating of the clastic wedges and correlation with their distal equivalents. The southernmost succession, exposed close to the boundary with Chad, contains elements of the *rugosa* group, namely *C. rugosa goldfussi* and *C. rugosa furcifera*, suggesting an Arenigian–Llanvirnian age for the Hawaz Formation. The overlying Memouniat Formation lacks trace fossils and probably records deposition in fluvial environments. Towards the north, a coarsening-upward succession is exposed, recording the vertical transition from black shale of the Tanezzuft Formation into the Akakus Sandstone. The presence of *Cruziana acacensis* indicates a Lower Silurian age for the sandstone wedge. Further north, the slightly younger *C. quadrata* and *C. pedroana* are present in the next overlying sandstone wedges. Interestingly, the only ichnosubspecies of *C. acacensis* recorded in the area is *C. acacensi plana*, a simpler variant that is assumed to be older than the most complex ichnosubspecies (*C. acacensis sandalina*, *C. acacensis retroversa*, and *C. acacensis laevigata*), which occur upward into the Acacus Sandstone, but in the Murzuk Basin of western Libya. Overall, the integration of *Cruziana* stratigraphy with graptolite data allows reconstructing the northward diachronic progradation of nearshore clastic wedges into shelf settings.

References: Seilacher (1996); Seilacher *et al.* (2002).

and others favoring comb-like exopodites (Bergström, 1973; Crimes and Marcos, 1976). Based on geographic distribution and size, the most likely tracemakers are asaphacean trilobites (Bergström, 1973, 1976; Fillion and Pickerill, 1990; Mángano *et al.*, 2001b; Neto de Carvalho, 2006).

Although *Cruziana* stratigraphy allows relative dating of sandstones lacking body fossils (Box. 13.1), it remains an underexplored paradigm. There are some possible reasons for this. First, this methodology requires a careful evaluation of fine morphological details, including determination of the "claw formula". Poorly preserved material or a small sample (that fails to represent the ethological variability of the ichnotaxon) are common problems. However, this may be overcome with critical analysis based on adequate sampling and avoiding determinations or proposal of new ichnotaxa based on fragmentary material. Second, anomalies within the model have created doubts about the validity of the proposed biostratigraphic scheme. In some cases (e.g. the *rugosa* group in Lower Cambrian rocks), subsequent re-analysis and solving of the anomaly has reinforced the model (Seilacher, 1994). In others (e.g. *rugosa* group in Caradocian rocks), additional research led to the extension of the originally proposed stratigraphic range of key *Cruziana* ichnospecies (e.g. Mángano and Buatois, 2003a; Egenhoff *et al.*, 2007). Third, several *Cruziana* ichnospecies are only known from their type localities or from a few localities, whose age in some cases has probed to be incorrect (e.g. *C. salomonis*, see Mángano *et al.*, 2007). To complicate matters, independent biostratigraphic evidence (e.g. body fossils and radiometric dating) is commonly absent in many of these localities. Finally, identification of *Cruziana* ichnospecies and ichnosubspecies requires a fair amount of background understanding about trilobite behavior and anatomy (Seilacher, 1970, 1985, 1992a; Bergström, 1973). In any case, specific technical expertise is required with any fossil group of biostratigraphic significance and, therefore, trace fossils are not an exception. Undoubtedly, there is a need for further studies, particularly in areas where independent paleontological evidence based on body fossils or radiometric dating may allow testing and further developing of the *Cruziana* stratigraphy paradigm.

13.3 ARTHROPHYCID STRATIGRAPHY

There is yet another group of trace fossils (*Arthrophycus*, *Daedalus*, and *Phycodes*), included in the ichnofamily Arthrophycidae, which has been proposed as yielding biostratigraphic significance (Seilacher, 2000). Although these trace fossils cannot be confidently assigned to a particular group of organisms, the different ichnotaxa included in this ichnofamily share regular transverse ridges and a teichichnoid spreite.

In particular, the ichnogenus *Arthrophycus* is abundant and widespread in Ordovician and Silurian strata, specifically in shallow-marine epeiric quartzites and quartzose sandstones. According to Seilacher (2000), *Arthrophycus* has a distinct stratigraphic range and can be used as a biostratigraphic index in Ordovician–Silurian rocks. Five ichnospecies are known at present: *A minimus*, *A. brongniartii* (= *A. linearis*), *A. alleghaniensis*, *A. lateralis*, and *A. parallelus* (Mángano *et al.*, 2005b; Brandt *et al.*, 2010). *Arthrophycus minimus* consists of shallow, small, long, regularly annulated hypichnial elements displaying subcircular to squarish cross-section and a ventral median groove; palmate, fan-like structures and scribbling patterns are absent, but a few side branches may occur (Mángano *et al.*, 2005b) (Fig. 13.7a). *Arthrophycus minimus* is known in Upper Cambrian (Furongian) to Lower Ordovician rocks and displays

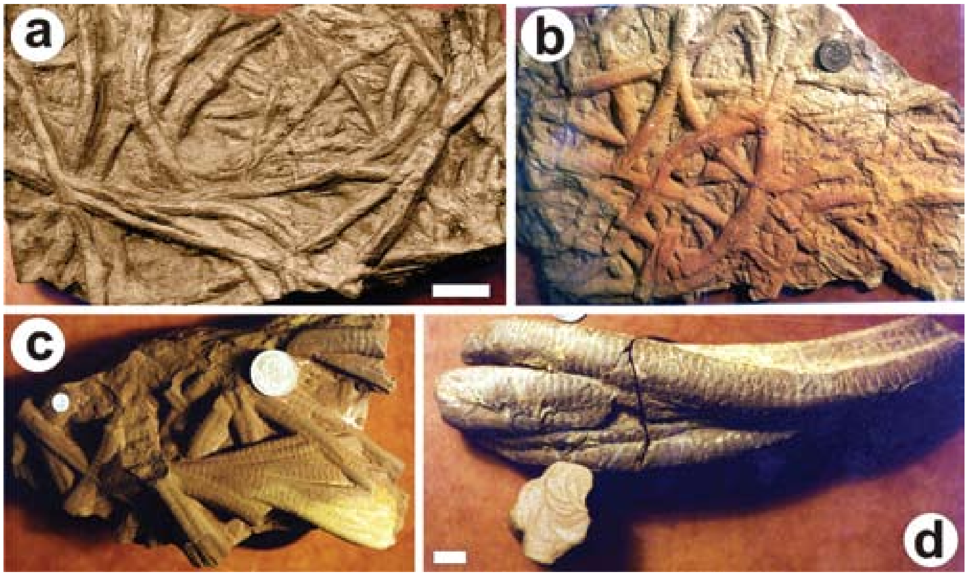

Figure 13.7 Typical *Arthrophycus* ichnospecies used in biostratigraphy. (a) *Arthrophycus minimus*. Upper Cambrian–Lower Ordovician, Santa Rosita Formation, Angosto del Morro de Chucalezna, northwest Argentina. Scale bar is 1 cm. See Mángano *et al.* (2005b). (b) *Arthrophycus brongniartii* (= *A. linearis*) *retrusiva*. Lower Silurian, Acacus Sandstone, Acacus Mountains, Libya. Coin is 1.9 cm. See Seilacher (2000). (c) *Arthrophycus alleghaniensis*. Lower Silurian, Medina Sandstone, Rochester, United States. Coin is 1.9 cm. See Seilacher (2000). (d) *Arthrophycus lateralis*. Lower Silurian, Acacus Sandstone, Takharkhuri Pass, Libya. Polished slab (lower left) shows spreiten pattern. Scale bar is 1 cm. See Seilacher (2000).

an exploratory behavioral pattern that is simpler than that of the younger *Arthrophycus* ichnospecies, which is consistent with its basal position within the arthrophycid lineage (Mángano *et al.*, 2005b). *Arthrophycus brongniartii* consists of shallow, straight to gently curved elements having no or few side branches (Seilacher, 2000; Rindsberg and Martin, 2003) (Fig 13.7b). This ichnospecies ranges from the Lower Ordovician to the Lower Silurian. *Arthrophycus alleghaniensis* comprises three-dimensional palmate bundles of tunnels typically displaying vertically retrusive spreite (Fig 13.7c), and *A. lateralis* consists of fan-shaped structures, in which branches bend only to one side having a horizontal protrusive spreite (Seilacher, 2000) (Fig 13.7d). Both ichnospecies are only known from the Lower Silurian. Finally, *A. parallelus* consists of elongate tunnels with well-developed annulations, showing a parallel to sub-parallel orientation (Brandt *et al.*, 2010). This ichnospecies has been introduced by Brandt *et al.* (2010) based on Carboniferous specimens and represents the youngest confident occurrence of this ichnogenus.

The ichnogenus *Daedalus* also seems to have biostratigraphic potential. While the ichnospecies *D. labechei*, *D. halli*, and *D. desglandi* are apparently restricted to the Lower Ordovician, *D. multiplex* is only known from the Middle Ordovician, and *D. verticalis* and *D. archimedes* occur in the Lower Silurian (Seilacher, 2000). According to Seilacher (2000), some ichnospecies of *Phycodes* may be useful in biostratigraphy. *Phycodes circinatum* is widespread in the Tremadocian, while *P. fusiforme* is only known from the Upper Arenigian. *Phycodes parallelum* ranges from the Upper Arenigian to the Lower Llanvirnian, and *P. flabellum* is only present in the Caradocian–Ashgillian.

In short, as in the case of *Cruziana* stratigraphy, the Arthrophycid stratigraphy provides an alternative to date and correlate lower Paleozoic quartzites and quartzose sandstones that commonly lack body fossils. The amount of evidence supporting the scheme is uneven. Some ichnospecies are widespread, while others are only known from one or two localities. We can certainly consider that this paradigm is still in a state of flux. Further fieldwork will most likely adjust and add to the original ichnostratigraphic proposal.

13.4 OTHER INVERTEBRATE ICHNOTAXA

Besides those ichnotaxa apparently restricted to the Lower Cambrian and those included in the *Cruziana* and arthrophycid stratigraphy, there are a few other invertebrate ichnofossils that seem to have a more restricted stratigraphic distribution. One of these ichnogenera is *Climactichnites* (Fig. 13.8a) and its associated resting trace *Musculopodus*, which are only known from the Upper Cambrian (Yochelson and Fedonkin, 1993; Getty and Hagadorn, 2008, 2009).

Heimdallia (Fig. 13.8b) is apparently restricted to Upper Ordovician–Devonian strata, mostly in nearshore settings, *H. chatwini* being the most typical ichnospecies (e.g. Bradshaw, 1981; Trewin and McNamara, 1995; Hunter and Lomas, 2003; Bradshaw and Harmsen, 2007). A potential Lower Ordovician occurrence of *H. chatwini* (Fillion and Pickerill, 1990) requires further analysis. Another ichnospecies, *H. zigzag*, occurs in the Lower Silurian (Seilacher and Alidou, 1988; Seilacher 2007b). A slightly younger representative, *Heimdallia mullaghmori*, is known from the Lower Carboniferous (Buckman, 1996).

The ichnogenus *Dictyodora* also displays a restricted stratigraphic distribution, which is of biostratigraphic significance (Seilacher 1967a; Benton and Trewin, 1980; Uchman, 2004a). *Dictyodora simplex* is Cambrian–Ordovician, while *D. scotica* and *D. tenuis* are Ordovician–Silurian. Others ichnospecies display more restricted ranges, such as the Ordovician *D. zimmermanni*, the Silurian *D. silurica*, and the Early Carboniferous *D. liebeana* (Fig. 13.8c).

Some graphoglyptids have narrower stratigraphic ranges than less complex ichnotaxa (Uchman, 2004a). For example,

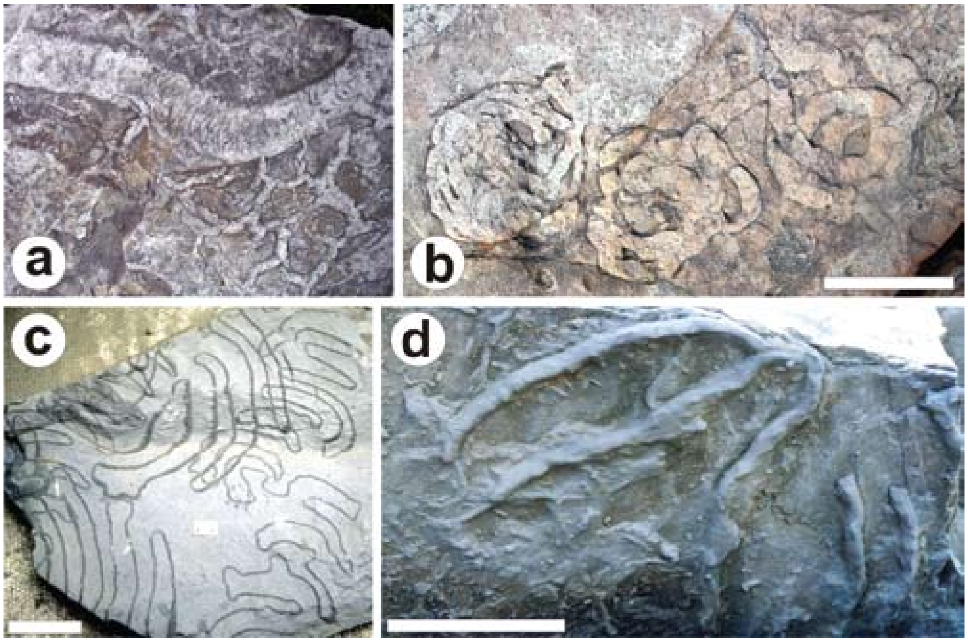

Figure 13.8 Other invertebrate trace fossils showing restricted stratigraphic ranges. (a) *Climactichnites wilsoni* cross-cutting desiccation cracks. Upper Cambrian, Cairnside Formation, Postdam Group, slab exhibited at the Fossil Garden at Buisson Point Archaeological Park, Melocheville, Quebec, Canada. Coin (upper center) is 2.4 cm. (b) *Heimdallia chatwini*. Ordovician, Peninsula Formation, Table Mountain Group, Matjiesgloof Farm, South Africa. Scale bar is 10 cm. (c) *Dictyodora liebeana*. Lower Carboniferous, Cabo de Favaritz Beds, Menorca, Spain. Scale bar is 3 cm. (d) *Glockerichnus alata*. Lower to Middle Eocene, Tarcau Sandstone, Teherau Valley, Romania. Scale bar is 10 cm.

Glockerichnus alata (Fig. 13.8d) is only known from the Eocene, while *Rotundusichnium zumayense* occurs in Maastrichtian–Eocene. However, most of graphoglyptid ichnotaxa have longer stratigraphic ranges, essentially from the Cretaceous to the Neogene (Uchman, 2003, 2004a).

Crustacean burrows having bilobate segments with scratch marks were originally referred to a new ichnospecies, *Cruziana seilacheri* (Zonneveld *et al*., 2002), but belong in some of the ichnogenera currently available for burrow systems, most likely *Spongeliomorpha* (Knaust, 2007). This form is at present only known from the Middle Triassic.

Genise (2004) reviewed the stratigraphic range of insect trace fossils in paleosols. Most of these ichnotaxa range from the Paleogene. Of these, *Eatonichnus* is only known from the Paleocene–Eocene, and *Teisseirei* from the Eocene–Oligocene. Although the temporal resolution of these ichnotaxa is too crude, the presence of some of these insect trace fossils may be useful to differentiate Cenozoic paleosols from older terrestrial strata (Genise *et al*., 2000).

The stratigraphic distribution of macro- and microborings has been reviewed by Bromley (2004), and Glaub and Vogel (2004). Bromley (2004) concluded that the temporal ranges of borings are too long to allow their use in biostratigraphy. However, first-appearance data may have some applications in biostratigraphy. More restricted temporal ranges are displayed by bioclaustrations (Tapanila, 2005; Tapanila and Ekdale, 2007). Although some of the most abundant forms (e.g. *Tremichnus*) have long temporal ranges, other less-widespread ichnogenera (e.g. *Catellocaula*, *Diorygma*, *Hicetes*, *Klemmatoica*, and *Torquaysalpinx*) seem to be restricted to one to four stages, a resolution unparalleled by any other ichnotaxa. Because many of these forms are poorly known, further documentation of these ichnotaxa may be necessary to test their biostratigraphic significance.

13.5 TETRAPOD TRACKWAYS

Tetrapod trackways are known since the early Middle Devonian (Niedźwiedzki *et al*., 2010), being particularly abundant in marginal-marine to continental deposits since the Carboniferous (Lucas, 2007). This group of trace fossils has been extensively used in biostratigraphy. In fact, the tradition of using trace fossils in biostratigraphy is more firmly entrenched among vertebrate ichnologists than among invertebrate ichnologists. Lucas (2007) provided an exhaustive review of tetrapod trackway biostratigraphy, addressing a series of limiting factors that complicate use of vertebrate footprints in this field.

As in the case of invertebrate ichnology, some of these problems are connected with taxonomy (see Section 2.6). The uneven quality of footprint ichnotaxonomy complicates the reliability of biostratigraphic zonations. Ichnotaxa based on extramorphological features result from a splitting approach to taxonomy. Biostratigraphic zonations based on this approach give the false appearance of stratigraphic resolution because they include a large number of biozones, which are, in fact, unsound and simple artifacts of poor taxonomic practice. Zonations based on better defined ichnotaxa are sound, albeit with limited resolution. This is because vertebrate ichnogenera do not correspond to tetrapod genera, but to higher-rank taxonomic levels (e.g. families and groups), and the most precise biostratigraphic schemes are based on genus- or species-level taxa (e.g. Baird, 1980; Carrano and Wilson, 2001; Lucas, 2007). Lucas (2007) also noted that, as in the case of invertebrate trace fossils, facies restrictions limit the utility of tetrapod footprints.

Despite all these problems, tetrapod trackways are effectively used in biostratigraphy, and Lucas (2007) recognized several global time intervals based on the footprint record. The recently discovered early Middle Devonian tetrapod trackways from

Poland (Niedźwiedzki *et al.*, 2010) predate the oldest tetrapod body fossils which are from the Upper Devonian (Ahlberg, 1991). The Late Devonian interval is characterized by trackways attributed to ichthyostegalians, which is consistent with the skeletal record (Warren and Wakefield, 1972; Rogers, 1990; Stössel, 1995; Clack, 2002, 2005). However, the trackway record is poor and no index taxa have been defined, restricting biostratigraphic utility (Lucas, 2007).

The Carboniferous trackway record is very rich, although mostly restricted to Laurussia. Lucas (2007) pointed out that taxonomic problems due to oversplitting complicate biostratigraphic schemes, but that three time intervals can be recognized: Early Carboniferous (Mississippian), Middle Carboniferous (roughly Westphalian), and Late Carboniferous (approximately Stephanian). The Early Carboniferous interval is mostly based on trackways from Nova Scotia (e.g. Sarjeant and Mossman, 1978; Hunt *et al.*, 2004b; Lucas *et al.*, 2004b) and, to a lesser extent, England (e.g. Scarboro and Tucker, 1995). Typical trackways are produced by temnospondyls and stem amniotes (captorhinomorphs), including the ichnogenera *Peratodactylopus*, *Megapezia*, *Baropezia*, *Hylopus*, and *Palaeosauropus*, although the latter three also occur in younger Carboniferous rocks (Lucas, 2007). Middle Carboniferous trackways are known essentially from Nova Scotia, eastern and western United States, Germany, France, and the Czech Republic (e.g. Sarjeant and Mossman, 1978; Cotton *et al.*, 1995). This interval is dominated by stem amniotes (captorhinomorphs) trackways (although temnospondyl footprints occur also), and is referred to as the *Pseudobradypus* biochron (Lucas, 2007). Other ichnogenera include *Notalacerta*, *Cincosaurus*, *Matthewichnus*, *Anthracopus*, *Salichnium*, and *Quadropedia*. The producers of Lower and Middle Carboniferous trackways are essentially the same, and distinction between these two global time intervals is therefore problematic. Upper Carboniferous footprints have been recorded in eastern and western United States, Germany, France, Italy, England, and Spain (e.g. Haubold and Sarjeant, 1973; Gand, 1975; Soler-Gijón and Moratalla, 2001). Lucas (2007) noted that this interval is characterized by the first appearance of *Batrachichnus*, *Ichniotherium*, *Dromopus*, *Gilmoreichnus*, and *Dimetropus*, marking the beginning of the *Dromopus* biochron, highlighting the consistency between the track and body-fossil record.

The Permian tetrapod trackway record is more widespread, including localities in Europe, South Africa, South America, and North America, and encompasses two intervals (Lucas and Hunt, 2006; Lucas, 2007). The Early Permian interval is represented by the continuation of the *Dromopus* biochron, and has been extensively recorded in southern and western United States, Canada, and Europe (e.g. Lucas *et al.*, 1999, 2004b; Haubold and Lucas, 2001; Avanzini *et al.*, 2001). Trackmakers are temnospondyls, "diadectomorphs", seymouriamorphs, procolophonids, and basal synapsids (pelycosaurs). Dominant ichnotaxa include *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Dromopus* (Fig. 13.9a), *Varanopus*, *Hyloidichnus*, *Ichniotherium*, *Dimetropus* (Fig. 13.9b), and *Gilmoreichnus* (Lucas, 2007). The Late Permian interval is illustrated by tetrapod footprints in Europe and South Africa (e.g. Smith, 1993), and has been referred to as the *Rhychosauroides* biochron (Lucas, 2007). According to this author, paraeiasaurs and dicynodonts are the most important trackmakers, with *Pachypes*, *Dicynodontipus*, and *Rhychosauroides* being characteristic ichnogenera. Interestingly, there seems to be a gap in the trackway record that is roughly equivalent to the Guadalupian (Middle Permian), and longer than the Olson's gap of the body-fossil record (Lucas, 2004).

The Triassic tetrapod trackway record is essentially worldwide and contains many ichnotaxa with biostratigraphic potential. Demathieu (1977, 1994) proposed three main intervals, from the Early to the Late Triassic, and Lucas (2007) added a fourth zone for the earliest Triassic. The lowermost interval is of Induan age (earliest Triassic) and is characterized by dicynodont tracks (e.g. Retallack, 1996). The second zone comprises the Olenekian–early Anisian (Early Triassic to early Middle Triassic), and is known as the Chirothere assemblage, which is dominated by archosaur trackways (e.g. Demathieu and Demathieu, 2004). *Chirotherium* is the most common ichnogenus; *Isochirotherium*, *Rotodactylus*, *Brachychirotherium*, and *Synaptichnium* are present locally (e.g. Demathieu, 1977, 1984; Avanzini and Lockley, 2002; King *et al.*, 2005). The late Middle Triassic interval is known as the Dinosauromorph assemblage (Lucas, 2007). Although chirothere footprints (e.g. *Brachychirotherium*) are also present, they are rare and the interval is distinguished from the Chirothere assemblage by the appearance of tridactyl bipedal trackways that have been attributed to dinosaur or dinosaur-like organisms (Demathieu, 1989; Haubold, 1999) (see Section 14.1.5). The Late Triassic interval is represented by the Dinosaur assemblage (Lucas, 2007). It is characterized by the higher diversity in dinosaur-like and dinosaur footprints, such as *Tetrasauropus*, *Pseudotetrasuropus*, *Grallator* (Fig. 13.9c), and *Atreipus*. Attempts have been made to further subdivide this interval (e.g. Olsen, 1980; Haubold, 1986; Lockley, 1993; Olsen and Huber, 1998; Lockley and Hunt, 1994, 1995).

The Jurassic tetrapod-footprint record is remarkably widespread, with dinosaur trackways found in all continents except Antarctica (Lucas, 2007). This author recognized two intervals within the Jurassic based on dinosaur trackways. The Early Jurassic interval is dominated by non-avian theropod footprints. This interval is characterized by and the appearance of a number of ichnotaxa (e.g. *Eubrontes*, *Anomoepus*, and *Ameghinichnus*) and the absence of some ichnogenera typical of the Triassic (e.g. *Brachychirotherium*). Of these, *Eubrontes* is the most abundant, and Lucas (2007) has referred to the base of this interval as the *Eubrontes* datum, stressing the biostratigraphic importance of this ichnogenus (e.g. Lockley *et al.*, 2004). However, this is not without problems because *Eubrontes* has been recorded in Upper Triassic rocks, probably reflecting the early appearance of large theropods (Lucas *et al.*, 2005). Lockley and Hunt (1995) noted that, although *Grallator* occurs in both Triassic and Jurassic rocks, it tends to be smaller in the Triassic. The Middle–Late Jurassic interval is characterized by a less sparse record and an increase in the size of tracks (Farlow, 1992).

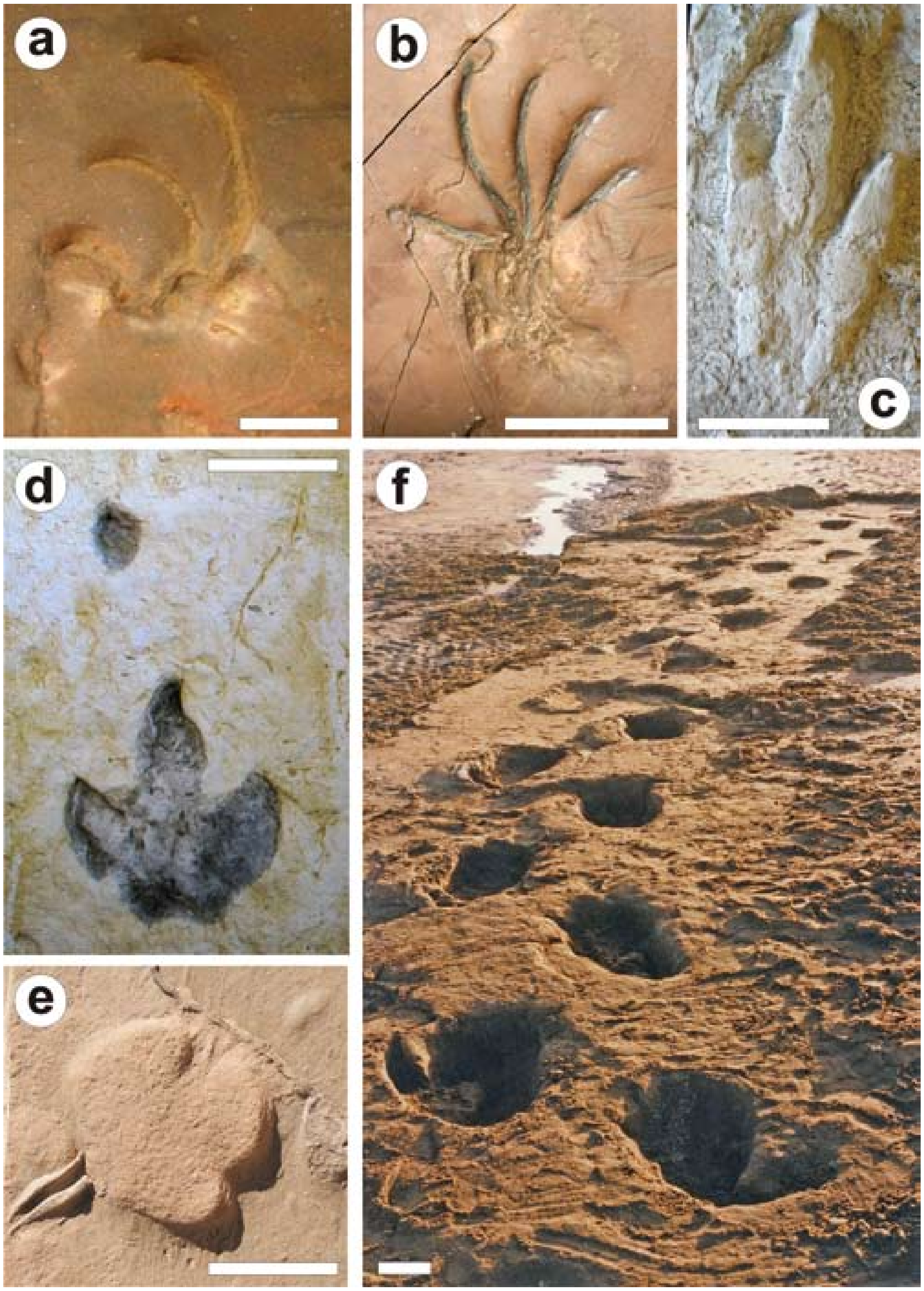

Figure 13.9 Vertebrate trackways showing restricted stratigraphic ranges and commonly used in biostratigraphy. (a) *Dromopus agilis*. Lower Permian, Hueco Formation, Robledo Mountains, New Mexico, United States. Scale bar is 1 cm. See Hunt *et al.* (2005). (b) *Dimetropus leisnerianus*. Lower Permian, Hueco Formation, Robledo Mountains, New Mexico, United States. Scale bar is 5 cm. See Hunt *et al.* (2005). (c) *Grallator sulcatus*. Upper Triassic, Brunswick Formation, Clark Quarry, near Milford, New Jersey, United States. Scale bar is 5 cm. See Olsen *et al.* (1998). (d) *Caririchnium leonardii*. Lower Cretaceous, Dakota Group, Dinosaur Ridge, Colorado, United States. Scale bar is 10 cm. See Lockley (1987). (e) *Macrauchenichnus rector*. Miocene, Toro Negro Formation, Quebrada de la Troya, near Vinchina, western Argentina. Scale bar is 10 cm. See Krapovickas *et al.* (2009). (f) *Neomegatherichnium pehuencoensis*. Upper Pleistocene, Pehuen-Co, southeastern coast of Buenos Aires Province, Argentina. Scale bar is 10 cm. See Aramayo and Manera de Bianco (1996, 2009).

Theropod (e.g. *Carmelopodus* and *Megalosauripus*), sauropod (e.g. *Gigantosauropus* and *Parabrontopodus*, *Breviparopus*), and ornithopod (e.g. *Dinehichnus*) trackways occur (Ishigaki, 1989; Lockley and Hunt, 1995; Lockley and Meyer, 2000; Lucas, 2007). Possible refinements in the Jurassic biostratigraphic scheme have been further proposed in other studies (e.g. Lockley, 1998; Lockley and Meyer, 2000).

As with the Jurassic record, the Cretaceous footprint record is global in nature, with tracksites known from every continent, including Antarctica (Olivero *et al.*, 2007). The record is overwhelmingly dominated by dinosaur tracks, but bird, pterosaur, and, more rarely, mammal trackways also occur (Lucas, 2007). According to this author, the main difference with respect to the Jurassic record is the abundance of large ornithopod trackways in the Cretaceous. Two global intervals have been identified, Early Cretaceous and Late Cretaceous. The Early Cretaceous tends to be dominated by sauropod trackways, including the ichnogenera *Parabrontopodus* and *Brontopodus*, particularly in southern United States. Nevertheless, ornithopod trackways occur also, with *Iguanodontipus* and *Caririchnium* (Fig. 13.9d) being typical ichnotaxon. Bird tracks are also abundant in the Early Cretaceous, commonly associated with lake-margin environments, and including the ichnogenera *Ignotormis* and *Aquatilavipes* (Lockley *et al*., 1992; Lockley and Rainforth, 2002). The Late Cretaceous dinosaur-track record differs from the Early Cretaceous one in the lower number of sauropod tracks and in the appearance of ceratopsian, tyrannosaurid, and hadrosaurid footprints (Lucas, 2007). Bird tracks are also abundant and include the ichnogenera *Yacoraitichnus* and *Magnoavipes* (Lockley and Rainforth, 2002).

Although mammal body fossils provide a high-resolution biostratigraphy for the Cenozoic, the mammal-track record still remains poorly explored (Lucas, 2007). To further complicate things, trackways produced by amphibians, reptiles, and birds are too uncommon to be used in biostratigraphy. Lucas (2007) recognized two global intervals, Paleogene and Neogene based on the track record. The Paleogene track interval is sparse, and characterized by the abundance of basal ungulates (e.g. Sarjeant and Langston, 1994; McCrea *et al*., 2004). Some Paleogene ichnotaxa include the crocodile trackway *Albertasuchipes* and two ichnotaxon attributed to creodont mammals (*Sarjeantipes*, *Quirtipes*) (Sarjeant *et al*., 2002; McCrea *et al*., 2004). The Neogene track interval is richer, and dominated by derived ungulates (e.g. Aramayo and Manera de Bianco, 1987a, b, 1996, 2009; Sarjeant and Reynolds, 1999; Lucas *et al*., 2002; Krapovickas *et al*., 2009). Some Neogene ichnotaxa attributed to mammals are *Macrauchenichnus* (Fig. 13.9e), *Venatoripes*, *Megatherichnum*, *Neomegatherichnum*, *Eumacrauchenichnus*, and *Odocoileinichnum* (e.g. Aramayo and Manera de Bianco, 1987a, b, 1996, 2009; Krapovickas *et al*., 2009).

In short, the review by Lucas (2007) indicated that global biochronology based on tetrapod trackways resolves geological time approximately 20–50% as well as the body-fossil record. This resolution is even better than that of invertebrate trace fossils used in biostratigraphy (e.g. *Cruziana* and *Rusophycus* ichnospecies). In addition, because resolution based on skeletal remains is uneven through geological time, the temporal resolution of tetrapod footprints may be as good as that of body fossils for time intervals characterized by a meager bone record (e.g. Carboniferous). As in the case of invertebrate trace fossils, tetrapod footprints are particularly useful in the absence of skeletal remains. The fact that trackways are commonly found in facies lacking body fossils underscores the potential of footprints to fill stratigraphic gaps and to provide biostratigraphic information (e.g. Lockley, 1991).

14 Trace fossils in evolutionary paleoecology

> There is nothing like the Cambrian until the Cambrian.
>
> Andrew Knoll
> *Life on a Young Planet: The First Three Billion Years of Evolution on Earth* (2004)

> Some of these ideas were already touched upon by Darwin, such as the notion that burrowing organisms have a proportionally large impact on their environment, which is now formalized in the concept of ecosystem engineering. Other ideas were unforeseen, such as the role that bioturbation had during the Cambrian explosion. This establishes a strong link between Darwin's bioturbation book and On the Origin of Species, a connection that would have certainly astounded the author.
>
> Filip Meysman, Jack Middelburg, and Carlo Heip
> "Bioturbation: a fresh look at Darwin's last idea" (2006)

> Timing is the complex part of simplicity.
>
> Keith Jarrett
> *The Art of Improvisation* (2005)

Because ichnological analysis commonly emphasizes the long temporal range of most ichnotaxa (see Section 1.2.8), trace fossils have been traditionally overlooked as a source of information in macroevolution. However, comparisons of ichnofaunas through geological time do reveal the changing ecology of organism–substrate interactions. The use of trace fossils in evolutionary paleoecology represents a relatively new trend in ichnology that is providing important information for our understanding of patterns and processes in the history of life. In particular, Bambach (1983) understood the history of life as a process of colonization that implies the exploitation of empty or underutilized ecospace (see also Bambach *et al.*, 2007). Trace fossils may provide crucial evidence for the recognition of spatial and temporal patterns and processes associated with paleoecological breakthroughs (e.g. Seilacher, 1956, 1974, 1977b; Crimes, 1994, 2001; Buatois and Mángano, 1993b; Buatois *et al.*, 1998c, 2005; Orr, 2001; Mángano and Droser, 2004; Uchman, 2004a; Carmona *et al.*, 2004; Jensen *et al.*, 2005; Seilacher *et al.*, 2005; Mángano and Buatois, 2007).

Droser *et al.* (1997) proposed a hierarchy of paleoecological levels that allow for the ranking of ecological changes through geological time. First-level changes, the highest level, indicate colonization of a new ecosystem (e.g. terrestrialization), and fourth-level changes, at the other end, indicate turnover at the community level. This scheme provides a useful way to frame ichnological data having implications in evolutionary paleoecology (e.g. Mángano and Droser, 2004). Additionally, we make extensive use of the ichnoguild concept (see Section 5.4) in order to evaluate ecospace colonization in specific ecosystems through geological time. In many instances, trace-fossil evidence demonstrates much greater evidence of ecological change than that revealed by body fossils alone. The distribution of biogenic structures through geological time reveals a process of colonization resulting from the exploitation of empty or underutilized ecospace. Secular trends include an increase in the diversity of biogenic structures, increase in the intensity of bioturbation, addition of new invaders, environmental expansion, and faunal turnovers. In this chapter, we summarize the significance of trace-fossil information in evolutionary paleoecology. In order to do so, we first turn our attention to a number of evolutionary events, such as the Cambrian explosion, the Ordovician radiation, and the different mass extinctions. Then, we will address how animal–substrate interactions in various ecosystems have changed through geological time.

14.1 EVOLUTIONARY EVENTS

14.1.1 THE EARLY RECORD OF COMPLEX LIFE

The question about the earliest ichnological evidence of complex life (i.e. metazoans) is one of the most controversial in the science of organism–sediment interactions. The history of research is plagued with frequent reinterpretations, resulting from both the continuous scrutiny of Precambrian structures and the specific complexities of Precambrian paleobiology. The issue is of utmost relevance to understand the origin of metazoans, particularly in the absence of consensus on the affinities of many Neoproterozoic body fossils (Glaessner, 1984; Seilacher, 1989; Narbonne, 2005).

Bergström (1990) and Crimes (1994) cleverly summarized the unfortunate fate of previous candidates for the "oldest trace fossil" award. Either structures are inorganic, the rocks are younger than originally thought, or the structures are biogenic but younger than the host rock, among other less likely alternatives. For example, structures interpreted by Hofmann (1967) as new ichnotaxa, *Rhysonetron lahtii* and *R. byei*, from Lower Proterozoic rocks (2.0 Ga) in Canada, were subsequently reinterpreted by the same author as inorganic (Hofmann, 1971). Supposed burrow systems described by Clemmey (1976) in Mesoproterozoic (1.0 Ga) rocks of Zambia later were reinterpreted as traces of modern termites (Cloud *et al.*, 1980).

More recently, two new candidates have been proposed. Seilacher *et al.* (1998) documented sinusoidal and branched structures (the so-called "Chorhat worm burrows") in rocks from India that were considered as Middle Proterozoic in age (1.1 Ga). The reception was rather mixed and the actual age of the rocks became a controversial issue in itself (Azmi, 1998; Bagla, 2000; Kumar *et al.*, 2000). Finally, two independent teams dated the rocks as 1.6 Ga (Rasmussen *et al.*, 2002a; Ray *et al.*, 2002), which would push far back in time the origin of metazoans. Considering that one has to wait for more than 1.0 Ga (well into the Ediacaran) to see truly convincing examples of trace fossils, this finding became problematic at best. Either the structures are inorganic and the gap is removed, or we are forced to admit that the first attempt of metazoan life was a failed experiment with a probable extinction event during Snowball Earth times. Unsurprisingly, the biogenic nature of the structures was subject to further scrutiny and the present view is more parsimonious: the structures are not trace fossils (Budd and Jensen, 2000, 2004; Conway Morris, 2002; Jensen, 2003; Hofmann, 2005; Seilacher, 2007a). The second challenging example consists of supposed body fossils (Ediacaran-like), sea anemone burrows (*Bergaueria*), and vermiform traces described in rocks dated between 1.2 and 2.0 Ga from Western Australia (Rasmussen *et al.*, 2002b; Bengtsön *et al.*, 2007). However, they have been reinterpreted as pseudofossils (Conway Morris, 2002; Jensen, 2003; Budd and Jensen, 2004).

Crimes (1994) considered the possibility of trace fossils in pre-Ediacaran rocks highly unlikely. The oldest convincing trace fossils come, in fact, from Ediacaran strata that postdate the Marinoan Ice Age (Jensen, 2003). Recently, possible trails have been reported from 565 My-old deep-water deposits of Mistaken Point, Newfoundland, eastern Canada (Liu *et al.*, 2010). Overall, the trace-fossil record is consistent with at least some of the more recent estimations based on molecular clocks, which suggest an Ediacaran origin for bilaterians (Peterson, 2005; Rokas *et al.*, 2005; Bromham, 2006; Peterson *et al.*, 2008).

14.1.2 EDIACARAN ECOSYSTEMS

Ediacaran rocks are characterized by a rather unusual suite of structures, containing a wealth of wrinkled surfaces, ripple patches, palimpsest ripples, and elephant skin structures, all suggestive of sediment stabilization by microbial binding (Seilacher and Pflüger, 1994; Seilacher, 1999; Gehling *et al.*, 2005; Dornbos *et al.*, 2006; Droser *et al.*, 2006; Bottjer and Clapham, 2006; Mángano and Buatois, 2007). In all probability, microbial mats were critical components in Ediacaran ecosystems. Benthic communities developed in direct association with resistant matgrounds setting up an anactualistic scenario for early marine ecosystems (Seilacher, 1999). Four major categories of organism–microbial mat interactions were established during the Ediacaran: mat encrusters (attached to the microbial mats), mat scratchers (organisms grazing on the microbial mats), mat stickers (organisms growing inside of the mats), and undermat miners (those who constructed tunnels below the mat). Mat encrusters (e.g. *Charniodiscus*) and mat stickers (e.g. *Cloudina*) are essentially represented by body fossils. On the other hand, evidence of the activity of undermat miners and mat scratchers is preserved in the ichnological record. Interestingly, undermat miners seem to be more common in lowermost Cambrian deep-marine deposits than in Ediacaran rocks, being represented by the ichnogenus *Oldhamia* (see Section 14.1.3).

Trace fossils produced by mat scratchers can be further subdivided into two main groups: those reflecting the activity of worm-like metazoans and those recording the interaction of vendozoans with the matground (Mángano and Buatois, 2007). The most abundant trace fossils in Ediacaran rocks are mat grazers that belong to this first group (Gehling, 1999; Seilacher *et al.*, 2005; Jensen *et al.*, 2006). These are represented by very simple feeding trace fossils, and nonspecialized grazing trails (e.g. *Helminthoidichnites*, *Helminthopsis*, *Gordia*) preserved on corrugated surfaces. Buatois and Mángano (2003a, 2004) placed these structures in the *Helminthopsis* ichnoguild, which consists of transitory, near-surface to very shallow-tier, mat-grazer structures produced by vagile vermiform animals that exploit organic matter concentrated within microbial mats below a thin veneer of sediment (Fig. 14.1a–d). Contrary to common belief, these simple trails are not emplaced on the surface, but rather within the sediment (Seilacher, 1999). However, caution should be exercised because some filamentous body fossils can easily be confused with grazing trails (Jensen *et al.*, 2006). In addition, the giant protist *Gromia sphaerica* has been observed producing trails on the modern sea bottom (Matz *et al.*, 2008). However, these structures are commonly quite straight and shorter than most grazing trails attributed to bilaterians. Segmented burrows reflecting peristaltic locomotion are less common, but may be represented by *Torrowangea* (Narbonne and Aitken, 1990; Seilacher *et al.*, 2005). Because of the controversial nature of most of the Ediacaran body fossils, these trace fossils represent the clearest evidence of triploblastic organisms in the Neoproterozoic (Seilacher, 1989).

In recent years, evidence accumulated to demonstrate a direct link between Ediacaran trace fossils and their producers. Ediacaran shallow-marine deposits of the White Sea and south Australia contain serially repeated resting traces of *Dickinsonia* and the related genus *Yorgia* (Ivantsov and Malakhovskaya, 2002; Fedonkin, 2003; Gehling *et al.*, 2005). The body fossils *Yorgia waggoneri* and *Dickinsonia tenuis* were found in direct association with their trace fossils (Ivantsov and Malakhovskaya, 2002). The absence of preserved trails linking the resting traces suggests that the substrate did not record any locomotion disrupting the biomats (Gehling *et al.*, 2005). Recently, Sperling and Vinther (2010) suggested that these trace fossils indicate that *Dickinsonia* externally digested the mat using its entire lower sole. In addition, these authors noted that the ability of *Dickinsonia* to move militates against an algal, fungal, or sponge affinity, and that the combined locomotion and feeding mode suggest affinities with placozoans. However, a different interpretation has been proposed by McIlroy *et al.* (2009) who, based on experimental work,

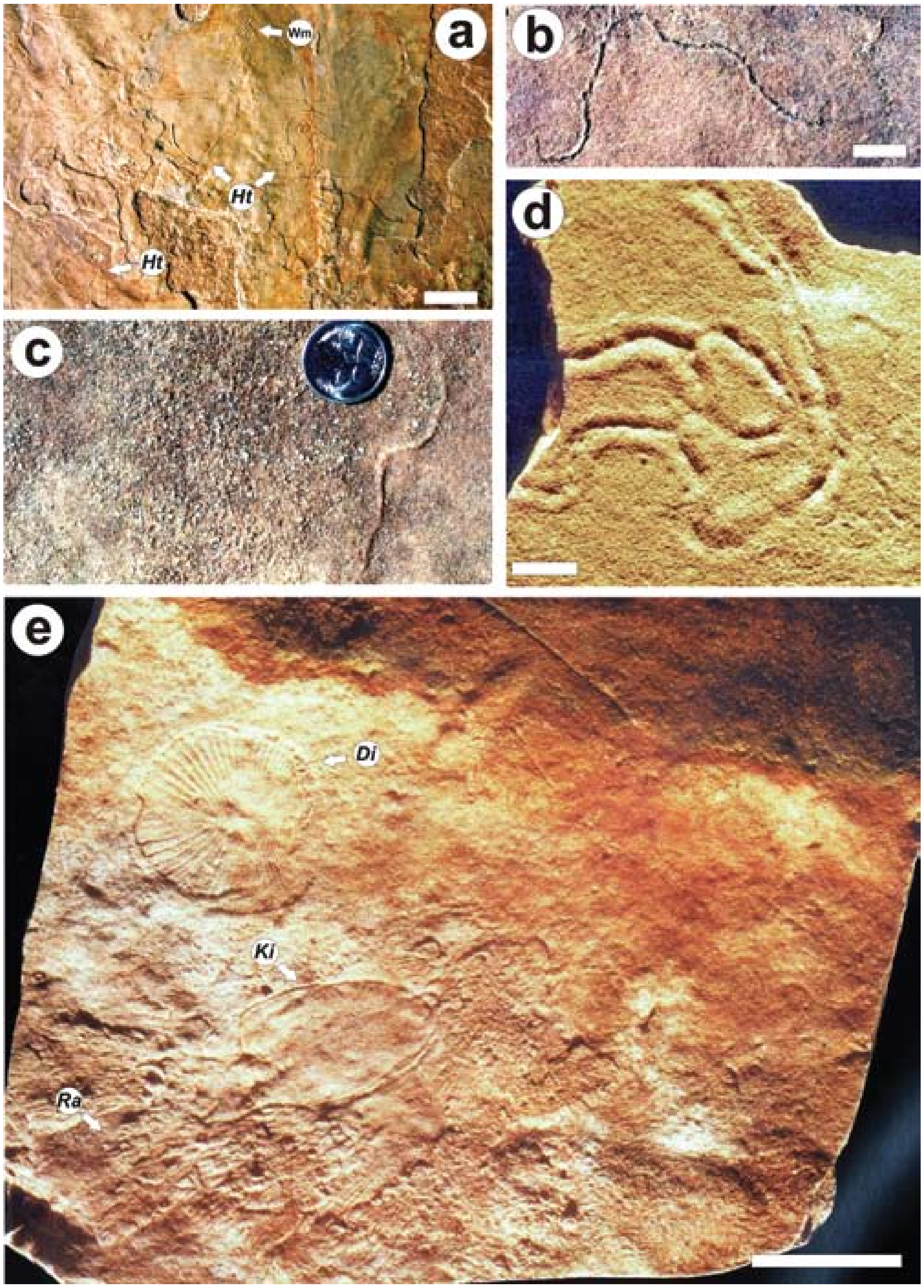

Figure 14.1 Representative trace fossils from the Ediacaran. (a) *Helminthoidichnites tenuis* (*Ht*) associated with wrinkle marks (Wm) suggestive of microbial mats. Arondegas Formation, Vanrhynsdorp Group, Arondegas Farm, South Africa. Scale bar is 1 cm. See Buatois *et al*. (2007c). (b) *Helminthopsis tenuis*. Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Scale bar is 1 cm. See Gehling *et al*. (2005). (c) *Helminthopsis tenuis* in unusually coarse-grained sandstone Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Coin is 1.9 cm. See Gehling *et al*. (2005). (d) *Archaeonassa fossulata*. Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Scale bar is 1 cm. (e) Radular marks attributed to the ichnogenus *Radulichnus* (*Ra*) in direct association with the producer, the protomollusck *Kimberella quadrata* (*Ki*). Note also the presence of *Dickinsonia* (*Di*). Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Scale bar is 5 cm. See Seilacher (2008).

suggested that the passive movement of dead organisms upon a microbial mat may have produced multiple impressions of body tissues mimicking a trace fossil.

Another match between producer and trace fossil is illustrated by the postulated primitive molluscan *Kimberella* (Fedonkin and Waggoner, 1997; but see Budd and Jensen, 2003, for a more basal phylogenetic position) and the scratches produced on microbial mats by its paired radular teeth (Seilacher, 1997; Fedonkin, 2003; Seilacher *et al*., 2005; Gehling *et al*., 2005; Fedonkin *et al*., 2007). Analysis of small specimens of

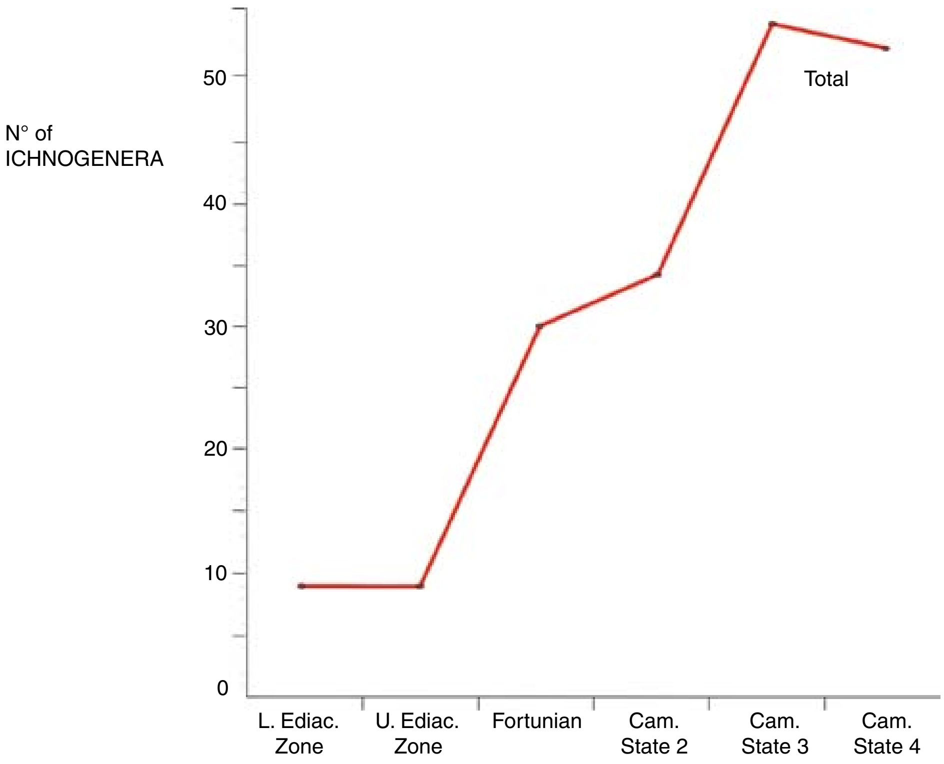

Figure 14.2 Ichnodiversity changes through the Ediacaran–Cambrian. No formal stratigraphic division is accepted yet for the Ediacaran, but two stratigraphic zones have been used here based on work by Jensen (2003). Although ichnodiversity levels remained more or less the same in these two zones, the upper Ediacaran zone is characterized by the appearance of more complex forms, such as *Treptichnus*, *Streptichnus*, and three-lobate trace fossils similar to *Curvolithus*. However, other forms present in the lower Ediacaran zone (e.g. *Radulichnus*, *Nenoxites*, Dickinsonid trace fossils) have not been recorded in the upper Ediacaran zone. Note sharp increase of trace-fossil diversity at the beginning of the Cambrian (Fortunian) and at the beginning of the Cambrian Series 2 (base of Cambrian Stage 3). The ichnodiversity curves were compiled at the ichnogenus level because the taxonomy is more firmly established than for ichnospecies.

Kimberella, and the fan-like arrangement of scratch marks indicate that the animal must have used a proboscis-like device to rasp on the microbial mat (Gehling *et al.*, 2005) (Fig. 14.1e).

The previous summary was essentially based on shallow-marine strata (e.g. Flinders Ranges, Australia, White Sea, Russia, Namibia, and South Africa) and, therefore, provides evidence on nearshore to offshore ecosystems. However, ichnological information is also available from deep-marine deposits (e.g. North Carolina, Mackenzie Mountains, Canada and central Spain), indicating that deep-sea bottoms were colonized by benthic animals already in Ediacaran times (Narbonne and Aitken, 1990; Vidal *et al.*, 1994; MacNaughton *et al.*, 2000; Orr, 2001; Crimes, 2001; Seilacher *et al.*, 2005; Liu *et al.*, 2010). In fact, the oldest trace fossils are known from deep-marine deposits rather than shallow-water deposits (Liu *et al.*, 2010). The colonization of the deep sea records a first-level ecological change. Ediacaran deep-marine ichnofaunas are poorly diverse and are dominated by nonspecialized grazing trails (e.g. *Helminthopsis*, *Helminthoidichnites*) associated with structures indicative of microbial mats (see Section 14.2.2). The body-fossil record further supports colonization of deep-sea bottoms during the terminal Proterozoic (Narbonne, 1998, 2005; Narbonne and Gehling, 2003; Clapham *et al.*, 2003; Grazhdankin, 2004).

Recent studies in Ediacaran ichnofaunas are changing our view of ichnodiversity levels by the end of the Proterozoic (Fig. 14.2). Previous studies listed a large number of ichnotaxa for the Ediacaran period (e.g. Runnegar, 1992a; Crimes, 1994). However, the emerging view is that Neoproterozoic ichnofaunas are of limited diversity and complexity (Jensen, 2003; Seilacher *et al.*, 2003, 2005; Mángano and Buatois, 2004c, 2007; Jensen *et al.*, 2005, 2006; Droser *et al.*, 2005, 2006). This shift reflects a reinterpretation of the trace-fossil nature of most ichnogenera that were considered exclusive of the Ediacaran (Group 1 of Alpert, 1977) (Haines, 2000; Gehling *et al.*, 2000, 2005; Jensen, 2003; Seilacher *et al.*, 2003, 2005; Jensen *et al.*, 2006). Supposedly guided meandering trails, such as *Yelovichnus* and *Palaeopascichnus*, have been reinterpreted either as algal remains (Haines, 2000) or body fossils of xenophyophorean protozoans (Seilacher *et al.*, 2003, 2005) or tubicolous animals (Shen *et al.*, 2007) (but see Zhuravlev *et al.*, 2009). *Harlaniella*, a rope-like structure regarded as a trace fossil, is now considered a body fossil related to *Palaeopascichnus*

(Jensen, 2003; Jensen *et al.*, 2006). The subcircular blob *Intrites* is now regarded as a body fossil of uncertain affinities (Gehling *et al.*, 2000). In particular, Jensen *et al.* (2006) provided a detailed table summarizing current re-evaluations of Ediacaran ichnofossils.

Problems also become evident with other ichnotaxa that occur through all or most of the Phanerozoic, and whose supposed presence in the Neoproterozoic has been pointed out in several compilations. For example, unquestionable specimens of vertical burrows, such as *Skolithos* or *Diplocraterion*, have not been documented from Ediacaran strata (Seilacher *et al.*, 2005; Jensen *et al.*, 2006). The presence of branched burrow systems in Ediacaran rocks is controversial. *Chondrites* has been mentioned in Ediacaran strata (e.g. Jenkins, 1995). However, these structures are commonly preserved as furrows that lack the characteristic burrow fill. More recently, they have been reinterpreted as poorly preserved specimens of body fossils or as overlap of unbranched trace fossils (Seilacher *et al.*, 2005; Jensen *et al.*, 2006). The radial structure *Mawsonites* is no longer considered a trace fossil (Runnegar, 1992b; Seilacher *et al.*, 2005; Jensen *et al.*, 2006). However, very shallow, three-dimensional burrow systems (*Treptichnus* and *Streptichnus*) occur in the uppermost Ediacaran, recording incipient exploitation of the infaunal ecospace and a slight increase in trace fossil complexity (Jensen *et al.*, 2000; Jensen and Runnegar, 2005). In addition, an increase in size seems to have occurred by the end of the Neoproterozoic as suggested by the presence of large horizontal trace fossils in Ediacaran rocks (Buatois *et al.*, 2007c).

14.1.3 THE CAMBRIAN EXPLOSION

The Ediacaran–Cambrian boundary constitutes a major divide in the history of life on Earth (Knoll *et al.*, 2006). Ediacaran biotas were dominated by soft-bodied organisms that are considered at least in part to be unrelated to modern metazoan faunas (Seilacher, 1992b; Seilacher *et al.*, 2003; Narbonne, 2004, 2005). On the other hand, the rapid development of almost all modern groups of animals, including the rise of skeletal faunas, took place during the Cambrian, in a major evolutionary event known as the Cambrian explosion (Conway Morris, 2000; Erwin, 2001; Droser and Li, 2001; Budd, 2003; Valentine, 2004; Marshall, 2006). Our understanding of the Cambrian explosion has implications for several key topics, including the origin of metazoan bodyplans, the role of developmental genetics, the validity of molecular clocks, and the influence of paleoenvironmental factors on macroevolution (Conway Morris, 2000). Although most evolutionary studies dealing with the Ediacaran–Cambrian transition have been based on the analysis of body fossils, the ichnological record provides an independent line of evidence to calibrate and evaluate the Cambrian explosion (Mángano and Buatois, 2007). This is of paramount importance because there is still no agreement whether the Cambrian explosion is a real evolutionary event or a preservational artifact that reflects an increase in fossilization potential (Valentine, 2004). It is evident that the Cambrian was a unique time in the history of life. Paraphrasing Andrew Knoll, it is also fair to say that there is nothing like the Cambrian after the Cambrian.

The diversity of Neoproterozoic ichnofaunas is generally low, and behavioral complexity is also limited (see Section 14.1.2). By the Fortunian (lowermost Cambrian), this picture changed with the appearance of much more diverse and complex ichnofaunas, particularly in shallow-marine environments (Fig. 14.2). Another increase in trace-fossil diversity again mostly in shallow-marine settings took place by the beginning of Cambrian Stage 3 (Fig. 14.2). Relatively diverse ichnofaunas composed of arthropod trackways, such as *Diplichnites* (Fig. 14.3a) and *Dimorphichnus*, the arthropod resting trace *Rusophycus*, complex grazing trace fossils (e.g. *Psammichnites*), the sinusoidal trail *Cochlichnus* (Fig. 14.3b), bilobate locomotion trace fossils (e.g. *Didymaulichnus*), branched feeding burrows of deposit feeders, including *Treptichnus pedum* (Fig. 14.3c), and complex feeding patterns included in the ichnogenus *Oldhamia* are known worldwide in lowermost Cambrian strata (Buatois and Mángano, 2004b, and references therein). Systematic guided meanders, such as those present in *Psammichnites saltensis* (Fig. 14.3d) and the elaborate feeding morphologies displayed by various ichnospecies of *Oldhamia* (Fig. 14.3e) reveal the onset of sophisticated grazing strategies that were notably absent during the Ediacaran (Seilacher *et al.*, 2005). Also, the large size of earliest Cambrian trace fossils (e.g. *Psammichnites*) contrasts with the typical small size of most Ediacaran trace fossils. In contrast to the rather monotonous aspect of Ediacaran ichnofaunas (see Section 14.1.2), Fortunian shallow-marine ichnofaunas display more varied behavioral patterns. This fact undoubtedly reflects the appearance of a number of body plans of soft-bodied organisms, which cannot be fully evaluated based on the analysis of the body fossil record alone.

Lowermost Cambrian trace fossils are typically oriented parallel to the bedding plane, and, therefore, they do not significantly disturb the primary sedimentary fabric (McIlroy and Logan, 1999; Buatois and Mángano, 2004b; Mángano and Buatois, 2004c, 2006). Fortunian trace fossils mostly reflect shallow to very shallow infaunal feeding activities of mobile, bilaterian metazoans. As a consequence of being restricted to bedding planes, the degree of bioturbation is only slightly higher than that of Ediacaran deposits. As in the case of Ediacaran rocks, there is a conspicuous absence of *Skolithos* pipe rock in Fortunian strata (Mángano and Buatois, 2004c, 2007). Vertically oriented trace fossils are only represented by shallow specimens of *Gyrolithes* (Droser *et al.*, 2002, 2004). This limited extent and depth of bioturbation resulted in the widespread development of relatively firm substrates and the virtual absence of a mixed layer within the substrate (Droser *et al.*, 2002, 2004; Dornbos *et al.*, 2004, 2005; Jensen *et al.*, 2005; Mángano *et al.*, 2007).

In contrast to Fortunian ichnofaunas, Cambrian Stage 2 trace-fossil assemblages are characterized by the appearance of vertical dwelling structures (*Skolithos*, *Diplocraterion*, and *Arenicolites*) of suspension feeders and passive predators, reflecting the onset of deep bioturbation, and the establishment

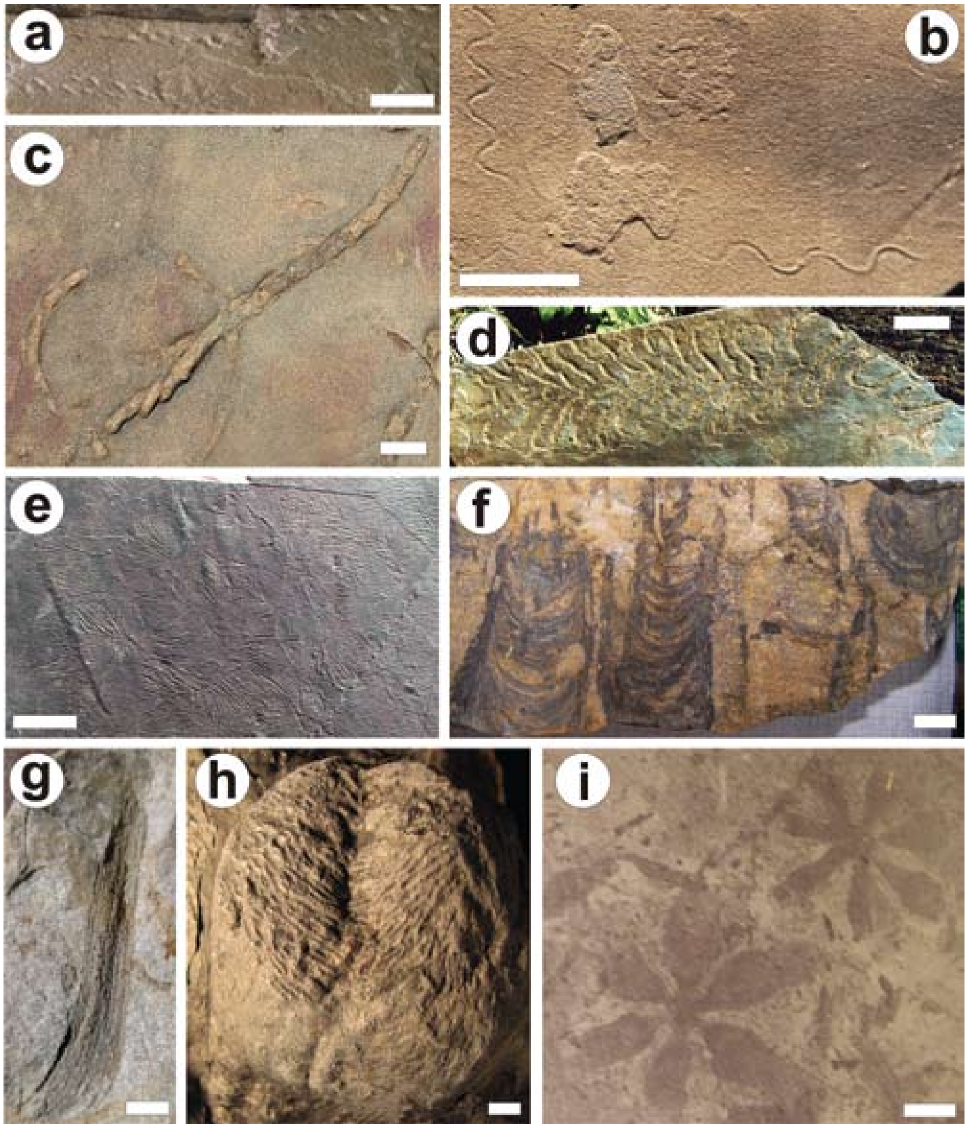

Figure 14.3 Trace-fossil variability and the Cambrian explosion. Note the wide variety of morphological patterns attained by the Early Cambrian. (a) *Diplichnites* isp. Puncoviscana Formation, San Antonio de los Cobres, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (b) *Cochlichnus anguineus*. Puncoviscana Formation, San Antonio de los Cobres, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (c) *Treptichnus pedum*. Klipbak Formations, Brandkop Subgroup, Gannabos Farm, South Africa. Scale bar is 1 cm. See Buatois *et al.* (2007c). (d) *Psammichnites saltensis*. Puncoviscana Formation, Cachi, northwest Argentina. Scale bar is 2 cm. See Buatois and Mángano (2004b). (e) *Oldhamia alata*. Puncoviscana Formation, el Mollar, Quebrada del Toro, northwest Argentina. Scale bar is 1 cm. See Seilacher *et al.* (2005). (f) *Diplocraterion parallelum*. Dividalen Group, Imobekken, northern Norway. Scale bar is 2 cm. See Bromley and Hanken (1991). (g) *Syringomorpha nilssoni* in an erratic block, Kiersgoube Pastz, Berlin, Germany. Scale bar is 1 cm. (h) *Rusophycus jenningsi*. Lake Louise Formation, Gog Group, Lake O'Hara, Canadian Rockies. (i) *Dactyloidites asteroides*. Metawee Slate Formation, vicinity of Middle Granville, New York State, northeastern United States. Scale bar is 1 cm.

of the *Skolithos* ichnofacies in high-energy settings (Fig. 14.3f). These vertical burrows may occur in prolific densities forming *Skolithos* pipe rock (Droser, 1991). Additionally, the J-shaped spreite trace fossil *Syringomorpha* (Fig. 14.3g) may occur in similar settings, forming distinct ichnofabrics (Mángano and Buatois, 2004b) (see Box 5.1). While Fortunian ichnofaunas were emplaced very close to the sediment–water interface, younger Lower Cambrian ichnofaunas reflect burrowing depths in the order of tens of centimeter, revealing an exponential increase in the depth of bioturbation of suspension-feeding organisms (Mángano and Buatois, 2004c, 2007). Also, detailed ichnological analysis in shallow-marine environments reveals a more complex tiering structure with the development of multiple guilds (Mángano and Buatois, 2004b). This increase in depth of bioturbation is not exclusive of high-energy nearshore areas, but also of lower-energy settings, where deep *Rusophycus*, such as *R. jenningsi* (Fig. 14.3h) and *R. dispar*, became common. In any case, the tiering structure is much simpler than that in younger ichnofaunas. During the Cambrian Stages 2 to 3, matgrounds became rare due to the onset of vertical bioturbation, and were replaced by mixgrounds in an event referred to as the "Agronomic Revolution" (Seilacher and Pfluger, 1994; Seilacher, 1999). This dramatic change at the biosphere scale was conducive to a remarkable change in the way living organisms interacted with the substrate ("Cambrian Substrate Revolution" of Bottjer *et al.*, 2000). Also, archaeocyathid reefs containing high densities of *Trypanites* are present in Lower Cambrian hardgrounds, revealing bioerosion by a macroboring biota (James *et al.*, 1977) (see Section 14.2.3). Additionally, increasing levels of predation were implicated in an arms race, spurring the development of complex predatory–prey interactions, and spurring evolutionary innovations (Vermeij, 1987). The role of predation as a triggering factor in the thorough exploitation of the infaunal ecospace has been a matter of debate. Evaluating extrinsic and intrinsic factors at the onset of the Cambrian explosion and the Agronomic Revolution is not easy (Marshall, 2006). In any case, evidence of predation has been detected in some Lower Cambrian deep burrowing *Rusophycus* directly associated with *Palaeophycus* (Jensen, 1990).

In addition to the noted changes in substrate conditions and predation intensity, it has recently been emphasized that the increased complexity and heterogeneity of marine environments may have played a major role as a driving force of evolutionary changes across the Ediacaran–Cambrian boundary (Plotnick, 2007; Plotnick *et al.*, 2010). The distribution of environmental signals in the marine ecosystem that an organism can potentially respond to has been termed its "information landscape". It has been hypothesized that a coevolutionary increase in the information content of the marine environment and in the ability of animals to obtain and process this information took place during the Cambrian explosion. According to this view, these facts may have resulted in the development of mobile bilaterians with macroscopic sense organs. This evolutionary event has been referred to as the "Cambrian Information Revolution" (Plotnick *et al.*, 2010). The trace-fossil record of this revolution is most likely expressed by the appearance of grazing trails and feeding burrows, displaying more sophisticated strategies to exploit resources in an heterogeneous landscape (e.g. Gámez Vintaned *et al.*, 2006) (Fig. 14.3d–e, and i).

The presence of multiple trophic guilds, and a well-established suspension-feeding infauna represented by abundant pipe rock in Cambrian Stages 2 to 3 strata provide evidence of a significant change in complexity of shallow-marine benthic communities, suggesting a coupling between plankton and benthos (Mángano and Buatois, 2004b, 2006, 2007; Mángano *et al.*, 2007). Butterfield (2001) suggested that the appearance of filter-feeding mesozooplankton were crucial in metazoan evolution. In fact, the addition of mesozooplankton to the trophic web may have acted as a trigger not only for the evolution of large metazoa, but also for the advent of the Agronomic Revolution. By repacking unicellular phytoplankton as nutrient-rich larger particles, zooplankton provides a more concentrated and exploitable resource for the benthos (Butterfield, 2001). This significant increase in the delivery of labile, nutrient-rich particles into the sediment may be behind the most significant change in the history of benthic ecology: the shift from matgrounds to mixgrounds. Mángano and Buatois (2004c, 2007) noted that ichnological evidence suggests that the presence of metazoa able to exploit the endobenthic environment preceded the establishment of a modern endobenthic ecological structure (i.e. mixground ecology). According to the decoupling hypothesis, the Cambrian evolutionary event consists of two phases: diversification of body plans during the Fortunian and a subsequent infaunalization and ecological shift during Cambrian Stages 2 and 3. Therefore, the Agronomic Revolution is not strictly coincident with the Ediacaran–Cambrian boundary. Although the body fossil record indicates the appearance of most of the major clades at the Cambrian Stage 3, the presence of rich ichnofaunas revealing diverse body plans during the Fortunian indicates the existence of a fuse time previous to what is commonly referred to as the Cambrian explosion (Mángano and Buatois, 2006).

Lower Cambrian ichnofaunas display segregation into two distinct environmentally related trace-fossil associations: shallow- and deep-marine (e.g. Buatois and Mángano, 2004b). Shallow-marine ichnofaunas are relatively diverse and complex (Box 14.1), but deep-marine trace-fossil assemblages essentially

Box 14.1 The Lower Cambrian Mickitzia Sandstone of Sweden and the Cambrian explosion

The Mickitzia Sandstone of Sweden contains one of the best documented Lower Cambrian ichnofaunas, and is essential to understanding the level of complexity reached by shallow-marine benthic communities at this early stage of metazoan evolution. Acritarch data indicate that this unit ranges in age from Cambrian Stage 3 to Stage 4. Forty one different ichnotaxa have been documented. The most outstanding feature of this ichnofauna is the wide variety of morphological and ethological types (Fig. 14.4a–e). The Mickitzia ichnofauna includes plug-shaped dwelling or resting burrows of actinarians (*Bergaueria perata*), sinusoidal grazing trails of nematodes or annelids (*Cochlichnus* isp.), arthropod locomotion (*Cruziana problematica* and *Cruziana rusoformis*, and *Cruziana* cf. *rusoformis*), resting (*Rusophycus dispar, Rusophycus jenningsi*, *Rusophycus eutendorfensis*), and dwelling (*Cheiichnus gothicus*) trace fossils commonly with distinctive scratch marks, vertical dwelling burrows (*Diplocraterion parallelum*, *Skolithos linearis*), concentrically filled conical vertical dwelling burrows of polychaetes (*Rosselia socialis*), spiral-shaped dwelling burrows of polychaetes (*Gyrolithes polonicus*), J-shaped vertical feeding burrows (*Syringomorpha nilssoni*), simple grazing trails of worm-like organisms (*Helminthoidichnites tenuis*), simple horizontal dwelling burrows of worm-like organisms (*Palaeophycus imbricatus*, *Palaeophycus tubularis*, *Palaeophycus tubularis*), annulated burrows (*Fustiglyphus* isp.), irregular feeding networks (*Olenichnus* isp.), branched feeding burrows of worm-like organisms, including priapulids (*Phycodes* cf. *curvipalmatum*, *Phycodes palmatus*, *Treptichnus bifurcus*, *Treptichnus pedum*), spreite simple feeding burrows possibly produced by annelids, priapulids, or trilobites (*Teichichnus ovillus* and *Trichophycus venosus*), spreite U-shaped feeding burrows (*Rhizocorallium jenense*), radiating feeding burrows (*Scotolithos mirabilis*), and spreite lobate feeding burrows (*Zoophycos* isp.). The Mickitzia ichnofauna displays a sharp contrast with their Ediacaran counterparts of shallow-marine environments, which are remarkably less diverse and much simpler. Characterization of the Mickitzia ichnofauna illustrates the profound ecological and evolutionary changes resulting from the Cambrian explosion and the Agronomic Revolution.

Reference: Jensen (1997); Jensen and Bergström (2000).

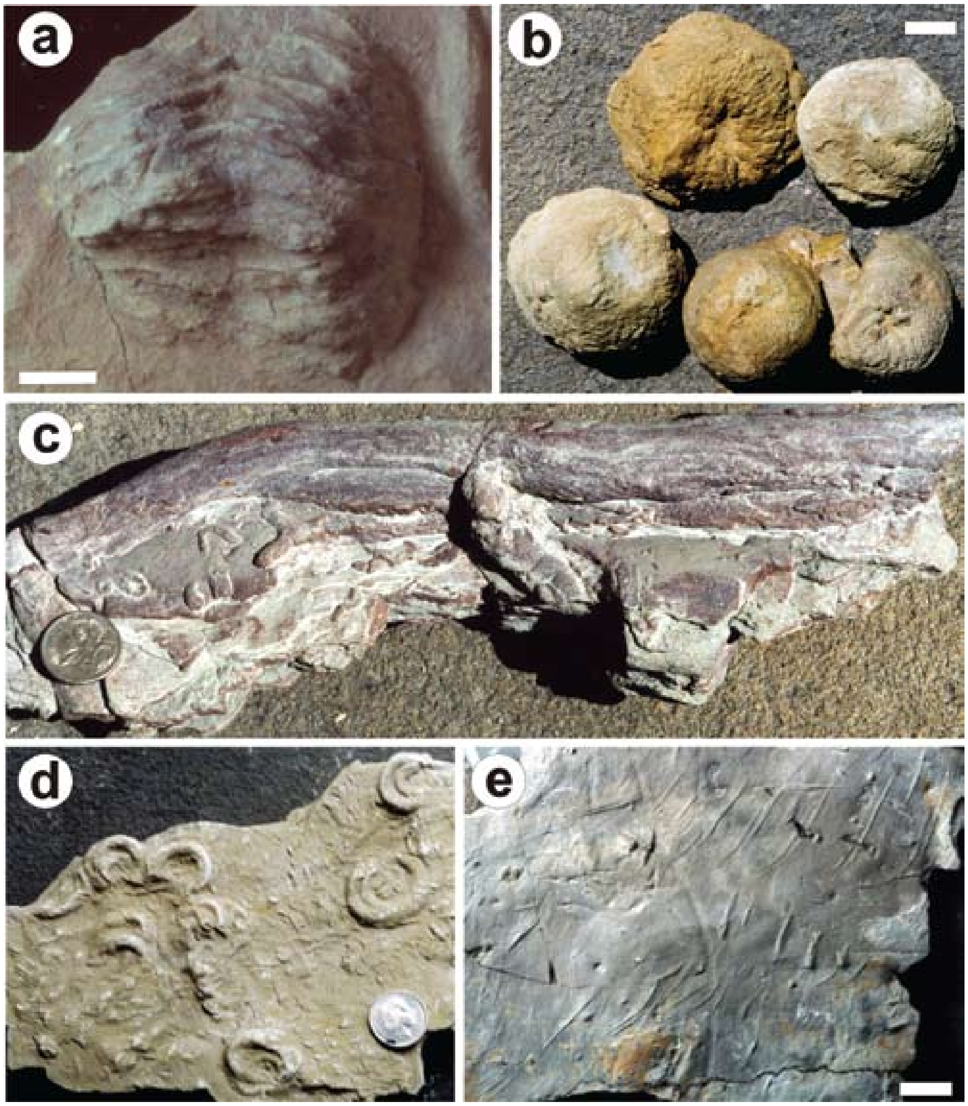

Figure 14.4 Selected trace fossils from the Lower Cambrian Mickitzia Sandstone, Västergötland, Sweden. See Jensen (1997). (a) *Rusophycus dispar*. Scale bar is 1 cm. (b) *Cheiichnus gothicus*. Scale bar is 2 cm. (c) *Trichophycus venosus*. Coin is 1.9 cm. (d) *Gyrolithes polonicus*. Coin is 1.9 cm. (e) *Dimorphichnus obliquus*. Scale bar is 2 cm.

consist of simple grazing trails, arthropod trackways, and different ichnospecies of the specialized undermat miner feeding structure *Oldhamia* (Buatois and Mángano, 2003a). This association indicates that microbial matground ecology persisted in the deep sea during the Early Cambrian, representing a Proterozoic "hangover" (see Section 14.2.2). This idea is consistent with the notion of archaic relics taking refuge in the deep sea (e.g. Conway Morris, 1989). *Oldhamia* flourished in Early Cambrian deep-marine environments, experiencing a remarkable behavioral diversification as revealed by a great diversity of ichnospecies (Seilacher *et al.*, 2005). *Oldhamia*-dominated assemblages in microbial-mat ecosystems persisted in the deep sea after the rise of vertical bioturbation in shallow seas, suggesting a gradual closure of a taphonomic window during the Ediacaran–Cambrian transition (Buatois and Mángano, 2004b). This is consistent with the recognition of Ediacara-type body fossils in Cambrian strata (Gehling *et al.*, 1998; Jensen *et al.*, 1998; Crimes and McIlroy, 1999; Hagadorn *et al.*, 2000; Shu *et al.*, 2006).

In addition to fully marine environments, Lower Cambrian ichnofaunas have been documented from marginal-marine settings (e.g. Mángano and Buatois, 2004b; Baldwin *et al.*, 2004; Mángano *et al.*, 2007), revealing that representatives of the Cambrian evolutionary fauna were able to colonize brackish-water environments (see Section 14.2.5). Although the scarcity of land plants was probably a major limiting factor in colonization of marginal-marine systems, documentation of Cambrian cryptospores suggests the presence of plants with one or more life-cycle phases on land (Strother and Beck, 2000; Strother, 2000). In contrast to complex modern estuarine food webs, Cambrian web chains in marginal-marine ecosystems were mostly marine-based, with acritarchs and algae being primary producers. However, a nascent terrestrial flora may have played a role in these ancient food webs (Mángano and

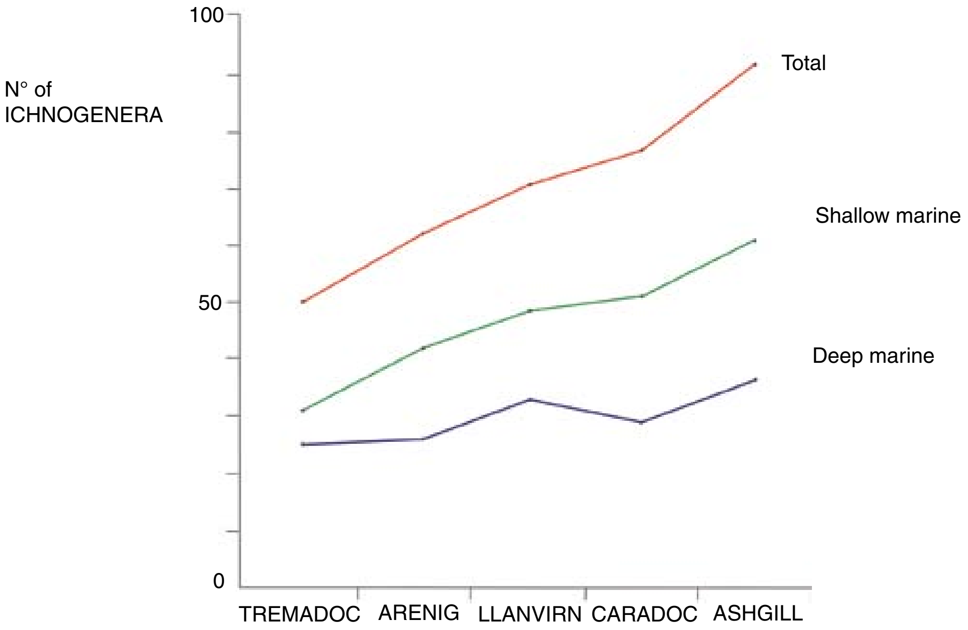

Figure 14.5 Ichnodiversity changes through the Ordovician (after Mángano and Droser, 2004). The ichnodiversity curves were compiled at the ichnogenus level. The ichnogeneric compilation was plotted as "range-through" data. Total curve includes not only shallow- and deep-marine ichnofossils but also continental trace fossils and boring ichnotaxa. The shallow-marine curve does not include borings.

Buatois, 2004b). Although tiering structure remains simple in marginal-marine environments, ichnoguild analysis reflects an incipient exploitation of food resources, recording the activity of a benthos that developed in the aftermath of the Agronomic Revolution (Mángano *et al*., 2007).

14.1.4 THE ORDOVICIAN RADIATION

As in the case of the Cambrian explosion, most of our knowledge of the Ordovician radiation comes from the body-fossil record (e.g. Sepkoski, 1995; Sheehan, 2001; Droser and Finnegan, 2003). Some studies, however, have focused on the information potential of ichnological data (Mángano and Droser, 2004). In contrast to previous views, analysis of ichnodiversity indicates a continuous increase in ichnogeneric diversity through the Ordovician, with the number of shallow-marine ichnogenera doubling from the Tremadocian to the Ashgill (Mángano and Droser, 2004) (Fig. 14.5). This increase parallels substantial changes in the nature of biofabrics (Kidwell and Brenchley, 1994; Li and Droser, 1999; Droser and Li, 2001) and compositional turnovers by the dominant bioturbators of shallow-water environments.

Lower Ordovician ichnofaunas from shallow-marine siliciclastic deposits tend to be dominated by trilobite trace fossils, which record a significant turnover in peri-Gondwanan settings. Elements of the *Cruziana semiplicata* group (Upper Cambrian–Tremadocian) are replaced by elements of the *Cruziana rugosa* group by the Late Tremadocian (see Section 13.2). This change in ichnotaxonomic composition parallels the replacement of olenid-dominated communities by saphid-dominated communities (Waisfeld *et al*., 1999, 2003). Other common components of the *Cruziana* ichnofacies in Lower Ordovician strata are vermiform structures such as *Planolites*, *Palaeophycus*, *Trichophycus*, *Treptichnus*, *Teichichnus*, and *Phycodes*.

Middle to Late Ordovician shallow-marine siliciclastic ichnofaunas commonly display more ethological variability. Although still relatively abundant, trilobite trace fossils are rarely the dominant component in open-marine clastic deposits, most likely reflecting the development of multiple tiers and the establishment of a well-developed mixed layer (Droser *et al*., 2004). Mángano and Droser (2004) noted that the dominant patterns include branched, spreiten burrow systems (e.g. *Phycodes* and *Trichophycus*), branched, annulated burrow systems (e.g. *Arthrophycus*), branched burrow mazes and boxworks (e.g. *Thalassinoides*), dumbbell-shaped traces (e.g. *Arthraria*), and chevronate structures (e.g. *Protovirgularia*). Most of these behavioral architectures were present in Cambrian and Lower Ordovician rocks already, but generally were subordinate in abundance and diversity to trilobite and other arthropod trace fossils.

In general, the tiering structure of Ordovician shallow-marine siliciclastic resident communities is more complex than that of Cambrian biotas. On the other hand, the post-depositional suite, which commonly reflects the work of opportunistic organisms, seems to be less sensitive to evolutionary events, being mostly recorded by vertical suspension feeder structures, such as *Skolithos*, *Arenicolites*, and *Diplocraterion* (Mángano and Buatois, 2003a).

In contrast to siliciclastic shallow-marine settings, carbonate softgrounds do not show a significant increase in ichnodiversity through the Ordovician, but rather reveal increased ecospace utilization and tiering complexity (Droser and Bottjer, 1989; Mángano and Droser, 2004). Colonization of carbonate substrates may have lagged behind that of siliciclastic deposits. Ichnofabric evidence indicates an onshore–offshore pattern. Intense bioturbation first developed in shallow-water environments and only later in the offshore (Droser and Bottjer, 1989). Inner-shelf carbonates of the Great Basin in the western United States reveal two major increases in the extent and depth of bioturbation during the early Paleozoic: the first one between pre-trilobite and trilobite-bearing Cambrian rocks, and the second between the Middle and Late Ordovician (Droser and Bottjer, 1989).

The Ordovician increase in bioturbation seems to have resulted, in part, from an increase in the size of discrete structures (Droser and Bottjer, 1989). Although *Thalassinoides* is present in Cambrian and Lower Ordovician rocks, specimens are typically small, architecturally simpler, and commonly form two-dimensional networks (e.g. Myrow, 1995). In contrast, Middle to Upper Ordovician *Thalassinoides* burrow systems tend to be larger and deeper, and display classic "T" and "Y" branching (Sheehan and Schiefelbein, 1984). These *Thalassinoides* burrow systems resemble modern structures produced by decapod crustaceans recording extensive reworking with severe obliteration of primary structures (Sheehan and Schiefelbein, 1984; Droser and Bottjer, 1989; Carmona *et al*., 2004). In spite of this general trend, *Thalassinoides* burrows from Upper Cambrian–Tremadocian lagoonal carbonates in the Argentinean Precordillera display unquestionable three-dimensional morphology, suggesting an earlier origin of boxwork architecture (Cañas, 1995; Mángano and Buatois, 2003a). Although Ordovician *Thalassinoides* has typical boxwork architecture, unquestioned scratch mark ornamentation has not been recorded in early Paleozoic galleries (Carmona *et al*., 2004). Furthermore, early Paleozoic examples largely predate the first occurrence of decapod crustacean body fossils in the Devonian (Schram *et al*., 1978). Therefore, these burrow systems were most likely produced by other malacostracans (e.g. phyllocarids) or unrelated clades (e.g. enteropneusts) as a result of behavioral convergence (Carmona *et al*., 2004). In addition to those changes operating in carbonate softgrounds, significant changes in the evolution of macroboring organisms occurred in shallow-water hardgrounds during the Ordovician, resulting in the so-called Ordovician Bioerosion Revolution (Wilson and Palmer, 2006) (see Section 14.2.3).

The Ordovician radiation was not restricted to shallow-marine environments, but also represents a breakthrough in the deep sea, where ichnofaunas attained a much more modern aspect in comparison with their Ediacaran–Cambrian counterparts marking the real onset of the *Nereites* ichnofacies (see Section 14.2.2). Further changes took place in marginal-marine (see Section 14.2.5) and continental (see Section 14.2.6) ecosystems, revealing the environmental breadth of the Ordovician radiation.

14.1.5 THE ORIGIN OF DINOSAURS

The oldest skeletal remains of dinosaurs are known from the Late Triassic (e.g. Sereno and Novas, 1992). However, Early and Middle Triassic trackways attributed to dinosaurs have been mentioned in the literature. Wills and Sarjeant (1970) documented several trackways from Lower Triassic borehole cores in England which were attributed to small coelurosaur dinosaurs. However, subsequent reviews reinterpreted these structures as ripple marks, mud rip-up clasts, and possible limulid trackways (Thulborn, 1990; King and Benton, 1996). Sarjeant (1967) documented a Middle Triassic tracksite from England, which included footprints attributed to small theropods and prosauropods. Subsequent work by King and Benton (1996) placed them in the archosaur trackway *Chirotherium*, while Sarjeant (1996) reinterpreted some of them as *Chirotherium* and others as crocodilian trackways.

The strongest ichnological evidence for an earlier origin of dinosaurs comes from the Middle Triassic of continental Europe and Argentina. In France, Demathieu (1989) described trackways that have a strong similarity with *Grallator*, a dinosaur trackway recorded in Late Triassic and Jurassic rocks. Lockley and Meyer (2000) concluded that these are either the oldest dinosaur trackways or they were produced by non-dinosaurian archosaurs. In Germany, Haubold and Klein (2000, 2002) documented tridactyl pedes of bipeds (*Grallator*) and quadrupeds (*Atreipus*), which were regarded as having been produced by early dinosaurs and dinosauriforms, respectively. Avanzini (2002) described isolated small tridactyl imprints from Italy and attributed them to dinosauromorphs. Middle Triassic rocks of western Argentina contain large tridactyl footprints attributed to theropods (Arcucci *et al*., 1995; Forster *et al*., 1995; Marsicano *et al*., 2004). A recent analysis by Marsicano *et al*. (2007) documented a more diverse track assemblage, but indicated that no synapomorphies are preserved in the three-toed footprints that might allow discrimination among theropods, basal saurischians, and basal ornithischian groups as trackmakers. In any case, the trace-fossil record seems to suggest a Middle Triassic history of dinosaurs, predating the earliest occurrence of body fossils (Marsicano *et al*., 2007) (Fig. 14.6).

14.1.6 MASS EXTINCTIONS

The potential of trace fossils to explain mass-extinction events has been realized only recently (e.g. Twitchett and Wignall, 1996; Twitchett and Barras, 2004). Of the "Big Five" mass extinctions, research has focused on the end-Permian (e.g. Twitchett and Wignall, 1996; Twitchett, 1999; Pruss and Bottjer, 2004; Wetzel *et al*., 2007) and end-Cretaceous (e.g. Ekdale and Bromley, 1984b; Savrda 1993; Rodríguez-Tovar, 2005; Rodríguez-Tovar and Uchman, 2006, 2008) events. A more limited ichnological dataset is available for the end-Ordovician, Late Devonian, and end-Triassic events.

Estimations indicate that approximately 85% of marine species went extinct during the Late Ordovician event as a result of a brief glacial episode (Brenchley *et al*. 2001; Sheehan 2001), although the ecological impact was comparatively low (McGhee *et al*., 2004). Only a few ichnological studies have been devoted to this mass extinction (McCann, 1990; Herringshaw and Davies, 2008). Information from shallow-marine strata of the Welsh Basin indicates overall low degrees of bioturbation and trace-fossil diversity during the Late Ordovician–Early Silurian transition, but no other clear patterns are apparent (Herringshaw and Davies, 2008). Examination of deep-marine deposits in the same basin reveals a sharp decrease in ichnodiversity across the Ordovician–Silurian boundary (McCann, 1990).

During the Late Devonian (Frasnian–Famennian) mass extinction approximately 70% of species disappeared, with the

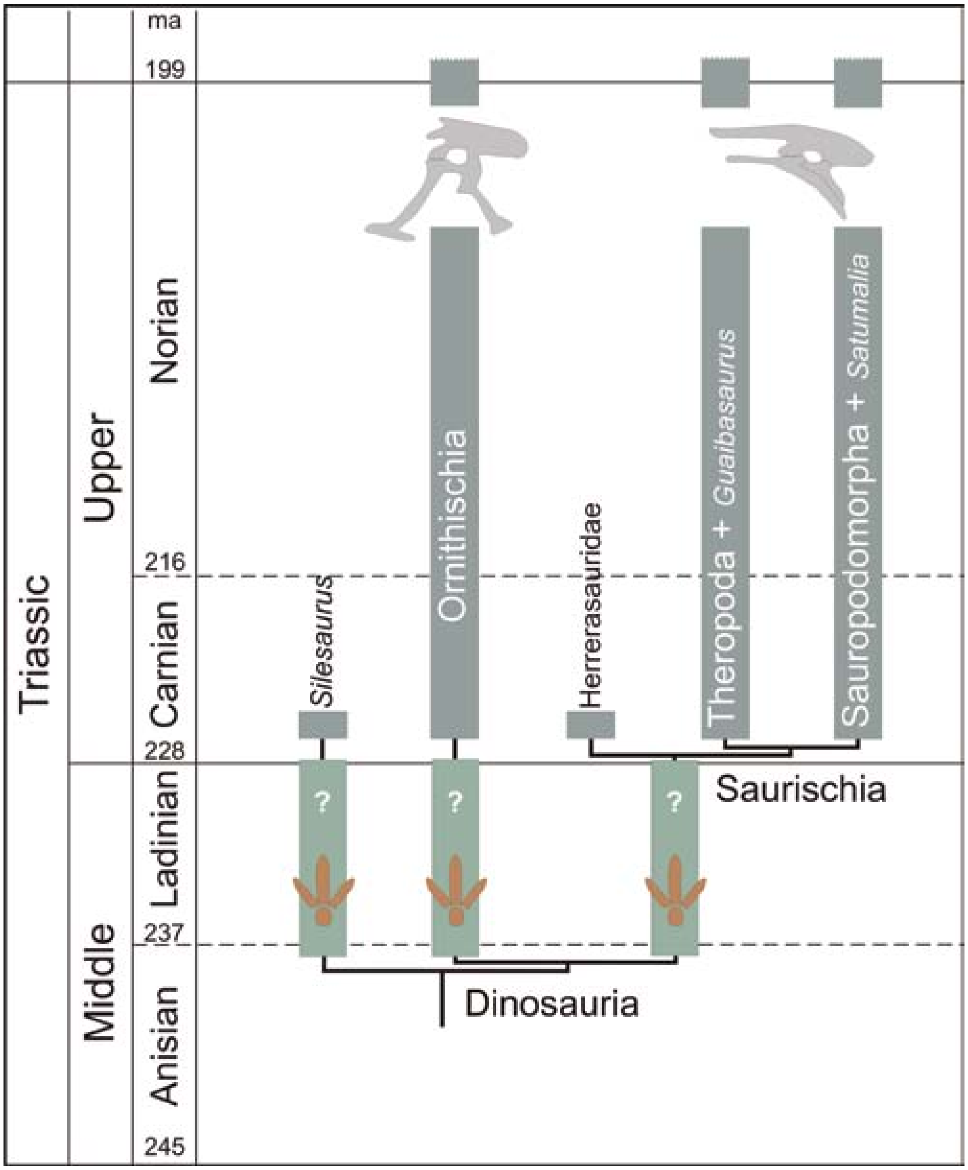

Figure 14.6 Calibrated phylogeny of early dinosaurs and its sister taxon taking into account not only the body-fossil record, but also the trace-fossil record. Addition of ichnological data implies the extension of the early diversification of dinosaurs and/or their closest relatives into the Middle Triassic. Based on Marsicano *et al.* (2007).

event affecting both marine and terrestrial organisms (McGhee, 1996). Global oceanic anoxia, global cooling, and multiple impacts of asteroids or comets have been proposed as potential causes (McGhee, 1996, 2001). Ichnological analysis of this event is still in its infancy and only one study has been published so far (Morrow and Hasiotis, 2007). Preliminary information indicates that the crisis is associated with a drop in ichnodiversity, reduction in bioturbation intensity, decreased depth of bioturbation, and decreased burrow size. A protracted post-extinction recovery is apparently marked by an increase in trace-fossil diversity by the middle Famennian, including *Cruziana* and *Rusophycus*. However, evaluation of environmental and facies controls needs to be addressed in more detail in this study. The suggested trends were based on a shallowing-upward succession from slope to offshore environments. Therefore, the appearance of trilobite burrows and the associated increase in ichnodiversity noted by these authors may simply reflect shallowing and the establishment of an offshore community rather than a true post-extinction recovery.

The end-Permian mass extinction was the largest of the entire Phanerozoic, and it has been estimated that up to 96% of species became extinct, (Raup, 1979; Hallan and Wignall, 1997; Benton, 2003; Erwin, 2006). This mass extinction displays the highest ecological severity in both marine and continental environments (McGhee *et al.*, 2004). Global anoxia has been suggested as the most likely cause of the extinction in the oceans (Hallam and Wignall, 1997; Wignall, 2001). Release of large volumes of volcanic carbon dioxide may have triggered a supergreenhouse climate, making large areas of Pangea uninhabitable. In turn, global warming may have affected global ocean circulation patterns by decreasing the generation of dense cold deep waters, resulting in stagnation and anoxia (Wignall, 2001). In recent years, trace-fossil information has been used to analyze the patterns of extinction and recovery across the critical

Permian–Triassic interval, and a more robust ichnological dataset is now available for this event (e.g. Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004; Pruss and Bottjer, 2004; Wetzel et al., 2007; Zonneveld *et al.*, 2007, 2010; Beatty *et al.*, 2008; Fraiser and Bottjer, 2009). Comparative ichnological analyses through the pre-extinction, post-extinction aftermath, and recovery phases are particularly useful for evaluating the endobenthic response to the end-Permian mass extinction event in shallow-marine settings (Twitchett and Barras, 2004). Pre-extinction deposits are intensely bioturbated and contain a wide variety of ichnotaxa. In contrast, ichnofaunas from the lowermost Triassic (immediate post-extinction aftermath) are typically monospecific and consist of small *Planolites*, indicating environmental stress in connection with a widespread anoxic event. Available information indicates that there was a stepwise appearance of ichnogenera through the Early Triassic, signaling the phase of recovery. Parallel to this increase in ichnodiversity, an increase in burrow size and depth of bioturbation has been noted. In addition, proliferation of microbial mat structures during the post-extinction aftermath provides further evidence of suppressed bioturbation and environmental stress (Pruss *et al.*, 2004, 2005; Mata and Bottjer, 2009). It has been suggested that there may have been a faster recovery at higher latitudes, as indicated by the presence of higher ichnodiversity levels (Beatty *et al.*, 2008; Zonneveld *et al.*, 2010). In addition, Wetzel *et al.* (2007) documented a deep-marine ichnofauna in Upper Triassic rocks of Oman, which displays unusually high diversity in contrast to age-equivalent deep-sea assemblages worldwide. According to these authors, some of these refuge habitats may have been located in warm-water, low-latitude shelf and continental-margin environments, allowing recolonization of the deep-sea floor after the Permian-Triassic mass extinction.

The end-Triassic mass extinction accounts for an approximately 76% loss in species diversity and is ranked third in terms of ecological severity, affecting both marine and continental communities (Raup, 1992; Tanner *et al.*, 2004; McGhee *et al.*, 2004). In comparison, less research has been done on this mass extinction and its causes are poorly understood, with hypotheses ranging from widespread eruptions of flood basalts to the release of methane hydrates and bolide impact-induced environmental degradation (Tanner *et al.*, 2004). Although ichnological aspects of this event have not been analyzed in the same detail as those of the end-Permian event, there is a growing volume of information suggesting changes in vertebrate and invertebrate ichnofaunas. The tetrapod footprint record indicates that large theropod dinosaurs appeared less than 10 000 years after the Triassic–Jurassic boundary and that dinosaur communities became dominant less than 100 000 years after the boundary (Olsen *et al.*, 1987). Marine invertebrate ichnofaunas of the pre-extinction Late Triassic are diverse, while lowermost Jurassic (Hettangian) deposits are characterized by low ichnodiversity, low bioturbation intensity, small burrow diameters, and an absence of deep-tier structures, illustrating the immediate post-extinction aftermath (Barras and Twitchett, 2007). A stepwise appearance of ichnogenera characterizes recovery times. Ichnological evidence seems to be consistent with an episode of marine anoxia (Barras and Twitchett, 2007).

The end-Cretaceous extinction accounts for 40–76% species loss, affecting both marine and terrestrial communities (Jablonski, 1995; Hallam and Wignall, 1997; Norris, 2001; Wolfe and Russell, 2001). This extinction most clearly illustrates the decoupling of taxonomic and ecological severity, being the least severe of the "Big Five" in terms of taxonomic diversity, but the second from an ecological standpoint (McGhee *et al.*, 2004). Most researchers favor the impact of a large bolide impact as the triggering cause of the extinction (Alvarez *et al.*, 1980; Kauffman and Hart, 1996), although other mechanisms, such as massive volcanism, have also been proposed (e.g. Keller, 2001, 2003). Ichnological research on the Cretaceous–Tertiary mass extinction focused on three different aspects: paleoenvironmental interpretation of the associated deposits, the nature of benthic colonization after the extinction, and changes in the types and intensity of arthropod–plant interactions. The first set of studies took place inland of the Gulf of Mexico, in Alabama (Savrda, 1993) and northeastern Mexico (Ekdale and Stinnesbeck, 1998). Both studies questioned the catastrophic nature of the deposits which were attributed to a tsunami. In the case of Alabama, ichnological and sedimentological analysis supports transgressive deposition in an estuarine incised valley (Savrda, 1993), while deposits in Mexico are intensely bioturbated, suggesting slow sedimentation rather than a catastrophic event (Ekdale and Stinnesbeck, 1998). The second set of studies was performed in Europe, more precisely in several sections in Denmark (Ekdale and Bromley, 1984b) and Spain (Rodríguez-Tovar, 2005; Rodríguez-Tovar and Uchman, 2004a, b; 2006, 2008; Rodríguez-Tovar *et al.*, 2006). In general, these studies documented intense bioturbation in earliest Danian strata, suggesting rapid substrate colonization and re-establishment of infaunal communities after the extinction event, and, therefore, arguing against the idea of a major restructuring of the infaunal benthic community. Also, it has been noted that deep burrowing may have transported Danian forams into the underlying Maastrichtian deposits, complicating positioning of the boundary (Rodríguez-Tovar and Uchman, 2006). Finally, evidence of insect traces preserved in fossil plants allowed an evaluation of the impact of the mass extinction in continental environments (e.g. Labandeira *et al.*, 2002a, b). These studies suggested a sudden and sustained drop in many categories of plant–insect interactions at the Cretaceous–Tertiary boundary. Similar levels of interactions to those of the latest Cretaceous were not attained until the Paleocene–Eocene boundary (Wilf *et al.*, 2001; Labandeira *et al.*, 2002a, b). Those categories of interactions that were most affected correspond to specialized associations in which monophagy defines plant–host specificity (Labandeira *et al.*, 2002a).

Also, ichnofaunas from various environments were differentially impacted by mass extinctions. Shallow-marine communities were the most affected. In contrast, the impact was lower on marginal-marine brackish-water faunas (Buatois *et al.*, 2005). Brackish-water faunas consist of opportunistic organisms that flourish under extreme conditions, and are able to rapidly colonize environments after a major disturbance, as it is the case of a mass extinction. Deep-water ichnofaunas have not been strongly affected by mass extinctions either (Uchman, 2004a). No major deep-water crisis has been associated with any of the "Big Five" mass extinctions. However, Uchman (2003) noted reduced diversity and abundance of graphoglyptids associated with the end-Ordovician and end-Cretaceous mass extinctions.

14.2 ANIMAL–SUBSTRATE INTERACTIONS AND ECOSYSTEMS THROUGH TIME

14.2.1 COLONIZATION OF SHALLOW-MARINE ENVIRONMENTS

Because nearshore to offshore-shelf strata typically contain a high diversity of body fossils, shallow-marine environments have been the focus of most studies in marine evolutionary paleoecology. Some of the most influential research on this topic was performed by Sepkoski (1981, 1991, 1992, 1997). In these studies, Sepkoski recognized the existence of three main evolutionary faunas in the Phanerozoic: the Cambrian, Paleozoic, and Modern evolutionary faunas. Each evolutionary fauna had a unique set of higher taxa and displays higher diversity and more ecological complexity than the previous one. This increase in ecological complexity has been further demonstrated through the analysis of Bambachian megaguilds (Bambach, 1983; Bambach *et al*., 2007; Bush *et al*., 2007). Although further studies based on more refined techniques and more extensive databases have questioned some aspects of this model (e.g. Alroy *et al*., 2001, 2008), this scheme has proved to be quite relevant to our understanding of ecological aspects of the history of life. Trace-fossil information is consistent with the body-fossil record of evolutionary faunas.

The Cambrian evolutionary fauna was dominated by trilobites, with inarticulate brachiopods, hyolithids, monoplacophorans, eocrinoids, and hexactinellid sponges as other components (Sepkoski, 1981). Deposit, detritus, and suspension feeders were the main trophic types, with predation being a relatively minor component (Sepkoski, 1981; Bambach, 1983; Burzin *et al*., 2000; Sheehan, 2001). The ecological structure of communities in this evolutionary fauna was relatively simple. Thirty modes of life (see Section 3.1) have been recognized for Lower to Middle Cambrian faunas, representing roughly one-third of the modes of life used by recent faunas (Bambach *et al*., 2007). Of these 30 modes of life, 19 were recorded based on skeletal faunas and the other 11 based on the analysis of soft-bodied animals preserved in Konservat-Lagerstätten. Overall, the Cambrian evolutionary fauna represents the occupation of 11 megaguilds (*sensu* Bambach, 1983). The Cambrian evolutionary fauna began in the Early Cambrian, increased in diversity during the Cambrian, gradually diminished in importance after the Ordovician, and was severely affected by the end-Permian mass extinction.

Of the typical components of the Cambrian evolutionary fauna, only trilobites and other arthropods are important trace-fossil producers, being inarticulate brachiopods makers of *Lingulichnus*. The increase and subsequent decrease in dominance and diversity of arthropod- and particularly trilobite-produced trace fossils certainly follows the trend displayed by the Cambrian evolutionary fauna (see Sections 14.1.3 and 14.1.4). Also, tiering analysis based on the study of ichnofaunas indicates relatively simple community structures and limited utilization of the infaunal ecospace. Deposit-feeding ichnoguilds are mostly shallow tier, while deep-tier ichnoguilds of suspension feeders are restricted to high-energy nearshore zones. Bambach (1993) has proposed that the paucity of deep deposit-feeding burrowers in offshore to deeper-water settings indicates limited amounts of food buried in the sediment. Limited durophagous predation is also suggested by the trace-fossil record, as illustrated by the scarcity of bored shells (see Section 14.2.3). Based on the existence of graphoglyptids in shallow-water deposits, it may be argued that farming and trapping strategies had already developed during the Cambrian, and later migrated into the deep sea (see Section 14.2.2). Because these sophisticated strategies are usually employed as a response to scarce food resources, this pattern seems to be consistent with comparatively limited food in shallow seas during the Cambrian (Buatois and Mángano, 2003b).

The Paleozoic evolutionary fauna was dominated by articulate brachiopods, rugose and tabulate corals, and crinoids; stenolaemate bryozoans, graptolites, and cephalopods were common also (Sepkoski, 1981). The benthos experienced a diversification in deposit feeders, detritus feeders, suspension feeders, and grazers, while suspension feeders and predators diversified in the pelagic setting (Bambach, 1983; Sheehan, 2001). Predation levels also increased and the ecological structure of the communities became more complex. As a result of the Ordovician radiation, the number of modes of life utilized by skeletal organisms increased to a total of 30 by the Late Ordovician; the scarcity of Konservat-Lagerstätten precludes analysis of soft-bodied faunas (Bambach *et al*., 2007; but see Van Ray *et al*., 2010). Of the 20 potential Bambachian megaguilds, 14 were filled by the Paleozoic fauna (Sheehan, 2001). The Paleozoic evolutionary fauna began in the Early Cambrian, but attained its maximum diversity in the Ordovician. Diversity was maintained during the Paleozoic and, although the fauna persisted into the Mesozoic and the Cenozoic, it was significantly affected by the end-Permian mass extinction, showing a rapid decline (Sepkoski, 1981).

The ichnological expression of the Paleozoic evolutionary fauna is mostly reflected by an increase in ichnodiversity and tiering complexity, as well as by an increase in degree and depth of bioturbation. As previously discussed, the number of shallow-marine ichnogenera doubled as a result of the Ordovician radiation (see Section 14.1.4). The tiering structure of ichnofaunas becomes more complex, both by the addition of deeper tiers and by the addition of a wider variety of behavioral patterns in previously occupied tiers, mostly in the case of offshore deposit-feeding faunas (Mángano and Droser, 2004; Mángano and Buatois, 2011). Interestingly, recent studies suggest that infaunalization by deposit feeders in offshore siliciclastic environments was most likely diachronic, with mid tiers being colonized first in Laurentia and Baltica, and subsequently in Gondwana (Mángano and Buatois, 2011). An overall increase in the depth of bioturbation seems to have occurred since the Ordovician and well into the Devonian (Larson and Rhoads, 1983). Bioturbation depths of 5–6 cm were common, locally with depths up to 30 cm (Bambach, 1993). Preliminary data suggest that these levels persisted into the Triassic (Aigner, 1985). Increased burrowing depths by deposit feeders have been linked to an increase in the amount of buried food (Bambach, 1993). In contrast, *Skolithos* pipe rock, a product of deep-tier suspension feeders which was widespread during the Cambrian, become less common through the Paleozoic (Droser, 1991; Desjardins *et al.*, 2010a). Although the reasons for this decline are unclear, increased disturbance of the substrate by deposit feeders may have impacted negatively on passive suspension feeders (Thayer, 1979; Miller and Byers, 1984) (see Section 6.6). In fact, the diversification of sediment bulldozers has been deemed responsible for the decline throughout the Phanerozoic of suspension feeders living in soft sediments (Thayer, 1979). Other potential factors involved in the decline of large sessile suspension-feeders may have been the radiation of predators (McIlroy and Garton, 2004) and greater spatial competition for the infaunal ecospace (Desjardins *et al.*, 2010a). Ichnological evidence of increased durophagous predation in the Paleozoic evolutionary fauna is indicated by a higher abundance of predatory holes. Overall, bioerosion increased significantly in both diversity and intensity (see Section 14.2.3).

The Modern evolutionary fauna is dominated by mollucks (bivalves and gastropods), echinoids, crustaceans, and different vertebrates; gymnolaemate bryozoans, demosponges, and ammonites are also members of this fauna (Sepkoski, 1981). A significant diversification occurs in the pelagic realm. The evolutionary innovations that took place during the Mesozoic have been referred to as "the Mesozoic marine revolution" by Vermeij (1987). This event led to a major restructuring of shallow-marine benthic communities. Some of these changes involved the acquisition of additional ecological guilds that were not present in the Cambrian and Paleozoic evolutionary faunas, particularly with respect to the exploitation of the deep infaunal ecospace (Thayer, 1983; Bambach, 1983). The intensification of grazing and the diversification of durophagous predators were conducive to increases in prey sturdiness and the frequency of shell repair (Vermeij, 1987; Kelley and Hansen, 2001) (see Section 14.2.3). The number of modes of life utilized increased up to present levels (Bambach *et al.*, 2007). All 20 Bambachian megaguilds were filled (Sheehan, 2001). Overall, the body-fossil record shows that by the late Cenozoic, marine paleocommunities have a much greater representation of infaunal organisms and higher proportion of motile animals than mid-Paleozoic communities (Bush *et al.*, 2007). The Modern evolutionary fauna began in the early Paleozoic, becoming dominant after the end-Permian mass extinction (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985).

The advent of the Modern evolutionary fauna is clearly reflected by the ichnological record (e.g. Carmona *et al.*, 2008). This is obvious not only from the composition of the ichnofaunas, but also from the complexity of tiering structure and intensity and depth of bioturbation. The imprint of malacostracan crustaceans is evidenced by the dominance of a wide variety of burrow systems produced by these organisms, such as *Thalassinoides*, *Ophiomorpha*, *Spongeliomorpha*, and, to a lesser extent, *Pholeus*, *Psilonichnus*, *Sinusichnus*, and *Maiakarichnus* (Carmona *et al.*, 2004; Verde and Martínez, 2004; Curran, 2007; Buatois *et al.*, 2009a). To this list we should add the double helicoidal burrow *Lapispira*, also possibly produced by decapod crustaceans (Lanes *et al.*, 2007). Crustacean burrows become dominant not only in offshore to shelf environments, but also in nearshore settings. In fact, *Ophiomorpha* replaced *Skolithos* as the dominant component of the *Skolithos* ichnofacies in post-Paleozoic strata (Droser and Bottjer, 1993). Another typical component of the Modern evolutionary fauna reflected in the trace-fossil record is irregular echinoid burrows, namely *Scolicia* and *Bichordites*, which are known since the Jurassic (Smith and Crimes, 1983). To this list we may add a number of post-Paleozoic morphologically complex ichnogenera (e.g. *Paradictyodora*, *Patagonichnus*) that are probably produced by unknown soft-bodied organisms (Olivero *et al.*, 2004; Olivero and López-Cabrera, 2005). The complex tiering structure commonly revealed by these ichnofaunas shows the development of a finely partitioned infaunal niche and an increase in degree of bioturbation. This is particularly obvious in the case of Neogene shallow-marine ichnofaunas, which typically display complex tiering patterns and a wide variety of ichnoguilds (e.g. Buatois *et al.*, 2003; Carmona *et al.*, 2008). Depth of bioturbation reached a maximum, with crustacean burrows colonizing the deep infaunal ecospace and reaching several meters below the sediment–water interface. Increased intensity of predation is revealed by the larger proportion of shells showing evidence of drilling holes produced by gastropods and breakage by crabs (Vermeij, 1987; Bambach, 1993). In addition, a remarkable increase in the diversity of bioerosion structures due to predation resulted from the Mesozoic marine revolution (see Section 14.2.3). Increased infaunalization and predation may also reflect an increase in the biomass of marine consumers (Bambach, 1993).

It has been suggested that evolutionary innovations commonly started in shallow water and subsequently migrated or expanded into deeper water. In fact, this pattern is also revealed by the evolutionary faunas themselves (Sepkoski and Miller, 1985) (see Sections 14.2.2 and 14.2.4). Also, the intensity of bioturbation first increased in shallow-water settings and only occurred later in the offshore (Droser and Bottjer, 1989). In addition, some ichnogenera seem to display an offshore–onshore trend. In the case of expansion, an ichnogenus that occurs for the first time in shallow water subsequently extends its environmental range into deeper water without loss of onshore representatives. In contrast, retreat involves migration into deeper water with loss of onshore representatives (Botjjer *et al.*, 1988; Stanley and Pickerill, 1993). For example, the ichnogenus *Zoophycos* is common in Paleozoic shallow-marine deposits. However, it migrated into deeper water throughout the Mesozoic, essentially disappearing from nearshore areas by the Cenozoic, providing an example of retraction (Bottjer *et al*., 1988). Another example of retraction into deep-water settings has been suggested for the ichnogenus *Fustiglyphus* (Stanley and Pickerill, 1993). The ichnogenus *Ophiomorpha*, restricted to shallow-marine environments during the late Paleozoic and early Mesozoic, expanded into deep water during the late Mesozoic (Bottjer *et al*, 1988; Tchoumatchenco and Uchman, 2001). *Scolicia* may have originated in shallow-marine settings, but expanded into deep water by the end of the Cretaceous, displaying an optimization of grazing patterns (Seilacher, 1986). Other ichnogenera, such as *Asteriacites*, seem to exhibit less straightforward distribution patterns (Mikuláš, 1992).

14.2.2 COLONIZATION OF THE DEEP SEA

The colonization of the deep sea was one of the first evolutionary processes addressed from an ichnological perspective (e.g. Seilacher, 1974, 1977b; Crimes, 1974). More recently, it has been discussed in detail in a number of papers (e.g. Orr, 2001; Uchman, 2003, 2004a). In particular, Uchman (2004a) provided a comprehensive analysis of the Phaneozoic history of deep-sea trace fossils supported by an extensive database. There is general agreement in that: (1) complex behavioral patterns initially evolved in shallow water, and subsequently migrated into the deep sea (Crimes and Anderson, 1985; Crimes and Fedonkin, 1994; Jensen and Mens, 1999), and (2) that there has been an increase in complexity and diversity of trace fossils throughout the Phanerozoic (Crimes, 1974; Seilacher, 1974, 1977b; Crimes and Crossley, 1991; Uchman, 2003, 2004a).

The earliest record of deep-marine trace fossils is Ediacaran, as indicated by poorly diverse, nonspecialized grazing trails (e.g. *Helminthopsis*, *Helminthoidichnites*) in connection with microbial mats (MacNaughton *et al*., 2000; Liu *et al*., 2010) (Fig. 14.7). These strategies linked to exploitation of microbial mats persisted well into the Cambrian with the addition of arthropod trackways (e.g. *Diplichnites*) and more sophisticated feeding strategies represented by different *Oldhamia* ichnospecies (Buatois and Mángano, 2003a) (Fig. 14.7).

Deep-marine ecosystems underwent significant changes by the end of the Cambrian, probably as a result of increased competition for ecospace and/or resources within shallow-marine ecosystems that forced animals into deeper-water settings (Crimes *et al*., 1992; Crimes, 2001; Orr, 2001; Mángano and Droser, 2004; Buatois *et al*., 2009b). The main lineages of deep-marine trace fossils (i.e. rosette, meandering, networks, and spirals) were established in deep-sea environments by the Early Ordovician, recording the first appearance of the *Nereites* ichnofacies (Orr, 2001; Mángano and Droser, 2004; Uchman, 2004a; Buatois *et al*., 2009b) (Fig. 14.7). Lower to Middle Ordovician deep-marine ichnofaunas seem to be moderately diverse, and fodinichnia commonly dominates rather than graphoglyptids (e.g. Orr, 1996). A significant diversity increase occurred in the Upper Ordovician–Lower Silurian, with ichnofaunas recording higher proportions of graphoglyptids (McCann, 1990; Orr, 2001; Mángano and Droser, 2004; Uchman, 2003, 2004a). In short, ichnological evidence records the advent of a deep-marine ecosystem of modern aspect during the Ordovician, representing a second-level change (*sensu* Droser *et al*., 1997). Interestingly, most of the Cambrian–Ordovician deep-marine trace fossils represent the activity of shallow-tier organisms. However, Orr (2003) documented Ordovician deep-marine ichnofabrics that record the activity of a climax suite that may have penetrated at least 40 cm into the substrate. Other examples of deep bioturbation (e.g. Pickerill and Williams, 1989) may have been produced by the activity of doomed pioneers transported from shallow- to deep-marine environments via turbidity currents (Waldron, 1992; Allison and Briggs, 1994).

Uchman (2004a) noted that Ordovician to Carboniferous deep-marine ichnofaunas were compositionally similar, typically containing *Dictyodora*, several ichnospecies of *Nereites*, and *Megagrapton*, among other ichnotaxa. In particular, *Dictyodora* records a clear evolutionary trend from the Upper Ordovician to the Carboniferous, as revealed by an increase in the height of the wall, and an improvement in feeding efficiency (Seilacher, 1967a; Benton, 1982). This pattern suggests a strategy of underground mining progressively deeper into the sediment through time (Seilacher, 1967a; Benton and Trewin, 1980; Benton, 1982; Seilacher-Drexler and Seilacher, 1999; Mángano and Droser, 2004).

A subsequent ichnodiversity peak is recorded in the Early Carboniferous (Orr, 2001; Uchman, 2004a). However, the rest of the Carboniferous experienced a constant decrease in ichnodiversity, culminating in overall low-ichnodiversity levels during the Permian to the Middle Jurassic (for an exception see Wetzel *et al*., 2007) (see Section 14.1.6). Uchman (2004a) linked the decrease in ichnodiversity during the Late Carboniferous–Permian to the deep-seawater temperature decrease resulting from the Gondwanan glaciations. He also noted that some typical earlier Paleozoic ichnotaxa disappeared from the fossil record (e.g. *Dictyodora* and *Spirodesmos*).

Significant innovations had taken place in the deep sea by the Late Jurassic–Early Cretaceous, when trace fossils produced by irregular echinoids (*Scolicia*) and large decapod crustaceans (*Ophiomorpha*) occurred for the first time (Tchoumatchenco and Uchman, 2001). These are efficient bioturbators and their arrival at deep-sea bottoms was conducive to intensive plowing of the sediment, deepening of the redox boundary, and expansion into deeper tiers (Uchman, 2004a). This author regarded this event as somewhat analogous to the Agronomic Revolution of Cambrian times (see Section 14.1.3). Also, an ichnodiversity peak is detected by the Late Jurassic–Early Cretaceous, followed by a remarkable decrease during the Albian, most likely as a result of widespread anoxia.

The maximum ichnodiversity peak is reached during the Eocene, accompanied by the largest contribution of graphoglyptids to global diversity (Uchman, 2003, 2004a). The Eocene optimum in graphoglyptid diversity has been linked to the advent of oligotrophic conditions in the oceans linked to global warming (Tunis and Uchman, 1996a, b). However, recent research on

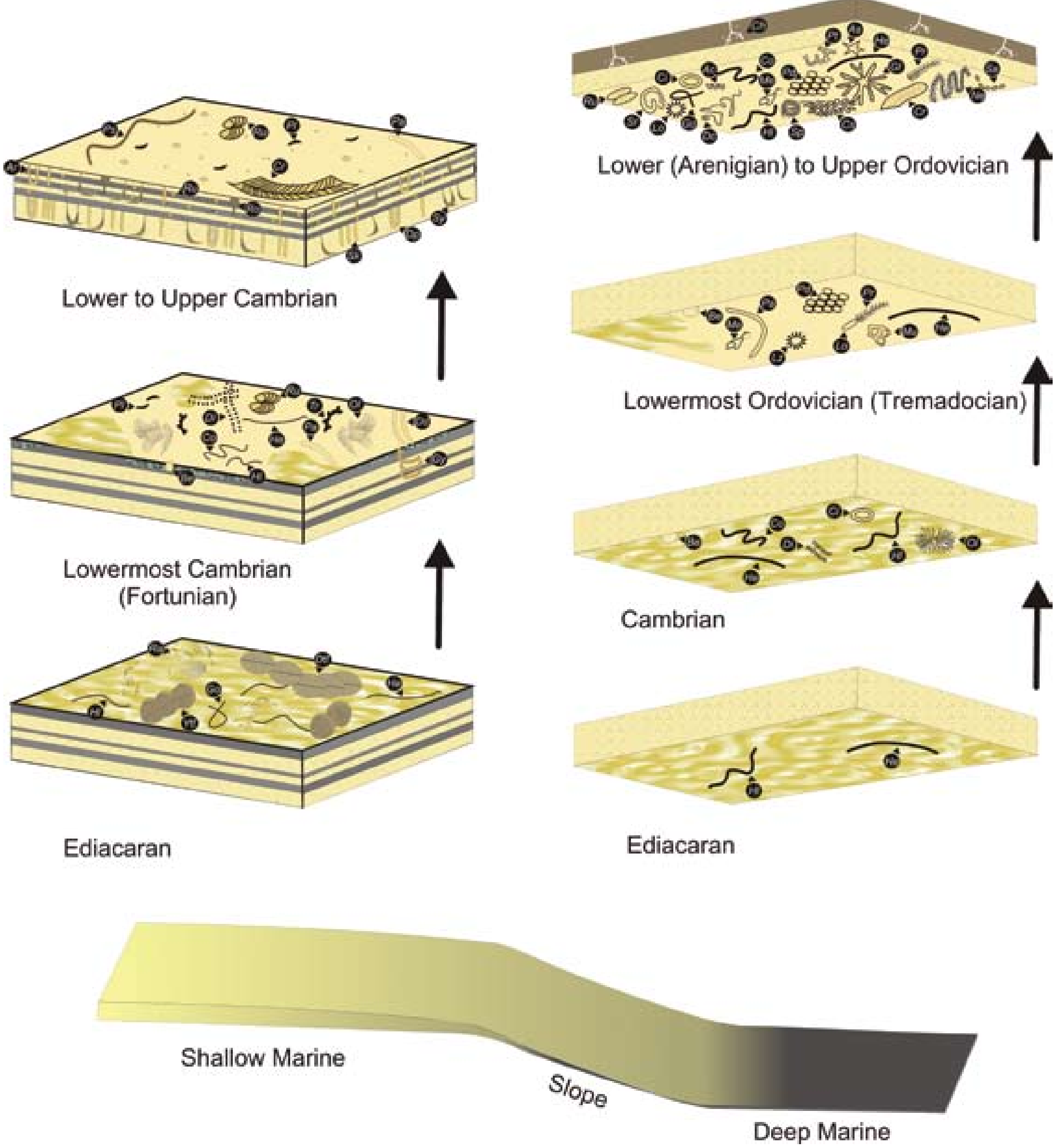

Figure 14.7 Early history of deep-sea colonization in comparison with evolutionary events in the shallow-marine realm. Colonization of deep-sea bottoms was delayed with respect to that of shallow-marine environments. By the Ediacaran, typical shallow-marine ichnofaunas consist of nonspecialized grazing trails, such as *Helminthopsis* (*Hl*), *Helminthoidichnites* (*He*), and *Gordia* (*Go*), the rasping trace *Radulichnus* (*Ra*), and trace fossils produced by *Dickinsonia* (*D*tf) and *Yorgia* (*Y*tf). Coeval deep-marine deposits contain less diverse ichnofaunas, essentially consisting of *Helminthopsis* (*Hl*) and *Helminthoidichnites* (*He*). Microbial mats are widespread in both settings. Lowermost Cambrian (Fortunian) shallow-marine deposits reflect a remarkable increase in ichnodiversity, and are dominated by branched burrows, typically *Treptichnus* (*Tr*), arthropod trace fossils such as *Diplichnites* (*Di*), *Rusophycus* (*Ru*), and *Diplopodichnus* (*Do*), the spiral-shaped burrow *Gyrolithes* (*Gy*), the plug-shaped burrow *Bergaueria* (*Be*), and simple burrows such as *Palaeophycus* (*Pa*) and *Planolites* (*Pl*). *Cochlichnus* (*Co*), *Helminthopsis* (*Hl*), and *Helminthoidichnites* (*He*) are also common. Some ichnospecies of *Oldhamia* (*Ol*) may occur in shallow-marine settings. Microbial matgrounds display a more patchy distribution. Later in the Early Cambrian other ichnotaxa become typical in shallow-marine environments. These include a wide variety of vertical burrows abundant in high-energy environments, such as *Skolithos* (*Sk*), *Diplocraterion* (*Dp*), *Arenicolites* (*Ar*), *Rosselia* (*Ro*), and *Syringomorpha* (*Sy*), together with other ichnogenera more typical of lower-energy settings, including *Psammichnites* (*Ps*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Rusophycus* (*Ru*), and *Cruziana* (*Cr*). Microbial mats became restricted to stressed settings, being rare in fully marine settings later in the Cambrian. Cambrian deep-marine ichnofaunas remained poorly diverse. Different ichnospecies of *Oldhamia* (*Ol*) are dominant, together with unspecialized grazing trails such as *Helminthoidichnites* (*He*), *Helmintopsis* (*Hl*), *Cochlichnus* (*Co*), the feeding trace *Circulichnis* (*Ci*), arthropod trackways such as *Diplichnites* (*Di*), and the plug-shaped burrow *Bergaueria* (*Be*). Matgrounds persisted in the deep sea during the Cambrian. Lowermost Ordovician (Tremadocian) deep-marine ichnofaunas are characterized by branched feeding burrows, typically *Multina* (*Mu*), simple trace fossils such as *Palaeophycus* (*Pa*) and *Helminthoidichnites* (*He*), and the bivalve locomotion trace *Protovirgularia* (*Pr*). Graphoglyptids also occur, including *Megagrapton* (*Me*), *Paleodictyon* (*Pd*), and *Lorenzinia* (*Lo*), although they do not seem to be abundant. The plug-shaped burrow *Bergaueria* (*Be*) persisted in this setting. Later in the Ordovician, a remarkable increase in trace-fossil diversity took place in deep-sea environments. These ichnofaunas consist of a wide variety of forms, including the graphoglyptids *Megagrapton* (*Me*), *Paleodictyon* (*Pd*), *Protopaleodictyon* (*Pt*), *Cosmorhaphe* (*Cs*), *Spirorhaphe* (*Sp*), *Acanthorhaphe* (*Ac*), *Glockerichnus* (*Gl*), and *Lorenzinia* (*Lo*). Other ichnotaxa include *Chondrites* (*Ch*), *Spirophycus* (*Sr*), *Dictyodora* (*Dc*), *Helminthoidichnites* (*He*), *Protovirgularia* (*Pr*), *Cruziana* (*Cr*), *Rusophycus* (*Ru*), *Nereites* (*Ne*), *Asteriacites* (*As*), *Cochlichnus* (*Co*), *Circulichnis* (*Ci*), *Helminthopsis* (*Hl*), *Gordia* (*Go*), and *Saerichnites* (*Sa*). Microbial mats show a remarkably patchy distribution. Modified from Mángano and Buatois (2007), and Buatois *et al*. (2009b).

ichnofaunas from Tierra del Fuego, southern Argentina, demonstrated a diversity peak accompanied by a cooling trend (López-Cabrera *et al.*, 2008). Accordingly, these authors suggested a link between diversification of graphoglyptids and constancy of relative oligotrophy, rather than temperature per se.

Most graphoglyptid ichnotaxa have their first occurrence in Upper Cretaceous–Eocene rocks (Uchman, 2003). Also, since the Late Cretaceous graphoglyptids displayed an accelerated evolution with farming becoming a widespread strategy in the deep sea (Seilacher, 1977b; Uchman, 2004a). After the Eocene, no new graphoglyptid ichnotaxa have been recorded (Uchman, 2004a). By the Oligocene, parallel to a decrease in water temperatures, ichnodiversity displayed a dramatic decrease, most likely linked to the Eocene–Oligocene boundary crisis, which negatively impacted on other groups, such as foraminiferans, dinoflagellates, and nanoplankton. No increase in ichnodiversity was recorded during climatic amelioration in the Miocene (Uchman, 2004a).

14.2.3 COLONIZATION OF HARD SUBSTRATES

Examination of trends displayed by marine bioerosion structures allows an understanding of evolutionary changes in marine hard substrate communities, including the role of drilling predation (e.g. Kowalewski *et al.*, 1998, 1999; Harper *et al.*, 1999; Perry and Bertling, 2000; Taylor and Wilson, 2003; Bromley, 2004; Glaub, 2004; Wilson, 2007; Tapanila, 2005, 2008). The oldest trace fossils known are microborings reported from Archean (3500 ma) pillow lavas from South Africa (Furnes *et al.*, 2004). These structures record microbial etching of glass along fractures and indicate biologically mediated corrosion. The presence of organic carbon in the margins of the microborings and isotopically low $\delta^{13}C$ values of carbonate in the glassy rims of the pillow support microbial fractionation and a biogenic origin for these structures. Bioerosion evidence is therefore consistent with an early origin of thermophilic microbes around deep-sea hydrothermal vents. Paleo- to Mesoproterozoic stromatolites were bored by cyanobacteria (Zhang and Golubic, 1987). Microbioerosion due to cyanobacteria has been also reported from Neoproterozoic oolites and pisolite grains (Knoll *et al.*, 1986).

Although bioerosion became more important during the Cambrian, borings provide evidence of incipient predation during the Ediacaran. Predatory holes (assigned to the ichnogenus *Oichnus*) in the tubular shell *Cloudina* suggest that shell-drilling predation may have been already present in the Ediacaran, representing the oldest evidence of macrobioerosion (Bengtsön and Yue, 1992; Hua *et al.*, 2003). The intensity of bioerosion increased as a result of the Cambrian explosion, but borings were very simple and diversity remained low with only *Trypanites* and *Oichnus* recorded (Wilson, 2007). High densities of *Trypanites* are present in Lower Cambrian archaeocyathid reefs, revealing domichnial bioerosion by a macroboring biota (James *et al.*, 1977; Kobluk *et al.*, 1978). The round hole *Oichnus* is present in Cambrian shells, representing increased predation levels, albeit significantly lower that those displayed by younger faunas (Matthews and Missarzhevsky, 1975; Conway Morris and Bengtson, 1994; Bromley, 2004). Bitten trilobites provide further evidence of predation in the Cambrian (Babcock, 1993; Pratt, 1998).

A significant rise in bioeroders probably occurred by the end of the Middle Ordovician (Kobluk *et al.*, 1978; Ekdale and Bromley, 2001b; Wilson and Palmer, 2001, 2006; Benner *et al.*, 2004), and has recently been referred to as "the Ordovician Bioerosion Revolution" by Wilson and Palmer (2006). This event is not only reflected in bioerosion domiciles but also in bioclaustrations (Tapanila, 2008). Early to Middle Ordovician bioerosion was dominated by simple borings such as *Trypanites* and *Palaeosabella*, although clavate borings (*Gastrochaenolites*), which are attributed to bivalves in younger rocks, have been recorded (Ekdale and Bromley, 2001; Ekdale *et al.*, 2002; Benner *et al.*, 2004). Late Ordovician hardground communities also included sponge borings (*Cicatricula*), bryozoan etchings (*Ropalonaria*), and bivalve borings (*Petroxestes*) (Wilson and Palmer, 2006; Wilson, 2007). The oldest record of green algae microborings (*Reticulina*) is known from the Ordovician, while that of red algae microborings (*Palaeoconchocelis*) is from the Silurian (Glaub and Vogel, 2004).

A subsequent increase in the diversity of macroborings had occurred by the Devonian ("Middle Paleozoic Marine Revolution" of Wilson, 2007, also referred to as a precursor of the "Mesozoic Marine Revolution" by Signor and Brett, 1984). Some of the bioerosion ichnotaxa which appeared by this time (e.g. *Entobia*, *Rogerella*, *Caulostrepsis*, *Talpina*) became dominant throughout the rest of the Phanerozoic (Bromley, 2004; Wilson, 2007). By the Carboniferous, the first *Gastrochaenolites* confidently attributed to bivalves has been recorded (Wilson and Palmer, 1998). Notably, diversification of macroborings and bioclaustrations is decoupled because the latter shows a decrease in diversity by the Late Devonian, most likely as a result of a decline in the host coralline taxa (Tapanila, 2005; Tapanila and Ekdale, 2007).

By the Jurassic, the Mesozoic Marine Revolution (Vermeij, 1977) is marked by an increase in the diversity, abundance, and size of macrobioerosion structures (Bromley, 2004; Wilson, 2007). An increase in diversity by the beginning of the Mesozoic is also evidenced by microborings (Glaub and Vogel, 2004). In addition, this event was characterized by the rise of boring echinoids and an increase in the abundance of sponge borings (Taylor and Wilson, 2003). A large number of ichnotaxa occurs for the first time in the Mesozoic, including the echinoid bite trace *Gnathichnus*, the echinoid boring *Circolites*, the cirriped etching scar *Centrichnus*, the bryozoan etching trace *Leptichnus*, and the bivalve wood boring *Teredolites*.

These evolutionary changes have a direct influence on the nature of some substrate-controlled ichnofacies. The *Teredolites* ichnofacies has not been recorded prior to the Cretaceous. In addition, the Jurassic represents a pivotal point for hardground ichnofacies because it marks the appearance of the *Gnathichnus* ichnofacies (Gibert *et al.*, 2007). Also, sponge and bivalve borings became common after the Jurassic, resulting in the appearance of the so-called *Entobia* association (Bromley and Asgaard, 1993a; Gibert *et al.*, 1998). Interestingly, Tapanila (2008) noted that, with the exception of echinoids, no new classes of organisms adopted an endolithic strategy during the Mesozoic Marine Revolution. By the beginning of the Cenozoic, a change is reflected in the dominant microbioeroding ichnotaxa, with the appearance of new ichnogenera whose oldest record is Paleogene (Glaub and Vogel, 2004).

14.2.4 COLONIZATION OF TIDAL FLATS

Tidal flats are geologically ephemeral systems, and at a given geographic region rarely last longer than 10^4 years as a result of transgressions and regressions (Reise, 1985). In contrast to the long-term temporal instability, tidal flats are, on a daily basis, highly predictable and controlled by tidal cyclicity. Tidal flats usually are regarded as harsh, heterogeneous, physically controlled environments (see Section 7.2). From a biological perspective, tidal flats are highly heterogeneous systems in which interspecific interactions are poorly regulated and open to numerous possibilities. Accordingly, ecological and environmental attributes of tidal-flat communities, together with the high genetic variability in populations inhabiting unstable environments, may have provided the appropriate ground for major steps in evolution (Reise, 1985).

Comparison of tidal-flat ichnofaunas through time helps to address the problem of onshore replacement and offshore migration of benthic faunas, and provides ground data to evaluate the notion that tidal flats may have served as sites of evolutionary innovations (Mángano *et al.*, 2002a). The earliest records of trace fossils in intertidal deposits are from the earliest Early Cambrian (Fortunian), and consist of monospecific occurrences of *Treptichnus pedum* (Buatois *et al.*, 2007c; Almond *et al.*, 2008). Younger early Paleozoic tidal-flat ichnofaunas are dominated by trilobite and other arthropod trace fossils (e.g. Durand, 1985; Astini *et al.*, 2000; Mángano *et al.*, 2001b; Mángano and Buatois, 2004b). Some aspects of early Paleozoic tidal flats are anactualistic in nature (Mángano and Buatois, 2004b). While modern tidal flats are characterized by abundant food supply derived from multiple sources, including terrestrially-derived organic particles, early Paleozoic intertidal trophic webs were almost entirely based on the organically rich marine source and significant autochthonous production. Modern intertidal organisms are exposed to a double set of predators: preyed on by marine organisms during submergence and by terrestrial organisms during emergence. Contrastingly, early Paleozoic intertidal environments may have functioned as refugia in the absence of continental predators, only being under the pressure of marine predators (Mángano and Buatois, 2004b). Another anactualistic aspect, particularly for Cambrian tidal flats, is the common presence of microbial matgrounds (Hagadorn *et al.*, 2002; Hagadorn and Belt, 2008). Tidal-flat deposits contain a wide variety of microbially induced structures that allowed preservation of medusa body fossils, and a peculiar suite of trace fossils consisting of the giant mollusk-like trail *Climactichnites*, its associated resting trace *Musculopodus*, and the arthropod trackway *Protichnites* (Yochelson and Fedonkin, 1993; Hagadorn *et al.*, 2002; Hagadorn and Belt, 2008; Seilacher, 2008; Getty and Hagadorn, 2008, 2009).

Although the picture that emerges from these early Paleozoic tidal flats is significantly different, they may have resembled modern ones in their ecological role as sites of reproduction and protection. Arthropod incursions in early Paleozoic tidal flats, recorded by the presence of *Rusophycus*, *Cruziana*, and *Dimorphichnus*, provide direct evidence of an early colonization of intertidal environments, and show that representatives of the Cambrian evolutionary fauna were not restricted to offshore settings, but were able to colonize very shallow-water environments. *Skolithos* and *Syringomorpha* pipe rock occurs in high-energy sand-flat areas. Depth and extent of bioturbation reveal colonization of a relatively deep-infaunal ecospace by endobenthic organisms at least in lower-intertidal areas, suggesting a significant landward expansion of the Agronomic Revolution (Mángano and Buatois, 2004b).

Molluscan trace fossils, in particular those of bivalves, are important components in late Paleozoic tidal-flat deposits (e.g. Rindsberg, 1994; Mángano *et al.*, 2002a; Mángano and Buatois, 2004a). Late Paleozoic intertidal ichnofaunas are remarkably different from those recorded in early Paleozoic tidal flats in that trilobite-dominated faunas were replaced by bivalve-dominated communities. Sepkoski and Miller (1985) documented onshore–offshore patterns of evolutionary faunas. Based on the analysis of body-fossil communities, these authors detected a replacement of trilobite-rich communities by mollusk-rich communities in shallow-water niches throughout the Paleozoic. Ichnological analysis of Paleozoic tidal-flat ichnofaunas provides further support to this model, and underscores the importance of tidal flats as nurseries of evolutionary innovations (Mángano *et al.*, 2002a). Bivalves, in contrast to articulate brachiopods, were particularly adaptable to physically unstable, stressful nearshore settings (Steele-Petrovic, 1979). The striking ecological segregation between articulate brachiopods and bivalves may indicate a higher tolerance of bivalves to unstable environments (Olszewski, 1996).

Analysis of late Paleozoic tidal-flat ichnofaunas also reflects patterns of colonization of the infaunal ecospace by bivalves. Presence of large specimens of *Lockeia siliquaria* in Carboniferous intertidal sandstone suggests relatively deep-bivalve burrowing below the sediment–water interface (Mángano *et al.*, 1998). These burrows have been attributed to the anomalodesmatan *Wilkingia*, also present in the same deposits, most likely illustrating siphon-feeding in the late Paleozoic, preceding the subsequent Mesozoic radiation of siphon-feeding infaunal bivalves (Mángano *et al.*, 1998) (Fig. 14.8). Although the deep-infaunal ecospace was colonized, late Paleozoic intertidal ichnofaunas contain a high diversity of shallow-tier trace fossils, suggesting that deep burrowers did not obliterate shallowly emplaced structures.

Mesozoic and Cenozoic tidal-flat ichnofaunas are quite different from their Paleozoic equivalents, but they share many similarities with Recent examples. Post-Paleozoic tidal-flat deposits tend to be dominated by deep- to mid-tier crustacean burrows together with a wide variety of polychaete and bivalve

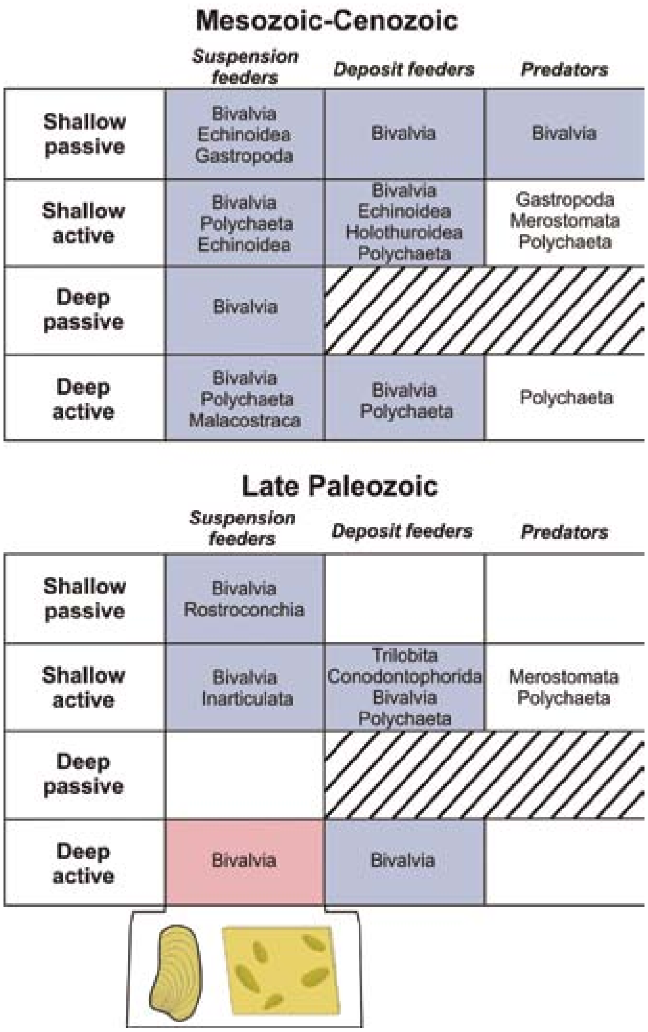

Figure 14.8 Evolutionary innovations in tidal flats. Boxes illustrate Bambachian megaguilds for infaunal ecospace based on body fossils after Bambach (1983). According to body-fossil information, no suspension feeders occupied deep tiers before the Mesozoic marine revolution. However, ichnological information (deep *Lockeia siliquaria*) indicates that suspension- feeding bivalves colonized the deep-infaunal ecospace in tidal-flat settings by the late Paleozoic. This prompted re-evaluation of associated body fossils, suggesting that the potential producer, the anomalodesmatan *Wilkingia*, was an efficient siphonate burrower (Mángano *et al.*, 1998).

trace fossils (Mángano *et al.*, 2002a). This seems to be the case in most modern tidal flats, where these groups dominate (e.g. Howard and Dörjes, 1972; Curran and Martin, 2003). In addition, crustaceans and polychaetes produce large quantities of argillaceous fecal pellets, and they are therefore important agents of biosedimentation and modifiers of substrate properties (Pryor, 1975; Bromley, 1990, 1996; Curran and Martin, 2003). In contrast to late Paleozoic tidal-flat ichnofaunas, Mesozoic to Cenozoic ichnofaunas are biased towards deeper tiers. Burrowing activities of crustaceans may have caused significant sediment reworking and obliteration of shallower tiers. Overall, post-Paleozoic tidal flats exhibit only moderate levels of ichnodiversity. This trend likely represents a taphonomic artifact resulting from the dominance of deep infaunal crustaceans in Mesozoic and Cenozoic tidal-flat ecosystems. Establishment of crustacean-dominated communities in tidal-flat ecosystems may have played a significant role in the offshore expansion of bivalves during the Mesozoic (Mángano *et al.*, 2002a).

14.2.5 COLONIZATION OF BRACKISH-WATER ENVIRONMENTS

The invasion of marginal-marine environments represents the appearance of an ecosystem and, therefore, qualifies as a first-level paleoecological event *sensu* Droser *et al.* (1997). The ichnological aspects of the colonization history of brackish-water environments have been recently explored (Buatois *et al.*, 2005). According to these authors, brackish-water ichnofaunas show an increase in ichnodiversity, an increase in the intensity of bioturbation, the addition of new invaders, environmental expansion, and faunal replacements through the Phanerozoic. The colonization of marginal-marine, brackish-water environments by fully marine organisms was a long-term process, but did not occur at a constant rate. Five major colonization phases have been proposed: Ediacaran–Ordovician, Silurian–Carboniferous, Permian–Triassic, Jurassic–Paleogene, and Neogene–Recent (Buatois *et al.*, 2005) (Fig. 14.9).

The first phase (Ediacaran–Ordovician) is a prelude to the major invasion that occurred during the rest of the Paleozoic. Although Ediacaran trace fossils have been recorded for the most part in open-marine strata, at least in one case, biogenic structures were described from deposits formed in a coastal environment subjected to rapid changes in salinity, as well as in sedimentation rate and turbidity (Netto and Martini da Rosa, 2001). This ichnofauna may represent one of the earliest attempts of benthic organisms to survive under marginal-marine conditions. As a result of the Cambrian explosion, a new array of characters invaded brackish-water settings. Among these, arthropods, including trilobites, trilobitomorphs, and eurypterids, were among the most successful (Selley, 1970; Mikuláš, 1995; Braddy and Almond, 1999; Webber and Braddy, 2004; Mángano and Buatois, 2003a). In Cambrian–Ordovician estuaries and embayments, trace fossils of trilobites and other arthropods occur in fine-grained deposits of low-energy zones, while high- to moderate-energy sandstones, such as those forming subtidal bars, are dominated by vertical burrows (e.g. *Skolithos*) (e.g. Martin, 1993; Mángano *et al.*, 2001b; Mángano and Buatois, 2003a; Baldwin *et al.*, 2004). Most of the lower Paleozoic ichnofaunas recorded in marginal-marine deposits are from tide-dominated estuaries, where salinity stress was probably attenuated by tidal mixing. Also, environmental expansion is recorded through the early Paleozoic. Cambrian trace fossils seem to be restricted to the outer regions of estuaries, but Ordovician ichnofaunas reveal a slight landward expansion, also being present in more central zones of the estuaries (Mángano and Droser, 2004). In any case, intensity of bioturbation and ichnodiversity levels remained relatively low.

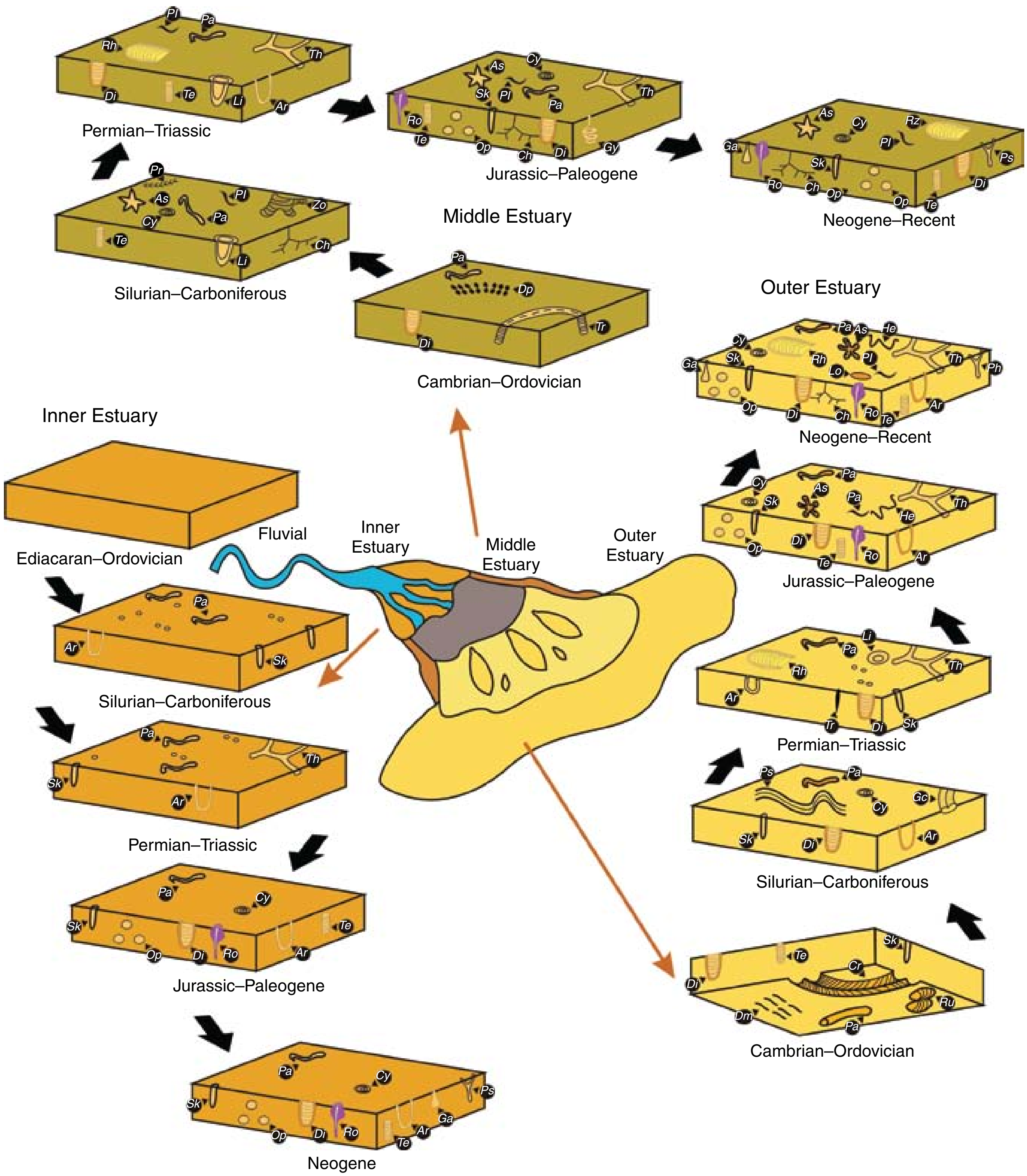

Figure 14.9 Colonization of brackish-water environments through geological time. The inner-estuary zone was essentially barren of biogenic structures during the Ediacaran–Ordovician. During the Silurian–Carboniferous, facies-crossing ichnotaxa, such as *Arenicolites* (*Ar*), *Palaeophycus* (*Pa*), and *Skolithos* (*Sk*), occur. Inner-estuarine Permian–Triassic deposits are characterized by the addition of the crustacean burrow *Thalassinoides* (*Th*). An increase in ichnodiversity in this environment took place during the Jurassic–Paleogene with the addition of a number of ichnotaxa, including *Ophiomorpha* (*Op*), *Rosselia* (*Ro*), *Teichichnus* (*Te*), *Cylindrichnus* (*Cy*), and *Diplocraterion* (*Di*). Neogene inner-estuarine ichnofaunas are similar to those from the Jurassic–Paleogene, but may contain *Psilonichnus* (*Ps*) and *Gastrochaenolites* (*Ga*) as well. Cambrian–Ordovician middle-estuarine deposits are typically sparsely burrowed, and contain *Diplichnites* (*Dp*), *Diplocraterion* (*Di*), *Trichophycus* (*Tr*), and *Palaeophycus* (*Pa*). A remarkable increase in trace-fossil diversity occurred in this environment during the Silurian–Carboniferous with the presence of a number of ichnotaxa, including *Palaeophycus* (*Pa*), *Planolites* (*Pl*), *Asteriacites* (*As*), *Cylindrichnus* (*Cy*), *Lingulichnus*

The second phase (Silurian–Carboniferous) is characterized by the appearance of more varied trace-fossil morphologies and behavioral strategies (Buatois *et al.*, 2005). As a result, a slight increase in ichnodiversity with respect to the previous phase is detected. While Cambrian–Ordovician ichnofaunas are dominated by arthropod trace fossils, those from the Silurian–Carboniferous also include ichnotaxa produced by other benthic organisms, in particular, bivalves, ophiuroids, and polychaetes. The replacement of trilobite-dominated ichnofaunas may have been a consequence of the end-Ordovician mass extinction, although an apparent decline in the abundance of trilobite trace fossils was already apparent by the Late Ordovician (Mángano and Droser, 2004) (see Section 14.1.4). The presence of more varied ichnofaunas may reflect an evolutionary rebound after the Late Ordovician mass extinction. Also, Silurian–Carboniferous benthic faunas experienced a remarkable environmental expansion, as illustrated by trace fossils present in inner- and middle-estuarine deposits as well (Buatois *et al.*, 2002b). The extensive colonization of terrestrial settings by land plants and animals may have promoted environmental expansion and increased complexity of estuarine food webs. Silurian–Carboniferous brackish-water ichnofaunas were essentially restricted to softgrounds, with very limited emplacement in firmgrounds. The intensity of bioturbation remains relatively low.

Our understanding of the third phase (Permian–Triassic) still suffers from a scarcity of studies. Permian brackish-water trace-fossil assemblages are more similar to those from the Mesozoic rather than Paleozoic ones (Buatois *et al.*, 2005, 2007b; Netto *et al.*, 2007). Despite these overall similarities, Permian–Triassic brackish-water deposits remain less bioturbated, and contain lower-diversity trace–fossil suites than those from the fourth phase. Accordingly, Permian-Triassic trace-fossil assemblages seem to represent a transitional phase between Paleozoic and Mesozoic marginal-marine ichnofaunas. Body-fossil data indicate that crustaceans radiated during the late Paleozoic, and that some of them adapted to brackish water (Briggs and Clarkson, 1990). Ichnological studies reveal the presence of numerous burrows that may have been produced by crustaceans, including *Thalassinoides* and *Gyrolithes* (Carmona *et al.*, 2004; Buatois *et al.*, 2007b; Netto *et al.*, 2007). Firmgrounds commonly contained the *Glossifungites* ichnofacies, reflecting adaptations to compacted muds (e.g. Tognoli and Netto, 2003; Buatois *et al.*, 2007b; Netto *et al.*, 2007).

The fourth phase (Jurassic–Paleogene) is marked by a notable increase in ichnodiversity and degree of bioturbation of brackish-water estuarine deposits (Buatois *et al.*, 2005). Although less diverse than their fully marine counterparts, relatively diverse ichnofaunas have been recorded (e.g. Beynon *et al.*, 1988; Beynon and Pemberton, 1992; MacEachern and Pemberton, 1994; MacEachern and Gingras, 2007). Also, Jurassic–Paleogene marginal-marine deposits tend to be more intensely bioturbated than older deposits. While older brackish-water substrates displaying trace fossils were essentially softgrounds and firmgrounds, hardgrounds and xylic substrates also become colonized during the late Mesozoic (e.g. Bromley *et al.*, 1984; Savrda *et al.*, 1993; Gingras *et al.*, 2004).

The fifth phase (Neogene–Recent) is characterized by the appearance of the modern brackish-water benthos. However, differences with respect to Jurassic–Paleogene ichnofaunas are subtle. Brackish-water ichnofaunas may reach moderately high diversities, typically in middle- and outer-estuarine regions. Also, the degree of bioturbation may be rather high in some deposits, such as those of estuarine tidal flats (e.g. Gingras *et al.*, 1999b). All types of substrates were colonized during the Neogene, including cemented surfaces, shells, and clasts. This pattern reflects the radiation of various groups of borers (e.g. sponges, polychaetes, gastropods, and bivalves) into brackish water (Gingras *et al.*, 2001).

Buatois *et al.* (2005) also noticed that although brackish-water ichnofaunas display clear evolutionary trends, some trace-fossil suites and ichnofabrics are remarkably persistent, reflecting the activity of conservative biotas. They proposed, as an example, the common occurrence in brackish-water fine-grained, heterolithic facies of *Teichichnus* forming monospecific suites, or associated with small *Planolites* (Fig. 14.10a–d). This assemblage, commonly associated with synaeresis cracks, occurs in stressed marginal-marine environments from the Cambrian to the Recent.

Caption for Figure 14.9 Continued
(*Li*), *Protovirgularia* (*Pr*), *Chondrites* (*Ch*), *Teichichnus* (*Te*), and *Zoophycos* (*Zo*). Permian–Triassic middle-estuarine ichnofaunas tend to be dominated by *Thalassinoides* (*Th*), *Diplocraterion* (*Di*), *Arenicolites* (*Ar*), *Lingulichnus* (*Li*), *Teichichnus* (*Te*), *Rhizocorallium* (*Rh*), *Planolites* (*Pl*), and *Palaeophycus* (*Pa*). By the Jurassic–Paleogene, crustacean burrows, including *Gyrolithes* (*Gy*), *Thalassinoides* (*Th*) and *Ophiomorpha* (*Op*), become dominant, but many other facies-crossing ichnotaxa are abundant also. Neogene middle-estuarine ichnofaunas are similar to those from the Jurassic–Paleogene, but with the addition of *Psilonichnus* (*Ps*) and *Gastrochaenolites* (*Ga*). Cambrian–Ordovician outer-estuarine deposits tend to display more ichnodiversity than coeval deposits formed further into the estuary. Ichnofaunas are dominated by vertical burrows such as *Skolithos* (*Sk*) and *Diplocraterion* (*Dp*), trilobite trace fossils including *Cruziana* (*Cr*), *Rusophycus* (*Ru*) and *Dimorphichnus* (*Dm*), *Teichichnus* (*Te*), and *Palaeophycus* (*Pa*). During the Silurian–Carboniferous, other ichnotaxa become dominant in outer-estuarine settings, including *Gyrochorte* (*Gc*), *Psammichnites* (*Ps*), *Arenicolites* (*Ar*), and *Cylindrichnus* (*Cy*). Permian–Triassic outer-estuarine deposits contain abundant vertical burrows, but also tend to show crustacean burrow galleries such as *Thalassinoides* (*Th*), together with *Rhizocorallium* (*Rh*), *Lingulichnus* (*Li*), *Trichichnus* (*Tr*), and *Palaeophycus* (*Pa*). Jurassic–Paleogene outer-estuarine ichnofaunas typically display more diversity than those of the Permian–Triassic. Crustacean burrows, including *Thalassinoides* (*Th*) and *Ophiomorpha* (*Op*), are dominant. Polychaete burrows, such as *Rosselia* (*Ro*), *Asterosoma* (*As*), and *Cylindrichnus* (*Cy*) are also common. Grazing trails, such as *Helminthopsis* (*Hl*), are less common. Neogene ichnofaunas are very similar to those of the Jurassic–Paleogene, but with the addition of *Psilonichnus* (*Ps*), *Gastrochaenolites* (*Ga*), and locally *Chondrites* (*Ch*). Modified from Buatois *et al.* (2005).

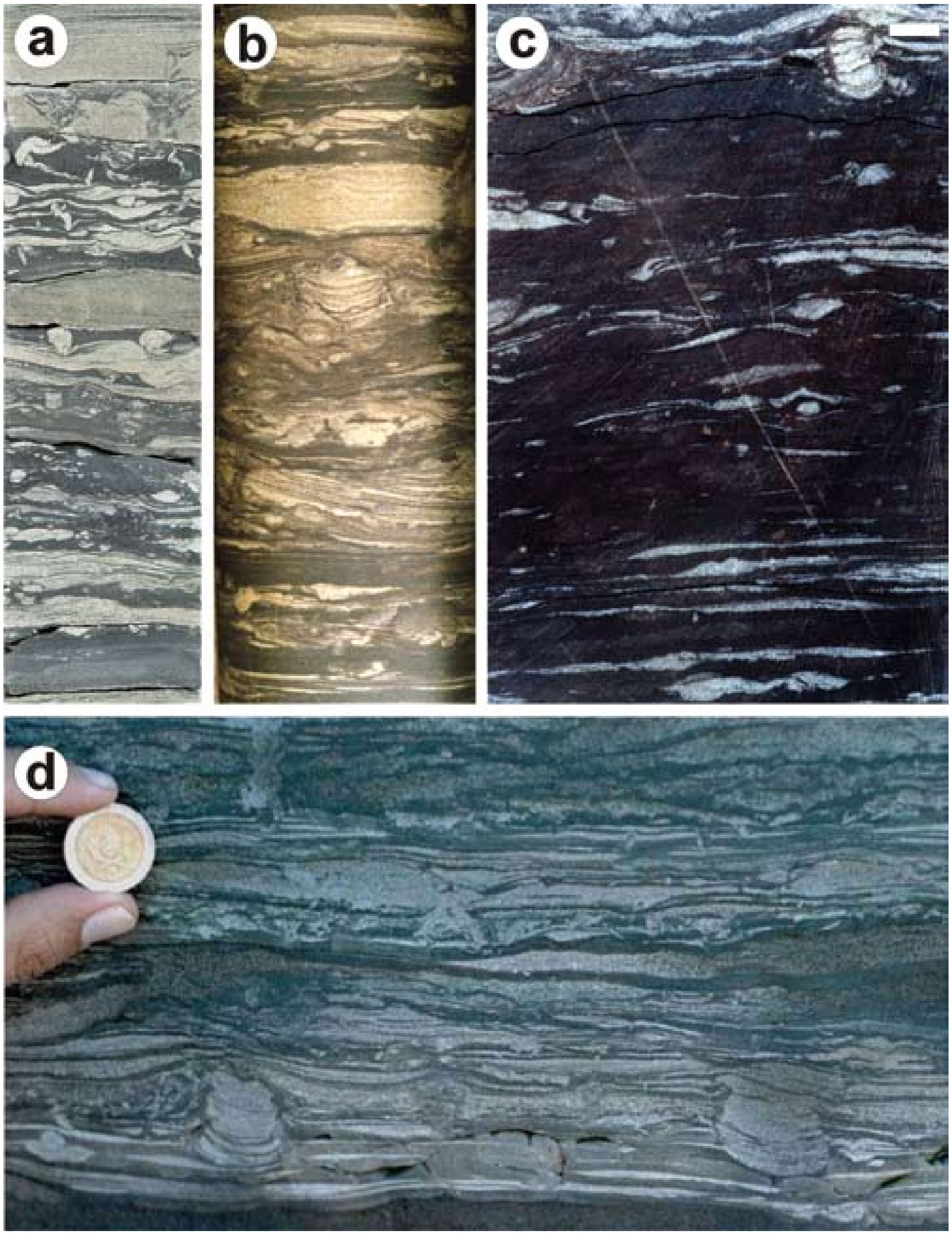

Figure 14.10 The *Teichichnus* ichnofabric as an example of a persistent trace-fossil association in Phanerozoic brackish-water environments. *Teichichnus* may form a monospecific suite or be associated with *Planolites*. Synaeresis cracks are typically present in this heterolithic facies. (a) Middle Cambrian, Earlie Formation, northeast of Edmonton, western Canada. Core width is 9 cm. (b) Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al.* (2007b). (c) Upper Cretaceous, Napo Formation, Shushufindi Field, Oriente Basin, Ecuador. Core width is 10 cm. (d) Lower Miocene Chenque Formation, Caleta Olivia, Patagonia, Argentina. See Carmona *et al.* (2009).

14.2.6 COLONIZATION OF FRESHWATER AND TERRESTRIAL ENVIRONMENTS

Continental ichnofaunas provide a wealth of information on evolutionary paleoecology, providing insights into the process of terrestrialization, evolutionary radiations, environmental faunal expansions, and exploitation of empty or underutilized ecospace (e.g. Miller, 1984; Maples and Archer, 1989; Buatois and Mángano, 1993b; Genise and Bown, 1994b; Buatois *et al.*, 1998c; Miller *et al.*, 2002; Cohen, 2003; Miller and Labandeira, 2003; Braddy, 2004; Genise, 2004; Mángano and Buatois, 2007) (Fig. 14.11).

Our knowledge of incipient Precambrian and early Paleozoic terrestrial ecosystems is patchy at best. Terrestrial microorganisms have been recorded in Upper Archean rocks (Watanabe *et al.*, 2000), probably becoming widespread by the late Mesoproterozoic to the early Neoproterozoic (Horodyski and Knauth, 1994; Prave, 2002). Spore-like microfossils or cryptospores are known since the Middle Cambrian, suggesting the establishment of a nascent semi-aquatic to subaerial flora of bryophyte grade (Strother, 2000; Strother and Beck, 2000). Spores indicative of land vegetation occur in Middle Ordovician rocks (Strother *et al.*, 1996), while spores and plant fragments have been documented in Upper Ordovician deposits (Wellman *et al.*, 2003). Fluvial style was dominantly sheet-braided with little mud preservation (Davies and Gibling, 2009). The earliest evidence of animal incursions into the land is trackways produced by an amphibious organism in Upper Cambrian to

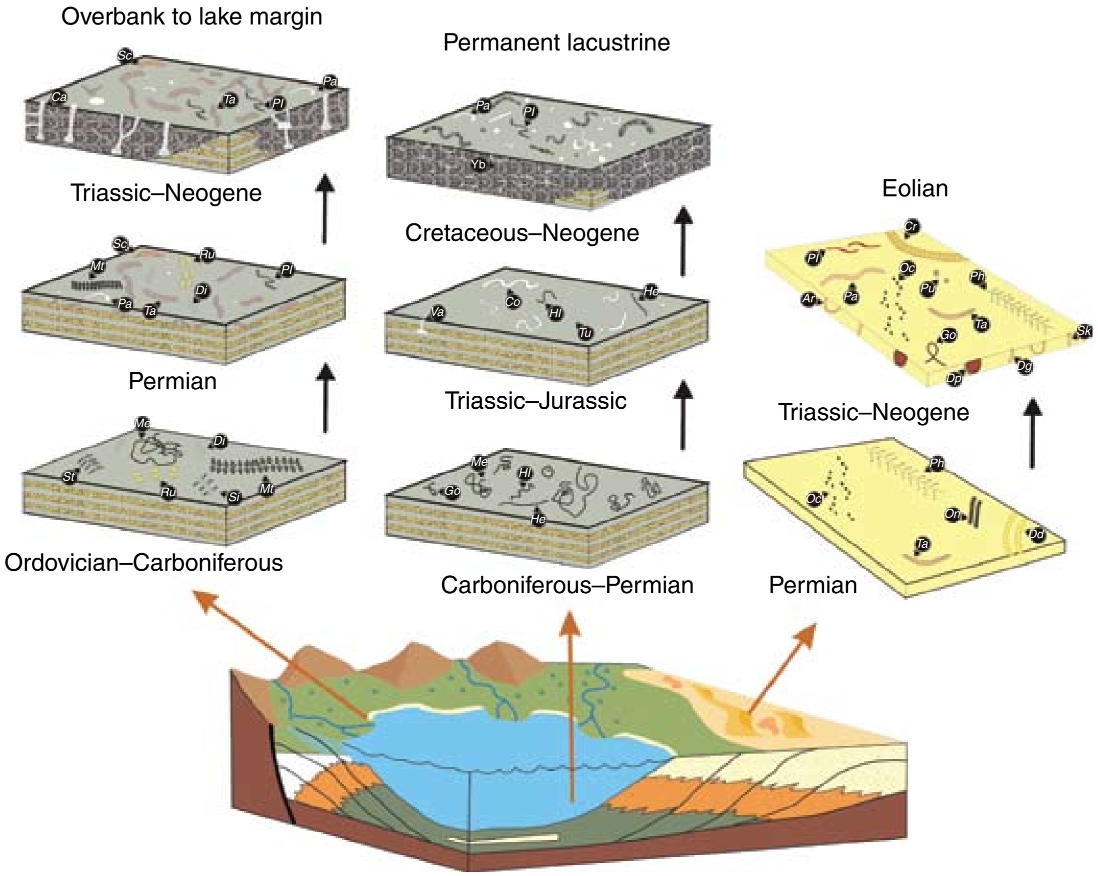

Figure 14.11 Colonization of continental environments. Invertebrate ichnofaunal changes occurred in the different continental environments throughout the Phanerozoic, with the colonization of lacustrine substrates being delayed with respect to that of overbank and lake-margin deposits. Ordovician to Carboniferous overbank to lake-margin deposits are dominated by arthropod trackways, including *Siskemia* (*Si*), *Stiaria* (*St*), *Diplichnites* (*Di*), and *Merostomichnites* (*Mt*), accompanied by bilobate traces such as *Rusophycus* (*Ru*) and grazing trails such as *Mermia* (*Me*). Permian deposits include the striated meniscate trace fossil *Scoyenia* (*Sc*), together with *Taenidium* (*Ta*), *Diplichnites* (*Di*), *Palaeophycus* (*Pa*), *Merostomichnites* (*Mt*), and *Rusophycus* (*Ru*). In contrast, Carboniferous–Permian ichnofaunas in permanent subaqueous portions of lacustrine systems are dominated by grazing trails such as *Mermia* (*Me*), *Helminthopsis* (*Hl*), *Helminthoidichnites* (*He*), and *Gordia* (*Go*). All these horizontal trace fossils are emplaced very close to the sediment–water interface, resulting in almost no disturbance of the primary sedimentary fabric. Overbank to lake-margin deposits display increased degree of bioturbation since the Triassic. Some of the typical elements are the backfilled trace fossils *Scoyenia* (*Sc*) and *Taenidium* (*Ta*), the crayfish burrow *Camborygma* (*Ca*), and simple burrows such as *Planolites* (*Pl*) and *Palaeophycus* (*Pa*). During the Triassic–Jurassic, an increase in depth of bioturbation occurred in permanent subaqueous lacustrine deposits with the appearance of branched burrows such as *Vagorichnus* (*Va*) and *Tuberculichnus* (*Tu*). Grazing trails, such as *Cochlichnus* (*Co*), *Helminthopsis* (*Hl*), and *Helminthoidichnites* (*He*), persisted but occupying a deeper-tier position. After the Cretaceous, mottled texture attributed to *Planolites* (*Pl*) and *Palaeophycus* (*Pa*) became common. Also, a number of biogenic structures attributed to chironomids, including Y-shaped burrows (Yb), are present. Paleozoic and post-Paleozoic eolian ichnofaunas are highly different. Little is known about pre-Permian eolian ichnofaunas, but Permian associations tend to be dominated by arthropod trackways, such as *Octopodichnus* (*Oc*), *Paleohelcura* (*Ph*), *Oniscoidichnus* (*On*), and *Diplopodichnus* (*Dd*); meniscate trace fossils, such as *Taenidium* (*Ta*), are less common. Post-Paleozoic invertebrate eolian ichnofaunas display much more variety of morphological types, including arthropod trackways such as *Octopodichnus* (*Oc*) and *Paleohelcura* (*Ph*), simple burrows such as *Planolites* (*Pl*) and *Palaeophycus* (*Pa*), the bilobate trace fossil *Cruziana* (*Cr*), the meniscate trace *Taenidium* (*Ta*), the grazing trail *Gordia* (*Go*), the small clustered burrow *Pustulichnus* (*Pu*), and various vertical burrows such as *Digitichnus* (*Dg*), *Arenicolites* (*Ar*), and *Diplocraterion* (*Dp*). Modified from Mángano and Buatois (2007).

Lower Ordovician coastal eolian-dune deposits (MacNaughton *et al.*, 2002). Meniscate trace fossils attributed to millipedes in paleosols (Retallack and Feakes, 1987; Retallack, 2001), and arthropod trackways (*Diplichnites* and *Diplopodichnus*) of myriapod-like invertebrates in pond deposits (Johnson *et al.*, 1994) are known from the Late Ordovician. However, marine influence has recently been detected in the deposits hosting the meniscate trace fossils (Davies *et al.*, 2010). Although myriapods are typically considered terrestrial, Early Ordovician to Late Silurian representatives were probably aquatic or amphibious (Almond, 1985).

A significant invasion of continental environments close to the Silurian–Devonian transition is indicated by trace-fossil data (Buatois *et al.*, 1998c). A terrestrial mobile arthropod epifauna representative of the *Diplichnites* ichnoguild was established in backshore, subaerial delta-plain, and floodplain environments

(Bradshaw, 1981; Woolfe, 1990; Trewin and McNamara, 1995; Draganits *et al.*, 2001; Neef, 2004a, b; Davies *et al.*, 2006). By the Devonian, ichnofaunas dominated by arthropod trackways become relatively common in lake-margin environments (Pollard *et al.*, 1982; Pollard and Walker, 1984; Walker, 1985) (Fig. 14.11). It has been suggested that the presence of these ichnofaunas in transitional alluvial-lacustrine deposits, rather than fully subaqueous environments may be a response to the concentration of land-derived plant debris along lake shorelines, particularly near the mouths of distributary channels (Buatois *et al.*, 1998c). Nutrient delivery to lakes may have been quite limited during the early Paleozoic before the onset of abundant upland terrestrial plant cover (Cohen, 2003). Ichnological evidence is consistent with body-fossil data, which indicate that before the Silurian lake inhabitants may have been rare, mostly linked to accidental incursions from marine habitats (Cohen, 2003). Also, by the Late Silurian to Early Devonian, vascular plants became common, an increase in the abundance of underground rooting systems took place, and muddy floodplains were widespread, allowing stabilization of channel banks. As a result, meandering systems became dominant and humic material built up in soils promoting colonization by organisms (Davies and Gibling, 2009).

While these ichnofaunas occur in low-energy, protected areas, vertical burrows seem to be common in relatively high-energy fluvial deposits, reflecting the establishment of a stationary, deep suspension-feeding infauna (*Skolithos* ichnoguild). However, the degree of marine influence in some of these deposits has been controversial (Bradshaw, 1981; Woolfe, 1990). A relatively deep-tier deposit-feeding infauna, represented by large (up to 250 mm wide) meniscate trace fossils (*Beaconites*–*Taenidium* ichnoguild), becomes widespread in abandoned fluvial-channel and overbank deposits by the Devonian and Carboniferous (e.g. Gevers *et al.*, 1971; Allen and Williams, 1981; Bradshaw, 1981; Gevers and Twomey, 1982; Graham and Pollard, 1982; Bruck *et al.*, 1985; Bamford *et al.*, 1986; Gordon, 1988; Keighley and Pickerill, 1997; Draganits *et al.*, 2001; Morrissey and Braddy, 2004). Ichnodiversity in these fluvial deposits is generally low. Based on the recurrent association of the meniscate trace fossils and large *Diplichnites*, as well as their similar size range, a myriapod (e.g. arthropleurid) producer has been invoked (Morrissey and Braddy, 2004). In particular, a potential producer, the arthropod *Bennettarthra annwnensis*, has been suggested recently (Fayers *et al.*, 2010).

Ordovician–Devonian ichnofaunas were restricted to alluvial and transitional alluvial-lacustrine environments, but Carboniferous trace fossils are also present in fully subaqueous lacustrine settings, signaling a significant environmental expansion of the benthic fauna (Buatois and Mángano, 1993b; Buatois *et al.*, 1998c) (Fig. 14.11). These lacustrine deposits were colonized by a moderately diverse, mobile detritus-feeding epifauna of the *Mermia* ichnoguild. It has been suggested that this expansion was probably linked to the rapid diversification, and increase in abundance of land plants. Vegetation changes may have introduced abundant organic detritus into previously nutrient-poor, lacustrine habitats (Maples and Archer, 1989). An analogous situation was proposed for terrestrial environments based on the migration of plants from geographically marginal areas (upland areas peripheral to major basinal wetlands) to the lowlands during the Carboniferous–Permian transition (DiMichele and Aronson, 1992). This pattern is consistent with environmental trends experienced by aquatic insects, which first originated in running water and later moved into lacustrine habitats (Wooton, 1988; Wiggins and Wichard, 1989). Ichnodiversity diagrams plotted as number of ichnogenera per million years show a rapid diversification during the Silurian–Devonian and then a continuous increase in trace-fossil diversity during the late Paleozoic (Buatois *et al.*, 1998c). However, these authors indicated that when the data are normalized to correct for differences in volume of continental deposits, the major diversification event seems to have occurred during the Carboniferous. This increase in ichnodiversity was accompanied by the diversification of freshwater organisms such as arthropods, annelids, fish, and mollusks (Maples and Archer, 1989). All continental sedimentary environments were colonized by the Carboniferous, and subsequent patterns indicate an increase of ecospace utilization within already colonized depositional settings (Fig. 14.11). For example, during the Permian the presence of striated and meniscate trace fossils of the *Scoyenia* ichnoguild record the establishment of a mobile, intermediate-depth, deposit-feeding infauna that was able to colonize firm, desiccated substrates in floodplain environments.

A decrease in diversity at familial level in lake environments took place during the Early Permian to the Middle Triassic. This was followed by a subsequent increase by the Late Triassic, in an evolutionary event referred to as the "Lacustrine Mesozoic Revolution" by Cohen (2003). In lake-margin and overbank environments, meniscate trace fossils of the *Scoyenia* ichnoguild became more abundant, leading to increased disturbance of the primary fabric since the Triassic (Buatois *et al.*, 1998c). Also in these settings, a stationary deep infauna attributed to freshwater crayfish, the *Camborygma* ichnoguild, was established by the Triassic (Hasiotis and Mitchell, 1993; Hasiotis *et al.*, 1993a) (Fig. 14.11). Parallel to this increase in burrowing extent and depth, a remarkable decrease in the abundance of arthropod trackways is apparent.

Changes also occurred in the permanent subaqueous portion of lacustrine systems with the appearance of penetrative trace fossils consisting of networks of irregularly branched burrows during the Middle to Late Triassic (Voigt and Hoppe, 2010). These burrow systems may reflect the activity of deposit-feeding oligochaetes or insect larvae. This mobile, intermediate-depth, deposit-feeding infauna is also illustrated by the *Vagorichnus* ichnoguild, recorded in Jurassic deep-lake deposits (Buatois *et al.*, 1996b, 1998c). In contrast to Paleozoic permanent subaqueous assemblages typified by surface trails, Mesozoic lacustrine ichnofaunas are dominated by infaunal burrows. Evolutionary innovations resulting from the Mesozoic lacustrine revolution were ultimately conducive to the establishment of modern lacustrine ecosystems and food webs by the Late Cretaceous (Cohen, 2003). High density of infaunal deposit-feeding traces of the *Planolites* ichnoguild has caused major disruption of lacustrine sedimentary fabrics since the Cretaceous (Buatois and Mángano, 1998; Buatois *et al.*, 1998c) (Fig. 14.11).

Interestingly, meniscate trace fossils of the *Beaconites–Taenidium* ichnoguild, which consist of large structures, occupying deeper tiers in the Paleozoic, are commonly smaller and occupied a middle-tier position during the Mesozoic and most of the Cenozoic (Buatois *et al.*, 2007a). This pattern is consistent with the idea of Morrissey and Braddy (2004) that a myriapod (e.g. arthropleurid) produced these large meniscate trace fossils in the Silurian–Carboniferous (see also Fayers *et al.*, 2010). However, by the Miocene large and deep backfilled burrows reoccupied deep tiers in similar overbank and abandoned-channel deposits (Buatois *et al.*, 2007a).

Freshwater ichnofaunas display an overall increase in extent and depth of bioturbation through the Phanerozoic (Miller, 1984; Buatois *et al.*, 1998c; Miller *et al.*, 2002; Miller and Labandeira, 2003). Comparative analysis of continental ichnofaunas in space and time suggests that increases in bioturbation depth and intensity took place progressively through time, from fluvial and lake-margin settings to permanent subaqueous lacustrine environments (Buatois *et al.*, 1998c). This increase in depth and intensity of bioturbation strongly influenced the nature of the stratigraphic record of continental environments, producing increasing disturbance of primary sedimentary fabrics.

Evolutionary aspects also play a major role in paleosol ichnology (Pemberton *et al.*, 1992b; Buatois *et al.*, 1998c; Genise, 2004). Late Jurassic to Early Cretaceous paleosols tend to be dominated by meniscate trace fossils (e.g. *Taenidium*, *Beaconites*), crayfish burrows (e.g. *Loloichnus baqueroensis*, *Dagnichnus titoi*, *Cellicalichnus meniscatus*) and earthworm boxworks (*Castrichnus*) (Genise *et al.*, 2008; Bedatou *et al.*, 2008, 2009). In addition, ichnological evidence suggests that fungiculture in social insects may have been attained by the Early Cretaceous (Genise *et al.*, 2010b). By the Late Cretaceous, bee nests (*Cellicalichnus chubutensis*) and pupal chambers of coleopterans (*Rebuffoichnus*) and insects of uncertain affinities (*Fictovichnus*, *Pallichnus*) became common (Johnson *et al.*, 1996; Genise *et al.*, 2002, 2007). The most important families of insect chambered trace fossils (Coprinisphaeridae, Pallichnidae, Krausichnidae, and Celliformidae) are virtually absent in pre-Cenozoic paleosols (Genise and Bown, 1994a, b; Genise *et al.*, 2002; Genise, 2004). Claims of Triassic bee cells and termite nests (Hasiotis and Dubiel, 1993, 1995; Hasiotis, 2002) and Jurassic termite nests, bee cells, dung-beetle nests, and ant galleries (Hasiotis, 2002, 2004) have met general rejection (e.g. Grimaldi, 1999; Engel, 2001; Genise, 2000, 2004; Grimaldi and Engel, 2005; Bromley *et al.*, 2007). This negative reception has been based on (1) the fact that these ecologically keystone insects have not been found in pre-existing non-angiosperm-dominated ecosystems, and (2) the reported Triassic and Jurassic trace fossils do not show diagnostic features supporting their attribution to these modern groups of insects (e.g. spiral closure cap in bee nests). In fact, recent re-examination of part of this material (the supposed Triassic bee nests) revealed that the observations claimed to identify these structures as produced by bees cannot be replicated (Lucas *et al.*, 2010b).

Diversification of modern insects is recorded by the abundance and complexity of structures produced by wasps (e.g. *Chubutolithes*), bees (e.g. *Celliforma*, *Uruguay*, *Ellipsoideichnus*, *Palmiraichnus*, and *Rosellichnus*), dung-beetles (e.g. *Coprinisphaera* and *Fontanai*) ants (e.g. *Attaichnus* and *Parowanichnus*), and termites (e.g. *Termitichnus*, *Vondrichnus*, *Syntermesichnus*, *Coatonichnus*, *Tacuruichnus*, *Fleaglellius*, *Krausichnus* and *Microfavichnus*) in Cenozoic paleosols (Genise and Bown, 1994a, b; Genise, 2004; Duringer *et al.*, 2006, 2007). This evolutionary event has been referred to as the "Paleogene Paleosol Revolution" (Buatois and Mángano, 2009b). This pattern reflects the appearance of ecologically keystone insects that coevolved with angiosperms by the mid Early Cretaceous (Thorne *et al.*, 2000; Grimaldi and Engel, 2005; Bromley *et al.*, 2007). In addition, nests produced by these groups of insects have a greater preservation potential than other continental biogenic structures because they are constructed structures and not merely excavated ones (Genise and Bown, 1994a).

Eolian environments also experienced significant ichnofaunal changes through the Phanerozoic (Fig. 14.11). An increase in diversity of trace fossils occurs in eolian deposits by the Permian–Triassic transition. Post-Paleozoic ichnofaunas display more varied behavioral patterns than their Paleozoic counterparts (Gradzinski and Uchman, 1994; Buatois *et al.*, 1998c). Many of the examples of Paleozoic eolian dune ichnofaunas are

Box 14.2 The impact of oribatid mites on plant tissue decomposition in late Paleozoic coal swamps

The field of arthropod–plant interactions has undergone an explosive development during the last 15 years. Trace fossils preserved in plant material provide a wealth of information for understanding food webs in terrestrial to coastal ecosystems. In modern temperate forest ecosystems, oribatid mites are key animals in converting plant litter and wood to organic residues. However, little is known of their fossil history and their body-fossil record commences in the Middle Devonian, but does not reappear until the Early Jurassic. The trace-fossil record, therefore, provides an independent source of data. Analysis of damage produced by oribatid mites in plant tissue preserved in Pennsylvanian coal-ball deposits of eastern North America helps to fill this gap. Examination of these coal balls reveals the presence of a number of trace fossils attributed to mites, including coprolites and tunnels within plant tissues. Virtually all the permineralized tissues from the dominant plant groups, namely lycopsids, calamites, ferns, seed ferns, and cordaites, have been attacked by oribatid mites. This study underscores the role of these arthropods as decomposers in late Paleozoic coal-swamp forests.

Reference: Labandeira *et al.* (1997).

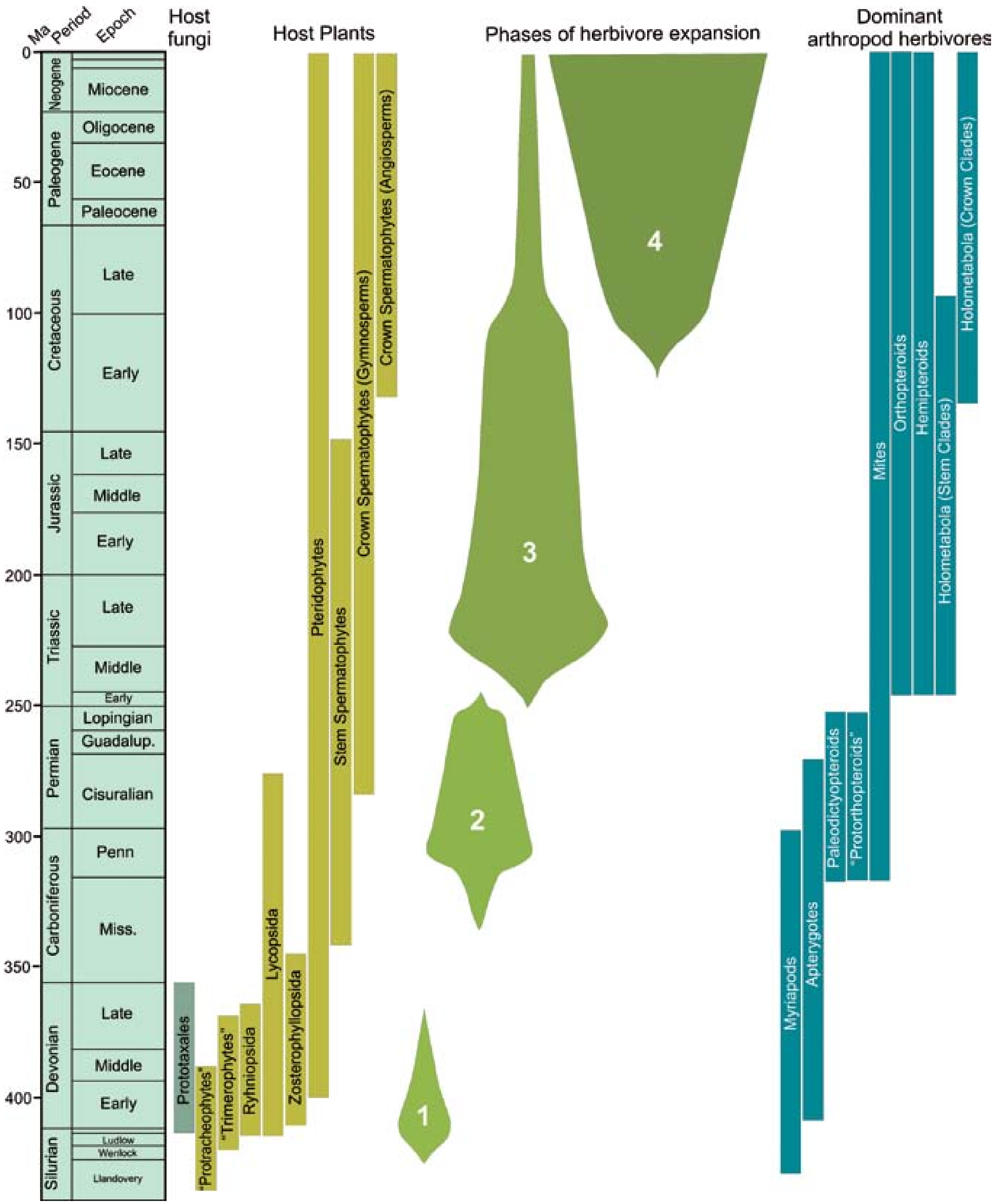

Figure 14.12. Expansion of arthropod herbivory during the Phanerozoic, showing arthropod producers, and host plants and fungi for the four phases of herbivory expansion. Based on Labandeira (2006).

dominated by arthropod and reptile trackways (e.g. Gilmore, 1926, 1927; Brady, 1947; Alf, 1968; Brand and Tang, 1991; Brand, 1992; Lockley, 1992; Loope, 1992; Sadler, 1993; Lockley *et al.*, 1994; Braddy, 1995; Kramer *et al.*, 1995; Brand and Kramer, 1996; Hunt and Lucas, 2007). Arthropod trackways include *Octopodichnus* (scorpions), *Oniscoidichnus* (isopods), *Diplopodichnus* (millipedes), *Paleohelcura* (scorpions), and *Permichnium* (insects). With respect to reptile trackways, the sinapsid ichnogenera *Laoporus* and *Chelichnus* are common (McKeever, 1991; Lockley *et al.*, 1994, 1995; Kramer *et al.*, 1995; Morales and Haubold, 1995). In particular, Lockley *et al.* (1995) noted that most of arthropod and vertebrate trackways were produced subaerially on dune faces.

Mesozoic eolian ichnofaunas are more varied rather than being dominated by arthropod trackways. Ichnofaunas from interdunes and dunes contain vertical U-shaped burrows (e.g. *Arenicolites* and *Diplocraterion*), short vertical burrows (*Digitichnus*), meniscate trace fossils (e.g. *Taenidium* and *Entradichnus*), grazing trails (e.g. *Gordia*), bilobate locomotion traces (e.g. *Cruziana*), simple horizontal feeding and dwelling traces (e.g. *Planolites* and *Palaeophycus*) (Ekdale and Picard, 1985; Netto, 1989; Fernandes *et al.*, 1990; Gradzinski and Uchman, 1994; Ekdale *et al.*, 2007). The typical vertebrate ichnogenus in eolian-dune deposits is the sinapsid trackway *Brasilichnium* (Leonardi, 1981; Lockley *et al.*, 1994; Lockley and Meyer, 2000; Hunt and Lucas, 2006c). Cenozoic eolian deposits may contain abundant vertebrate trackways. For example, Fornós *et al.* (2002) documented superbly preserved trackways of the ruminant goat *Myotragus balearicus* in Pleistocene eolianites formed in cliff-front coastal echo dunes.

14.2.7 ARTHROPOD–PLANT INTERACTIONS THROUGH THE PHANEROZOIC

Analysis of arthropod–plant interactions based on the study of traces produced in fossil leaves and other plant remains is revealing an amazing wealth of data which helps to explain the evolution of terrestrial ecosystems through the Phanerozoic (e.g. Labandeira, 1997, 1998, 2000, 2002, 2006, 2007) (Box 14.2). Labandeira (2007) outlined the main advantages of arthropod–plant associational data, namely (1) they are common in deposits that lack insect body fossils; (2) they are more abundant and useful than insect body fossils in the same deposits; (3) they frequently predate the insect body fossil record; (4) they provide behavioral information unavailable from the body-fossil record; and (5) they supply critical information for testing paleobiological and macroevolutionary hypotheses.

Based on this dataset, Labandeira (2006) suggested that the history of arthropod herbivory can be summarized in four main phases of expansion (Fig. 14.12). Each phase is defined by: (1) a temporally constrained and taxonomically distinctive suite of plant–host clades; (2) a coeval assemblage of arthropod herbivore clades in association with plant host clades; and (3) the presence of a representative associational biota early within the development of the phase. An analysis of the evolutionary history of palynivory and nectarivory results in the delineation of similar phases (Labandeira, 2000).

The first phase spans the Late Silurian to Late Devonian, and mostly consists of structures produced by myriapods and, to a lesser extent, apterygote hexapods and possibly true insects. The host plants are basal clades of vascular plants (primitive land plants) and prototaxalean fungus. Arthropod–plant associations include three functional feeding groups, namely external foliage feeding, piercing-and-sucking, and boring. Coprolites containing spores provide the earliest evidence of palynivory (Edwards *et al.*, 1995). Evidence for this phase comes essentially from the coastal plains of Euramerica.

The second phase encompasses the mid Carboniferous to end Permian, and includes structures produced by a wider array of makers than in the previous phase, including not only myriapods and apterygote hexapods, but also mites, and paleopterous and neopterous insects (the Paleozoic insect fauna of Labandeira, 2000). The host plants are mostly medulosan and glossopterid pteridosperms, and, to a lesser extent, lyginopterid pteridosperms and cordaites (early seed plants and ferns). With respect to functional feeding groups, three more types are added to those previously present in phase 1, galling, seed predations, and non-feeding oviposition. Considerably more evidence of spore feeding is available from this phase. Information comes from wetlands in fluvial and coastal plains mostly from Euramerica, although information from Gondwana has been added in recent years (e.g. Adami-Rodrigues *et al.*, 2004).

The third phase is Middle Triassic to Recent in age, and is represented by structures produced by mites, orthopteroids, hemipteroids, and basal holometabolan clades (earlier phase of the Modern insect fauna of Labandeira 2000). The host plants are pteridophytes and gymnosperms (seed plants). Leaf mining is added to the previous groups and, accordingly, the seven functional feeding groups that characterize modern ecosystems were already present in the early Mesozoic. The dataset for this phase comes from a wide variety of environmental settings in all continents.

The fourth phase spans the mid Early Cretaceous to Recent, and includes structures produced by Modern-aspect orthopteroids and derived hemipteroid and holometabolous insects (later phase of the Modern insect fauna of Labandeira 2000). Angiosperms are the host plants, and the seven functional feeding groups are present. This phase is evidenced by the largest dataset, encompassing a wide array of terrestrial and coastal environments and all continents, although most information comes from North America and western Europe. Most insect mouthpart classes, functional feeding groups, and dietary guilds were established by the end of the Cretaceous (Labandeira, 2002).

15 Ichnology in paleoanthropology and archaeology

> And what had he felt, I asked Mario, when he'd seen it there, the *huella*?
> "One thing is to see artifacts presumably made by somebody and another is to see the *pisada* someone made, what their foot left in the earth. That's what gives you the sense of humanity, right?"
>
> Ariel Dorfman
> *Desert Memories* (2004)

While the previous chapter deals with processes occurring at the scale of deep time, we now move into a more recent past, a time witnessing human activities. For the implications of trace fossils in paleoanthropology, information is based on the study of human fossil footprints (Kim *et al.*, 2008a). Human footprints also play a major role in archaeology, although sources of information are found in many other ichnological datasets, such as bioerosion and bioturbation structures, and other vertebrate tracks as well (Baucon *et al.*, 2008). The aim of this chapter is to review recent research in the area of ichnological applications in paleoanthropology and archaeology. The first half of the chapter will be devoted to review the fossil record of human footprints, from the Pliocene to the Holocene. The second half will explore the uses of ichnology in archaeology.

15.1 APPLICATIONS IN PALEOANTHROPOLOGY

Hominid fossil footprints represent a rich record with examples in all continents with the exception of Antarctica (Kim *et al.*, 2008b) (Fig. 15.1). A recent review indicates the existence of at least 63 reported hominid tracksites (Lockley *et al.*, 2008a). Specifically, the term "hominid ichnology" was introduced by Lockley (1998) for the study of all traces made by hominids. Although, in a broad sense, the field of hominid ichnology includes not only footprints, but also butchering and feeding traces, evidence of stone tool industries, and even any evidence of built structure, it is advisable to restrict the field to avoid full overlap with other disciplines (Kim *et al.*, 2008a). As noted by these authors, fossil footprints are the main field of hominid ichnology and, therefore, we will focus on their implications in paleoanthropology.

15.1.1 THE PLIOCENE RECORD

The only recorded Pliocene hominid footprints are those from Laetoli, Tanzania, which represent the oldest hominid tracks known (Leakey and Hay, 1979; Hay and Leakey, 1982; Suwa, 1984; Leakey and Harris, 1987; Tuttle *et al.*, 1990; Raichlen *et al.*, 2008; Meldrum *et al.*, 2011). The Laetoli site contains three trackways preserved in volcanic ash dated to 3.56 million years ago (Leakey, 1981, 1987). Abundant mammal and avian fossil tracks also occur in the Laetoli area (Musiba *et al.*, 2008). The composition of these vertebrate ichnofaunas suggests a number of microhabitats, such as open grasslands and wooded galleries, in a mosaic landscape.

The original and standard interpretation is that the trackways were produced by *Australopithecus afarensis*, which is essentially consistent with the age of the site and the associated bone record (Suwa, 1984). However, alternative interpretations have been suggested, and some authors have noted the remarkably modern aspect of the tracks, suggesting that they are indistinguishable from those produced by the genus *Homo* (Tuttle, 1987, 1996, 2008; but see Meldrum *et al.*, 2011). Based on these uncertainties, the Laetoli trackways have been classified only at ichnogeneric level as *Hominipes* isp. (Kim *et al.*, 2008b).

15.1.2 THE EARLY PLEISTOCENE RECORD

There is a significant gap between the age of the Laetoli tracksite and the next oldest fossil site (1.5–1.6 million years ago), which is that of the Koobi Fora on the shores of Lake Turkana, Kenya (Behrensmeyer and Laporte, 1981; Lockley *et al.*, 2008a). A hominid trackway consisting of seven tracks occurs in a sandy mudstone layer accumulated in a lake-margin environment. Associated footprints include those of pigmy hippopotamuses and wading birds, which is consistent with the envisaged environmental setting (Behrensmeyer and Laporte, 1981). The hominid trackway is inferred to have been produced by *Homo erectus*. As in the case of the Laetoli trackways, that from Koobi Fora should be classified only at ichnogeneric level as *Hominipes* isp.

15.1.3 THE MIDDLE PLEISTOCENE RECORD

The Middle Pleistocene marks an expansion in the hominid footprint fossil record, with occurrences outside of Africa, specifically in Europe (Italy and France) (Lockley *et al.*, 2008a). Of these two recordings, the best documented is that of the Roccamonfina Volcano site in Italy, dated between 385 000 and 325 000 years old (Mietto *et al.*, 2003; Avanzini

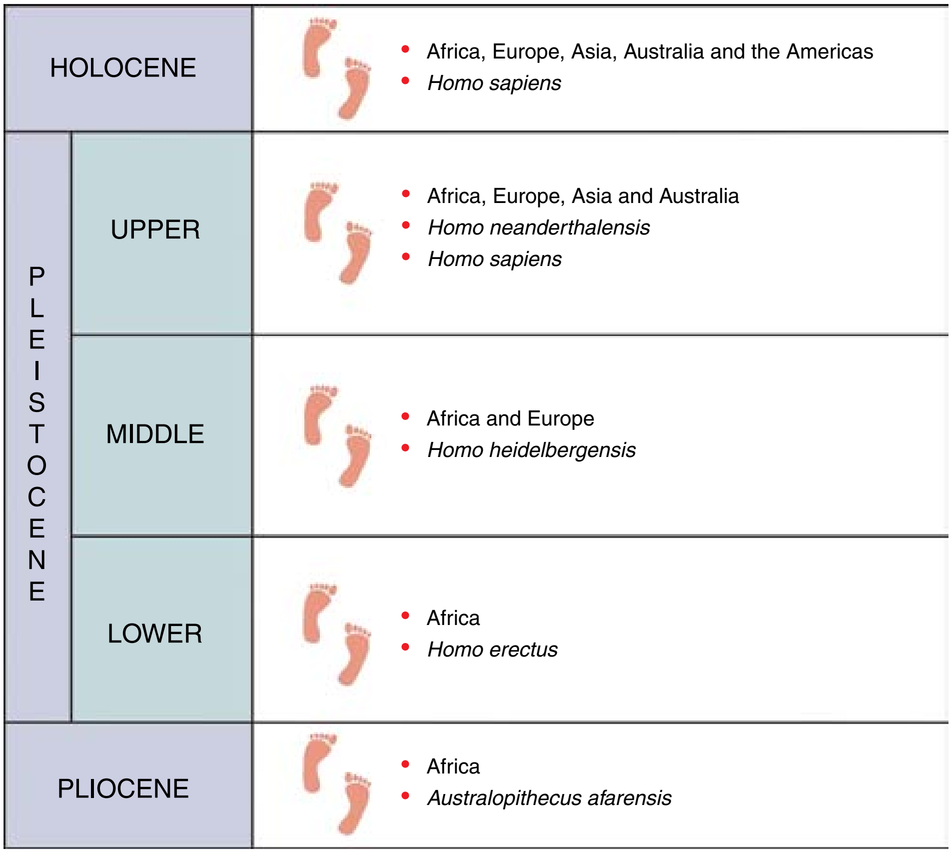

Figure 15.1 Stratigraphic and geographic distribution of human fossil footprints, including the most likely hominid producers. The consistency between the bone and trace-fossil record may be in part an artifact based on the fact that at least some of the footprints are attributed to specific hominids on the basis of age and the bone record itself. The trackway record is not continuous. A large gap exists between the 3.56 million years old Laetoli site (Pliocene) and the 1.5–1.6 million years old Koobi Fora (Early Pleistocene).

et al., 2008). Three trackways have been documented from volcanic ash deposited from pyroclastic flows on a volcano slope. Although fine morphological details are not preserved, the age of the unit is consistent with production by a pre-*Homo sapiens* or pre-*Homo neanderthalensis* species, *H. heidelbergensis* being the most likely candidate.

15.1.4 THE LATE PLEISTOCENE RECORD

Late Pleistocene human trackways are more abundant and widespread and provide definite evidence of the appearance of *H. sapiens* (Lockley *et al.*, 2008a). Early Late Pleistocene hominid tracks of the last interglacial are recorded in two different sites (Nahoon and Langebaan) in South Africa (Roberts, 2008). They are preserved in a coastal-eolian calcarenite, and associated with hyena and bird tracks. As noted by Lockley *et al.* (2008a), these recordings are particularly relevant because they may represent evidence of the presence of *H. sapiens* in Africa close to the Middle to Late Pleistocene transition. The only other Late Pleistocene record in Africa is represented by a single track assigned to *H. sapiens* in Lake Bogoria, Kenya (Scott *et al.*, 2008). The footprint is preserved on a siltstone formed in a lacustrine mud flat and is associated with a wide variety of mammal and bird tracks.

The most extensive Late Pleistocene hominid record occurs in Europe, including tracksites in France, Spain, Italy, Romania, and Greece (Lockley *et al.*, 2008a). European human tracks are almost invariably preserved in caves, such as Lascaux in France (Barriere and Sahly, 1964) or Vârtop in Romania (Onac *et al.*, 2005), reflecting a higher preservation potential. Associated tracks are mostly those of carnivores (Lockley *et al.*, 2008a). The oldest of these are the tracks recorded in Vârtop Cave, which has been attributed to *Homo neanderthalensis* (Onac *et al.*, 2005). Most of the other recordings most likely correspond to *H. sapiens*.

The Late Pleistocene is characterized by the first occurrence of human tracks worldwide, with records extending to Australia (Webb *et al.*, 2005), Tibet (Zhang and Li, 2002), and Korea (Kim *et al.*, 2009). The Tibet finding is particularly significant because no other evidence of humans has been recorded in the area (Zhang and Li, 2002).

15.1.5 THE HOLOCENE RECORD

The Holocene record reveals an expansion into the Americas, with sites recorded in United States (Willey *et al.*, 2009), Mexico (Rodriguez-de la Rosa *et al.*, 2004), Guatemala (Lockley *et al.*, 2008a), El Salvador (Haberland and Grebe, 1957), Honduras (Lockley *et al.*, 2008a), Nicaragua (Lockley *et al.*, 2008b), and Argentina (Bayón and Politis, 1996). In addition, Holocene human footprints have been recorded in Europe, including England (Roberts, 2009), Wales (Lockley *et al.*, 2008a), Spain

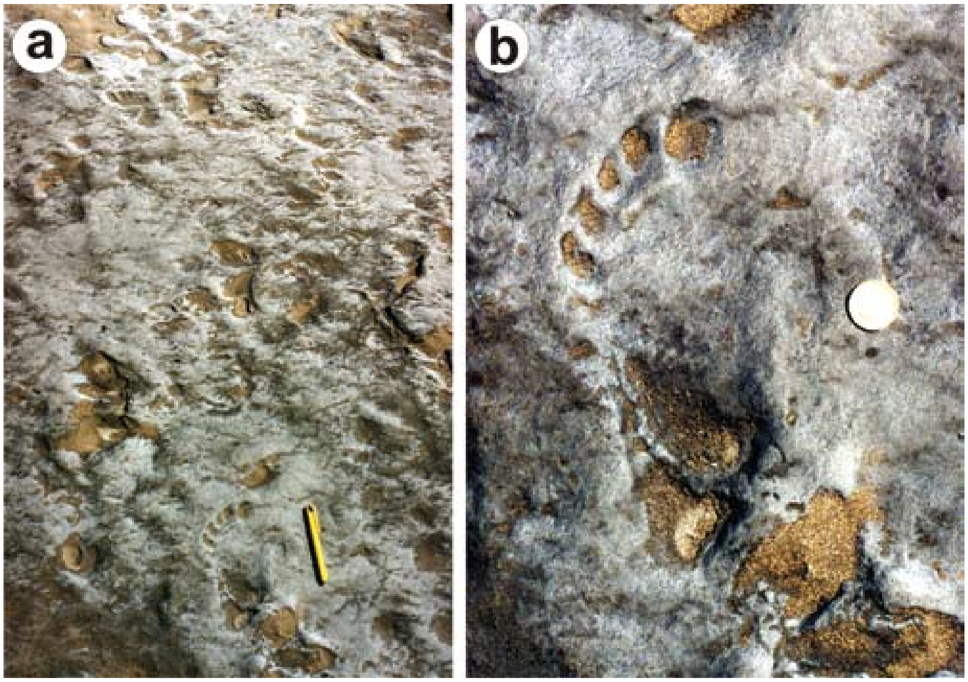

Figure 15.2 Human footprints from the Monte Hermoso site, Buenos Aires Province, Argentina. (a) General view of trackway. Pen is 16 cm. (b) Close up of a track. Coin is 1.5 cm. See Bayón and Politis (1996).

(Lockley *et al.*, 2008a), Italy (Mastrolorenzo *et al.*, 2006), Greece (Bromley *et al.*, 2009b), and Turkey (Westaway *et al.*, 2006). Examples in Africa and Asia are restricted to Mauritania (Mafart, 2006) and Japan (Harada and Noto, 1984), respectively. Additional recordings have been reported from Australia (Lockley *et al.*, 2008a) and New Zealand (Nichol, 1982).

The Acahualinca Footprint Museum site in Nicaragua has been regarded as the most important fossil human tracksite (Lockley *et al.*, 2008b). These authors noted that the site combines accessibility, a large number of well-preserved trackways, and reliable dating. Accordingly, Kim *et al.* (2008b) selected these trackways as the type sample for *Hominipes modernus*, inferred to be produced by *Homo sapiens*. The tracksites in Monte Hermoso and Pehuen-Co, Argentina, are particularly remarkable because they host hundreds of hominid trackways (Fig. 15.2a–b) together with mammal and bird footprints, and invertebrate trace fossils (Bayón and Politis, 1996; Aramayo, 2009; Aramayo and Manera de Bianco, 2009). These sites record the activities of human communities living in the proximity of a coastal lake.

15.2 APPLICATIONS IN ARCHAEOLOGY

The applications of ichnology in archaeology or ichnoarchaeology (Baucon *et al.*, 2008) represent a relatively new field. However, archaeological studies have commonly incorporated trace-fossil information without necessarily referring to the conceptual framework of ichnology (e.g. Pierce, 1992; Milner and Smith, 2005). Only a very few papers have dealt with archaeological aspects from an ichnological perspective (e.g. Mikuláš and Cílek, 1998; West and Hasiotis, 2007; Rodríguez-Tovar *et al.*, 2010b, c). As a result, Baucon *et al.* (2008) noted that a uniform, systematic approach has been lacking. Undoubtedly, ichnoarchaeology is a vibrant new field undergoing expansion particularly in the Mediterranean region (see review by Baucon *et al.*, 2008). In this section, we briefly review some of its most recent developments.

15.2.1 BIOGENIC STRUCTURES IN NATURAL AND ARTIFICIAL SUBSTRATES

Ichnology traditionally deals with biogenic structures produced in natural substrates. In archaeology, trace-fossil information is preserved not only in natural substrates but also in artificial ones. In the case of natural substrates, bioturbation structures may provide information, but their preservation potential is usually low because diagenetic processes have acted for insufficient time (Baucon *et al.*, 2008). Where preserved, footprints may yield valuable insights, as illustrated by human and horse tracks formed in a ceramic manufacturing workshop of the Bronze Age in Qatna, Syria (Baucon *et al.*, 2008). Burrows have received comparatively little attention in archaeological contexts. Burrows may record emplacement contemporaneous with the archaeological site or reveal a later bioturbation event. In the latter case, animals are responsible for significantly mixing sediment at the archaeological sites (Araujo and Marcelino, 2003). Borings are common in archaeological contexts because of their high preservation potential in natural substrates, and have been used to decipher sea-level changes in rocky shorelines, mostly in the Mediterranean region (e.g. Pirazzoli *et al.*, 1982). Work on wood bioerosion essentially reflects the fact that xylophagous insects may significantly damage wood materials, but the potential of wood borings as sources of information remain unexplored in ichnoarchaeology (Baucon *et al*., 2008).

Artificial substrates commonly help in the preservation of biogenic structures in archaeological sites. Bricks help to preserve tracks because of their geotechnical properties, open-air drying, rapid diagenesis, resistance, and abundance (Baucon *et al*., 2008). Bird and mammal footprints in bricks of Roman and Medieval sites have been extensively studied (Higgs, 2001). Borings are also preserved in artificial substrates, those in the pillars of the Temple of Serapis, Italy, being the classic example, as illustrated by Lyell (1830).

Also, bones comprise substrates for the preservation of human-produced structures. Of these, human skulls have been modified for various cultural purposes, including surgical or religious ones (e.g. Rytel, 1962; Lillie, 1998). The study of these structures, although technically within the field of ichnoarchaeology, falls close to the boundaries of the discipline (Baucon *et al*., 2008). Finally, study of trace fossils in archaeological objects (e.g. flint artifacts) offers the opportunity to identify the geological sources of raw material exploited in tool construction (Rodríguez-Tovar *et al*., 2010b, c) (Box 15.1).

15.2.2 ICHNOLOGICAL HIEROPHANIES

Hierophanies are physical manifestations of the holy or sacred (Eliade, 1959). Baucon *et al*. (2008) noted that some geological features (e.g. sacred rocks) qualify as hierophanies (“geological hierophanies”) because ancient cultures have linked them to the divine and the magical. These authors also noted that some biogenic structures in archaeological context may play a similar role, and referred to them as ichnohierophanies or ichnological hierophanies. Baucon *et al*. (2008) proposed a classification of these features in cultural (ichnofossils interpreted

Box 15.1 Identifying the source of archaeological artifacts through ichnological analysis

A recent study has presented a new ichnological technique to identify the source of archaeological tools. This is a non-destructive technique which allows matching the trace fossils present in the tools of an archaeological site with those of outcrops in the same region. This technique has been successfully developed to identify raw materials of flaked artifacts used by Late Neolithic and Copper Age communities of the Iberian Peninsula. This study focuses on blade cores from various archaeological sites in southern Spain. These artifacts contain a distinctive ichnofauna characterized by *Phycosiphon incertum* (Fig. 15.3) and subordinate small specimens of *Chondrites* isp. A survey of outcrops and chert quarries in the region indicates that the same ichnofauna is only present in deep-marine cherts of the Campo de Gibraltar Complex. Accordingly, it has been suggested that these rocks were the most likely source of the artifacts. Flint knappers appear to have preferred cherts from the Campo de Gibraltar over other material located near the settlements.

References: Rodríguez-Tovar *et al*. (2010b, c).

Figure 15.3 Blade core from the Copper Age (*c*. 3000–2500 BP) containing *Phycosiphon incertum*. Los Reconcos, Valle del río Turón, southern Spain. Photograph courtesy of Francisco Rodríguez-Tovar, Antonio Morgado, and José A. Lozano (University of Granada). See Rodríguez-Tovar *et al*. (2010b, c).

Figure 15.4 "Graphoglyptids" from Ancient Greece. National Archaeological Museum, Athens, Greece.

as manifestation of supernatural realities), morphological (inorganic structures interpreted as organic traces of supernatural entities), anthropic (human-generated structures based on ichnological motifs), scientific (trace fossils misinterpreted by archaeologists as cultural artifacts), and composite (superposition of ichnohierophanies of various types).

Mayor and Sarjeant (2001) noted that the fascination of early humans with footprint-shaped marks in rock have led to attribution of these structures to either familiar or fabulous once-living creatures, representing an example of morphological or cultural ichnohierophanies. Envisaged tracemakers range from gods, devils, heroes, and saints to occasionally more accurate interpretations. Early Jurassic dinosaur footprints in the Holy Cross Mountains, Poland, were formerly regarded as imprints produced by the Devil while traveling to participate in occult gatherings (Mayor and Sarjeant, 2001). These authors noted that the Bushmen of Lesotho depicted footprints in cave paintings in an area where dinosaur tracks were abundant. In addition, these paintings also depicted relatively accurate reconstructions of iguanodont-like animal as potential producers. Spiral designs from Ancient Greece may have been inspired by turbidite trace fossils (Fig. 15.4). Ichnology has a long history indeed!

References

Abbassi, N. and Lockley, M. (2004). Eocene bird and mammal tracks from the Karaj Formation, Tarom Mountains, northwestern Iran. *Ichnos*, 11, 349–356.

Aberhan, M., Kiessling, W., and Fürsich, F.T. (2006). Testing the role of biological interactions in the evolution of mid-Mesozoic marine benthic ecosystems. *Paleobiology*, 32, 259–277.

Abrams, P.A. (1987). On classifying interactions between populations. *Oecologia*, 73, 272–281.

Adami-Rodrigues, K., Iannuzzi, R. and Pinto, I.D. (2004). Permian plant-insect interactions from a Gondwana flora of southern Brazil. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, Fossils and Strata, 51, 106–125.

Ahlberg, P.E. (1991). Tetrapod or near tetrapod fossils from the Upper Devonian of Scotland. *Nature*, 354, 298–301.

Ahlbrandt, T.S., Andrews, S. and Gwynne, D.T. (1978). Bioturbation in eolian deposits. *Journal of Sedimentary Petrology*, 48, 839–848.

Aigner, T. (1985) Storm depositional systems. Dynamic stratigraphy in modern and ancient shallow-marine sequences. *Lecture Notes in Earth Sciences*, 3, 174.

Aigner, T. and Reineck, H.E. (1982). Proximality trends in modern storm sands from the Helgoland Bight (North Sea) and their implications for basin analysis. *Senckenbergiana Maritima*, 14, 183–215.

Aitken, A.E. (1990). Fossilization potential of Arctic fjord and continental shelf macrofaunas. In *Glacimarine Environments: Processes and Sediments*, ed. J.A. Dowdeswell and J.E. Scourse, Geological Society Special Publication, 53, 155–176.

Aitken, A.E., Risk, M.J. and Howard, J.D. (1988). Animal–sediment relationships on a subarctic intertidal flat, Pangnirtung Fjord, Baffin Island, Canada. *Journal of Sedimentary Research*, 58, 969–978.

Akpan, E.B. (1986). Depth distribution of endolithic algae from the Firth of Clyde: implications for delineation and subdivision of the photic zone. *Journal of the Marine Biological Association of the United Kingdom*, 66, 269–275.

Akpan, E.B. and Farrow, G.E. (1984). Depth of deposition of early Holocene raised sediments at Irvine deduced from algal borings in mollusc shells. *Scottish Journal of Geology*, 20, 237–247.

Alf, R.M. (1968). A spider trackway from the Coconino Formation, Seligman, Arizona. *Southern California Academy of Sciences, Bulletin*, 67, 125–128.

Allen, G.P. (1991). Sedimentary processes and facies in the Gironde estuary: a model for macrotidal estuarine systems. In *Clastic Tidal Sedimentology*, ed. D.G. Smith, G.E. Reinson, B.A. Zaitlin and R.A. Rahmani, Canadian Society of Petroleum Geologists, Memoir, 16, 219–226.

Allen, G.P. and Posamentier, H.W. (1993). Sequence stratigraphy and facies model of an incised valley fill: The Gironde Estuary, France. *Journal of Sedimentary Petrology*, 63, 378–391.

Allen, J.R.L. and Williams, B.P.J. (1981). *Beaconites antarcticus*: a giant channel–associated trace fossil from the Lower Old Red Sandstone of South Wales and the Welsh Borders. *Geological Journal*, 166, 255–269.

Allison, M.A. and Nittrouer, C.A. (1998) Identifying accretionary mud shorefaces in the geologic record: insights from the modern Amazon dispersal system. In *Mudstones and Shales: Recent Progress in Shale Research*, ed. J. Schieber, W. Zimmerle and P.S. Sethi, Stuttgart: Schweizerbart Publishers, pp. 147–161.

Allison, P.A. and Briggs, D.E.G. (1994). Reply to "Exceptional fossil record. Distribution of soft-tissue preservation through the Phanerozoic". *Geology*, 22, 184.

Almond, J.E. (1985). The Silurian-Devonian fossil record of the Myriapoda. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 309, 227–237.

Almond, J.E., Buatois, L.A., Gresse, P.G. and Germs, G.J.B. (2008). Trends in metazoan body size, burrowing behaviour and ichnodiversity across the Precambrian-Cambrian boundary: ichnoassemblages from the Vanrhynsdorp Group of South Africa. *Conference programme and abstracts, 15th Biennial Meeting of the Palaeontological Society of South Africa, Matjiesfontein*, pp. 15–20.

Alonso, R. (1985). Icnitas de aves como control de niveles boratiferos. *Sociedad Cientifica del Noroeste Argentino*, 1, 37–42.

Alonso-Zarza, A.M. (2003). Palaeoenvironmental significance of palustrine carbonates and calcretes in the geological record. *Earth Science Reviews*, 60, 261–298.

Alonso-Zarza, A.M. and Silva, P.G. (2002). Quaternary laminar calcretes with bees nests; evidence of small scale climatic fluctuations, eastern Canary Islands, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 178, 119–135.

Alonso-Zarza, A.M., Genise, J.F. and Verde, M. (2010). Calizas del Queguay: stratigraphy, sedimentology and trace fossils. *18th International Sedimentological Congress, Abstracts and Program*, p. 106.

Alpert, S.P. (1974). Systematic review of the genus *Skolithos*. *Journal of Paleontology*, 48, 661–669.

Alpert, S.P. (1977). Trace fossils and the basal Cambrian boundary. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 1–8.

Alroy J, Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J. Jr., Sommers, M.G., Wagner, P.J. and Webberal, P.J. (2001). Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences, USA*, 98, 6261–6266.

Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J.W., Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.J., Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J., Bonuso, N., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A., Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nürnberg, S., Powers, C.M., Sessa, J.A., Simpson, C., Tomaovch, A. and Visaggi, C.C. (2008). Phanerozoic trends in the global diversity of marine invertebrates. *Science*, 321, 97–100.

Alvarez, L.W., Alvarez, W., Asaro, F. and Michel, H.V. (1980). Extraterrestrial Cause for the Cretaceous-Tertiary Extinction. *Science*, 208, 1095–1108.

Anderson, A.M. (1976). Fish trails from the early Permian of South Africa. *Palaeontology*, 9, 397–409.

Anderson, B.G. and Droser, M.L. (1998). Ichnofabrics and geometric configurations of *Ophiomorpha* within a sequence stratigraphic framework: an example from the Upper Cretaceous US Western Interior. *Sedimentology*, 45, 379–396.

Anderson, J.G. and Meadows, P.S. (1978). Microenvironments in marine sediments. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, 76, 1–16.

Anderson, K.S., Graham, S.A. and Hubbard, S.M. (2006). Facies, architecture and origin of a reservoir-scale sand-rich succession within submarine canyon fill: Insights from Wagon Caves Rock (Paleocene), Santa Lucia Range, California. *Journal of Sedimentary Research*, 76, 819–838.

Angulo, S. and Buatois, L.A. (2009). Sedimentological and ichnological aspects of a sandy low-energy coast: Upper Devonian–Lower Mississippian Bakken Formation, Williston Basin, southeastern Saskatchewan. In *Summary of Investigations 2009, Volume 1, Saskatchewan Geological Survey*, Saskatchewan Ministry of Energy and Resources, Miscellaneous Report 2009–4.1, Paper A–5, 17.

Angulo, S. and Buatois, L.A. (2010). Sedimentary facies distribution of the Upper Devonian–Lower Mississippian Bakken Formation, Williston Basin, Southeastern Saskatchewan: implications for understanding reservoir geometry, paleogeography and depositional history. In *Summary of Investigations 2010, Saskatchewan Geological Survey*, Saskatchewan Ministry of Energy and Resources, Miscellaneous Report 2010, 1–18.

Ansell, A.D. (1962). Observations on burrowing in the Veneridae (Eulamellibranchia). *Biological Bulletin, Woods Hole*, 123, 521–530.

Ansell, A.D. and Trueman, E.R. (1968). The mechanism of burrowing in the anemone *Peachia hastata* Gosse. *Journal of Experimental Marine Biology and Ecology*, 2, 124–134.

Anthony, E.J. and Orford, J.D. (2002) Between wave- and tide-dominated coasts: the middle ground revisited. *Journal of Coastal Research, Special Issue*, 36, 8–15.

Aquino, R., Buatois, L.A., Somoza, D., Briceño, M. and Moreno, J. (2001). Integration of ichnology, palynology, foraminiferal paleoecology, sedimentology and sequence stratigraphy in reservoir characterization: Oligocene–Lower Miocene, Pirital Field, north of Monagas, Oriental Basin of Venezuela. *VI International Ichnofabric Workshop, Abstracts*, Isla Margarita & Puerto La Cruz, pp. 22–23.

Aramayo, S.A. (2009). A brief sketch of the Monte Hermoso Human Footprint Site, South Coast of Buenos Aires Province, Argentina. *Ichnos*, 16, 49–54.

Aramayo, S.A. and Manera de Bianco, T. (1987a). Hallazgo de una icnofauna continental (Pleistoceno tardío) en la localidad de Pehuen-Co (partido de Coronel Rosales), provincia de Buenos Aires, Argentina. Parte I: Edentata, Litopterna, Proboscidea. *4º Congreso Latinoamericano de Paleontología (Bolivia), Actas*, 1, 516–531.

Aramayo, S.A. and Manera de Bianco, T. (1987b). Hallazgo de una icnofauna continental (Pleistoceno tardío) en la localidad de Pehuen-Co (partido de Coronel Rosales), provincia de Buenos Aires, Argentina. Parte II: Carnivora, Artiodactyla y Aves. *4º Congreso Latinoamericano de Paleontología (Bolivia), Actas*, 1, 532–547.

Aramayo, S.A. and Manera de Bianco, T. (1996). Edad y nuevos hallazgos de icnitas de mamíferos y aves en el yacimiento paleoicnológico de Pehuen-Co (Pleistoceno Tardío), provincia de Buenos Aires, Argentina. *Asociación Paleontológica Argentina, Special Publication*, 4, 47–57.

Aramayo, S.A. and Manera de Bianco, T. (2009). Late Quaternary palaeoichnological sites from the Southern Atlantic Coast of Buenos Aires Province, Argentina: mammal, bird and hominid evidence. *Ichnos*, 16, 25–32.

Araujo M.A.G. and Marcelino J.C. (2003). The role of armadillos in the movement of archaeological materials: an experimental approach. *Geoarchaeology: An International Journal*, 18, 433–460.

Archer, A.W. (1984). Preservational control of trace-fossil assemblages: Middle Mississippian carbonates of South-Central Indiana. *Journal of Paleontology*, 58, 285–279.

Archer, A.W. and Maples, C.G. (1984). Trace-fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwestern Indiana. *Journal of Paleontology*, 58, 448–466.

Archer, A.W., Feldman, H.R., Kvale, E.P. and Lanier, W.P. (1994). Comparison of drier- to wetter-interval estuarine roof facies in the Eastern and Western Interior coal basins, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 106, 171–185.

Arcucci, A.B., Forster, C., Abdala, F., May, C. and Marsicano, C. (1995). "Theropods" tracks from the Los Rastros Formation (Middle Triassic), La Rioja Province, Argentina. *Journal of Vertebrate Paleontology*, 15, supplement 3, 16A.

Astini, R.A., Mángano, M.G. and Thomas, W.A. (2000). El icnogénero *Cruziana* en el Cámbrico Temprano de la Precordillera Argentina: El registro más antiguo de Sudamérica. *Revista de la Asociación Geológica Argentina*, 55, 111–120.

Atkinson, R.J.A. (1974). Spatial distribution of *Nephrops* burrows. *Estuarine and Coastal Marine Science*, 2, 171–176.

Augustinus, P. (1978). *The Changing Shoreline of Surinam (South America)*. Utrecht: Foundation for Scientific Research in Surinam and Netherlands.

Augustinus, P. (1989). Cheniers and chenier plains: a general introduction. *Marine Geology*, 90, 219–229.

Augustinus, P. (2002). Biochemical factors influencing deposition and erosion of fine-grained sediment. In *Muddy Coasts of the World: Processes, Deposits, and Function*, ed. T. Healy, Y. Wang and J.A. Healy, *Proceedings in Marine Science*, 4, 203–228.

Ausich, W.I. and Bottjer, D.J. (1982). Tiering in suspension feeding communities on soft substrate throughout the Phanerozoic. *Science*, 216, 173–174.

Avanzini, M. (2002). Dinosauromorph tracks from the Middle Triassic (Anisian) of the Southern Alps I (Valle di Non, Italy). *Bolletino della Società Paleontologica Italiana*, 41, 37–40.

Avanzini M. and Lockley M. (2002) Middle Triassic archosaur ontogeny and population structure: interpretation based on *Isochirotherium delicatum* fossil footprints (Southern Alps, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 185, 391–402.

Avanzini, M., Ceoloni, P., Conti, M.A., Leonardi, G., Manni, R., Mariotti, N., Mietto, P., Nicosia, U., Santi, G. and Spezzamonte, M. (2001). Tetrapod footprints as key elements of the Permo–Triassic continental biochronology. *Natura Bresciana, Annuario del Museo Civico di Storia Naturale di Brescia, Monografia*, 25, 89–107.

Avanzini, M., Piubelli, D., Mietto, P., Roghi, G., Romano, R. and Masetti, D. (2006). Lower Jurassic (Hettangian-Sinemurian) dinosaur track megasites, southern Alps, northern Italy. In *The Triassic-Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G.

Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 207–216.

Avanzini, M., Mietto, P., Panarello, A., De Angelis, M. and Rolandi, G. (2008). The Devil's Trails: Middle Pleistocene human footprints preserved in a volcanoclastic deposit of Southern Italy. *Ichnos*, 15, 179–189.

Azpeitia-Moros, F. (1933). Datos para el estudio paleontológico de la costa Cantábrica y de algunos otros puntos de España. *Boletín del Instituto Geológico y Minero de España*, 53, 1–65.

Azmi, R.J. (1998). Discovery of lower Cambrian small shelly fossils and brachiopods from the Lower Vindhyan of Son Valley, Central India. *Journal of the Geological Society of India*, 52, 381–389.

Babcock, L.E. (1993). Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology*, 67, 217–229.

Babcock, L.E. and Robinson, R.A. (1989). Preferences of Palaeozoic predators. *Nature*, 337, 695–696.

Bagla, P. (2000). Team rejects claim of early Indian fossils. *Science*, 289, 1273.

Baird, D. (1980). A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*, ed. L.L. Jacobs, Flagstaff, AZ: Museum of Northern Arizona Press, pp. 219–230.

Bajard, J. (1966). Figures et structures sédimentaires dans la zone intertidale de la partie orientale de la Baie du Mont-Saint-Michel. *Revue de Géographie physique et de Géologie Dynamique*, 8, 39–111.

Bak, K. (1995). Trace fossils and ichnofabrics in the Upper Cretaceous red deep-water marly deposits of the Pieniny Klippen Belt, Polish Carpathians. *Annales Societatis Geologorum Poloniae*, 64, 81–97.

Baker, M.E. and B.V. Barnes. (1998). Landscape ecosystem diversity of river floodplains in northwestern Lower Michigan, USA. *Canadian Journal of Forestry Research*, 28, 1405–1418.

Baldwin, C.T. (1975). The stratigraphy of the Cabos series in the section between Cadavedo and Luarca, Province of Oviedo, NW Spain. *Breviora Geologica Asturica*, 19, 4–9.

Baldwin, C.T. (1977). The stratigraphy and facies associations of trace fossils in some Cambrian and Ordovician rocks of north western Spain. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 9–40.

Baldwin, C.T., Strother, P.K., Beck, J.H. and Rose, E. (2004). Palaeoecology of the Bright Angel Shale in the eastern Grand Canyon, Arizona, USA, incorporating sedimentological, ichnological and palynological data. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society of London Special Publication*, 228, 213–236.

Balistieri, P.R.M.N., Netto, R.G. and Lavina, E.L.C. (2002). Ichnofauna from the Upper Carboniferous–Lower Permian rhythmites from Mafra, Santa Catarina State, Brazil: Ichnotaxonomy. *Revista Brasileira de Paleontologia*, 4, 13–26.

Balistieri, P.R.M.N., Netto, R.G. and Lavina, E.L.C. (2003). Icnofauna de ritmitos do topo da Formação Mafra (Permo-Carbonífero da bacia do Paraná) em Rio Negro, Estado do Paraná (PR), Brasil. In *Icnología: Hacia una convergencia entre geología y biología*, ed. L.A Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 131–139.

Bambach, R.K. (1983). Ecospace utilization and guilds in marine communities through the Phanerozoic. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenus Press, pp. 719–746.

Bambach, R.K. (1993). Seafood through time; changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology*, 19, 372–397.

Bambach, R.K., A.H. Knoll and J.J. Sepkoski Jr. (2002). Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proceedings of the National Academy of Sciences, USA*, 99, 6854–6859.

Bambach, R.K., Bush, A.M. and Erwin, D.H. (2007). Autecology and the filling of ecospace: Key metazoan radiations. *Palaeontology*, 50, 1–22.

Bamford, M.L.F., Bruck, P.M., Cooper, M.A., Forbes, W.H. and MacCarthy, I.A.J. (1986). *Beaconites*–type burrows from the Old Red Sandstone of Hook Head, Co. Wexford, Ireland. *Proceedings Geological Association*, 97, 59–71.

Banks, N.L. (1970). Trace fossils from the late Precambrian and Lower Cambrian of Finmark, Norway. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 19–34.

Barnes, R.S.K. and Hughes, R.N. (1999). *An Introduction to Marine Ecology.* 3rd edn. Oxford, UK: Blackwell Science.

Barnes, R.S.K., Calow, P. and Olive, P.J.W. (1993). *The Invertebrates: A New Synthesis*. Oxford, UK: Blackwell Science.

Barras, C.G. and Twitchett, R.J. (2007). Response of the marine infauna to Triassic-Jurassic environmental change: ichnological data from southern England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 244, 223–241.

Barriere, C. and Sahly, A. (1964). Les empreintes humaines de Lascaux. In *Miscelanea en homenaje a Abate H. Breuil*. Barcelona: Instituto de Prehistoria y Arqueología, pp. 173–180.

Barthel, K.W., Swinburne, N.H.M. and Conway Morris, S. (1990). *Solnhofen: A Study in Mesozoic Palaeontology*. Cambridge, UK: Cambridge University Press.

Basan, P.B. and Frey, R.W. (1977). Actual-palaeontology and neoichnology of salt marshes near Sapelo Island, Georgia. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 41–69.

Bates, C.C. (1953). A rational theory of delta formation as exemplified by the present-day Mississippi Delta. *Journal of Sedimentary Petrology*, 23, 132–133.

Batra, S.W.T. (1984). Solitary bees. *Scientific American*, 250, 120–127.

Baucon, A. (2008). Neoichnology of a microbial mat in a temperate, siliciclastic environment: Spiaggia al Bosco (Grado, Northern Adriatic, Italy). In *Italian Ichnology*, ed. M. Avanzini and F. Petti, *Studi Trentini di Scienze Naturali Acta Geologica*, 83, 183–203.

BauconA.,PriviteraS.,MorandiBonacossiD.,CanciA.,NetodeCarvalhoC., Kyriazi E., Laborel-Deguen F., Morhange C. and Marriner N. (2008). Principles of ichnoarchaeology: new frontiers for studying past times. In *Italian Ichnology*, ed. M. Avanzini and F. Petti, *Studi Trentini di Scienze Naturali Acta Geologica*, 83, 43–72.

Bayón, C. and Politis, G. (1996). Estado actual de las investigaciones en el sitio Monte Hermoso 1 (Prov. de Buenos Aires). *Arqueología*, 6, 83–116.

Beall, A. (1968). Sedimentary processes operative along the western Louisiana shoreline. *Journal of Sedimentary Petrology*, 38, 869–877.

Beatty, T.W., Zonnenveld, J.-P. Henderson, C.M. (2008). Anomalously diverse Early Triassic ichnofossil assemblages in Northwest Pangea: a case for a shallow-marine habitable zone. *Geology*, 36, 771–774.

Bechtel, D.J., Yuill, C.N., Ranger, M.J. and Pemberton, S.G. (1994). Ichnology of inclined heterolithic stratification of the Fort McMurray Formation, northwestern Alberta. In *Mannville Core Conference*, ed. S.G. Pemberton, D.P. James and D.M. Wightman, Canadian Society of Petroleum Geologists, Exploration Update, pp. 351–368.

Bedatou, E., Melchor, R.N., Bellosi, E.S. and Genise, J.F. (2008). Crayfish burrows from Late Jurassic–Late Cretaceous continental deposits of Patagonia: Argentina: their palaeoecological, palaeoclimatic and palaeobiogeographical significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257, 169–184.

Bedatou, E., Melchor, R.N. and Genise, J.F. (2009). Complex palaeosol ichnofabrics from Late Jurassic–Early Cretaceous volcaniclastic successions of Central Patagonia, Argentina. *Sedimentary Geology*, 218, 74–102.

Behrends, G. and Michaelis, H. (1977). Zur Deutung der Lebensspuren des Polychaeten *Scolelepis squamata*. *Senckenbergiana Maritima*, 9, 47–57.

Behrensmeyer, A.K. and Laporte, L.F. (1981). Footprints of a Pleistocene hominid in northern Kenya. *Nature*, 289, 167–169.

Bell, C.M. (2004). Asteroid and ophiuroid trace fossils from the Lower Cretaceous of Chile. *Palaeontology*, 47, 51–66.

Bellwood, D.R. and Wainwright, P.C. (2006). The history and biogeography of fishes on coral reefs. In *Coral reef fishes: Dynamics and Diversity in a Complex Ecosystem*, ed. P.F. Sale, Burlington, VT: Academic Press, pp. 5–32.

Bengtsön, S. and Yue, Z. (1992). Predatorial borings in Late Precambrian mineralized exoskeletons. *Science*, 257, 367–369.

Bengtsön, S., Rasmussen, R. and Krape, B. (2007). The Paleoproterozoic megascopic Stirling biota. *Paleobiology*, 33, 351–381.

Benner, J.S., Ekdale, A.A. and Gibert, J.M. de (2004). Macroborings *Gastrochaenolites* in Lower Ordovician hardgrounds of Utah: sedimentologic, paleoecologic, and evolutionary implications. *Palaios*, 19, 543–550.

Benner, J.S., Ridge, J.C. and Knecht, R.J. (2009). Timing of post-glacial reinhabitation and ecological development of two New England, USA, drainages based on trace fossil evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 212–231.

Benton, M.J. (1982). Trace fossils from Lower Palaeozoic ocean-floor sediments of the Southern Uplands of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 73, 67–87.

Benton, M.J. (2003). *When Life Nearly Died: The Greatest Mass Extinction of All Time*. London: Thames and Hudson.

Benton, M.J. and Trewin, N.J. (1980). *Dictyodora* from Silurian of Peeblesshire, Scotland. *Palaeontology*, 23, 501–513.

Berger, W.H., Ekdale, A.A. and Bryant, P.P. (1979). Selective preservation of burrows in deep-sea carbonates. *Marine Geology*, 32, 205–230.

Bergström, J. (1973). Organization, life and systematics of trilobites. *Fossils and Strata*, 2, 1–69.

Bergström, J. (1976). Lower Palaeozoic trace fosils from eastern Newfoundland. *Canadian Journal of Earth Sciences*, 13, 1613–1633.

Bergström, J. (1990). Precambrian trace fossils and the rise of bilaterian animals. *Ichnos*, 1, 3–13.

Berkenbusch, K. and Rowden, A.A. (2003). Ecosystem engineering: moving away from "just-so" stories. *New Zealand Journal of Ecology*, 27, 67–73.

Bertling, M. (1997). Bioerosion of Late Jurassic reef corals: Implications for reef evolution. *8th International Coral Reef Symposium, Proceedings*, 2, 1663–1668.

Bertling, M. (1999). Taphonomy of trace fossils at omission surfaces (Middle Triassic, East Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 149, 27–40.

Bertling, M. and Hermanns, K. (1996). Autochtone Muschelbohrungen im Neogen des Rheinischen Braunkohlenreviers und ihre sedimentologische Bedeutung. *Zentralblatt für Geologie und Paläontologie Teil I*, 1/2, 33–44.

Bertling, M., Braddy, S.J. and Bromley, R.G. (2006). Names for trace fossils: a uniform approach. *Lethaia*, 39, 265–286.

Bertness, M.D. (1999). *The Ecology of Atlantic Shorelines*. Sunderland, MA: Sinauer Associates.

Beukema, J.J. (1976). Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Nethearlands Journal of Sea Research*, 10, 236–261.

Beynon, B.M. and Pemberton, S.G. (1992). Ichnological signature of a brackish water deposit: an example from the Lower Cretaceous Grand Rapids Formation, Cold Lake oil sands area, Alberta. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, Society for Sedimentary Geology Core Workshop, 17, 191–221.

Beynon, B.M., Pemberton, S.G., Bell, D.A. and Logan, C.A. (1988). Environmental implications of ichnofossils from the Lower Cretaceous Grand Rapids Formation, Cold Lake Oil Sands Deposit. In *Sequences, Stratigraphy, Sedimentology: Surface and Subsurface*, ed. D.P. James and D.A. Leckie, *Canadian Society of Petroleum Geologists Memoir*, 15, 275–290.

Bhattacharya, J.P. (2006). Deltas. In *Facies Models Revisited*, ed. H. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 237–292.

Bhattacharya, J.P. and Giosan, L. (2003). Wave-influenced deltas, geomorphological implications for facies reconstruction. *Sedimentology*, 50, 187–210.

Bhattacharya, J.P. and MacEachern, J.A. (2009). Hyperpycnal rivers and prodeltaic shelves in the Cretaceous seaway of North America. *Journal of Sedimentary Research*, 79, 184–209.

Bhattacharya, J.P. MacEachern, J.A., Garrison J.R. Jr., Ryer, T.A. and Pemberton, S.G. (2007). *Integrated sedimentology and ichnology of fluvial-dominated and wave-influenced deltas in the Cretaceous seaway: Ferron Sandstone and Panther Tongue, Utah*. Society for Sedimentary Geology Research Conference, Ichnological Applications to Sedimentological and Sequence Stratigraphic Problems, Field Trip Guidebook, Price.

Billett, D.S.M., Lampitt, R.S., Rice, A.L. and Mantoura, R.F.C. (1983). Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature*, 302, 520–522.

Bishop, G.A. (1975). Traces of predation. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 261–281.

Blair, T.C. and McPherson, J.G. (1994). Alluvial Fan Processes and Forms. In *Geomorphology of Desert Environments*, ed. A.D. Abrahams and A.J. Parsons, London: Chapman & Hall, pp. 354–402.

Bockelie, J.F. (1991). Ichnofabric mapping and interpretation of Jurassic reservoir rocks of the Norwegian North Sea. *Palaios*, 6, 206–215.

Bockelie, J.F. (1994). Plant roots in core. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 177–199.

Bockelie, J.F., Eldoy, A., Gran, K. and Porturas, F. (1998). Ichnofabric analysis using borehole and core images: examples of the Norwegian sector of the North Sea. *American Association of Petroleum Geologists, Annual Meeting* (Salt Lake City), *Expanded Abstracts*, A77.

Bohacs, K.M, Carroll, A.R., Neal, J.E. and Mankiewicz, P.J. (2000). Lake-Basin type, source potential, and hydrocarbon character: an integrated sequence-stratigraphic-geochemical framework. In *Lake Basins through Space and Time*, ed. E. Gierlowski-Kordesch and K. Kelts, *American Association of Petroleum Geologists Studies in Geology*, 46, 3–34.

Bohacs, K.M, Hasiotis, S.T. and Demko, T.M. (2007). Continental ichnofossils of the Green River and Wasatch Formation, Eocene, Wyoming: a preliminary survey, proposed relation to lake-basin type, and application to integrated paleo-environmental interpretation. *Mountain Geologist*, 11, 79–108.

Bosence, D. and Wilson, J. (2003). Sequence stratigraphy of carbonate depositonal systems. In *Sedimentary Record of Sea-Level Change*, ed. A.L. Coe, Ambridge, UK: Cambridge University Press and Open University, pp. 234–255.

Bottjer, D.J. (1985). Trace fossils and paleoenvironments of two Arkansas Upper Cretaceous discontinuity surfaces. *Journal of Paleontology*, 59, 282–298.

Bottjer, D.J. and Clapham, M.E. (2006). Evolutionary paleoecology of Ediacaran Benthic marine animals. In *Neoproterozoic Geobiology and Paleobiology*, ed. S. Xiao and A.J. Kaufman, Dordrecht: Springer, pp. 91–114.

Bottjer, D.J. and Droser, M.L. (1991). Ichnofabric and basin analysis. *Palaios*, 6, 199–205.

Bottjer, D.J., Droser, M.L. and Jablonski, D. (1988). Palaeoenvironmental trends in the history of trace fossils. *Nature*, 333, 252–255.

Bottjer, D.J., Hagadorn, J.W. and Dornbos, S.Q. (2000). The Cambrian substrate revolution. *GSA Today*, 10, 1–8.

Bouma, A.H. (2000a). Coarse-grained and fine-grained turbidite systems as end member models: applicability and dangers. *Marine and Petroleum Geology*, 17, 137–143.

Bouma, A.H. (2000b). Fine-grained, mud-rich turbidite systems: model and comparison with coarse-grained, sand-rich systems. In *Fine-Grained Turdidite Systems*, ed. A.H. Bouma and C.G. Stone, *AAPG Memoir 72/SEPM Special Publication*, 68, 9–20.

Bouma, A.H. (2004). Key controls on characteristics of turbidite systems. In *Confined Turbidite Systems*, ed. S.A. Lomas and P. Joseph, *Geological Society Special Publication*, 222, 9–22.

Bown, T.M. 1982. Ichnofossils and rhizoliths of the nearshore fluvial Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 40, 255–309.

Bown, T.M. and Laza, J.H. (1990). A Miocene termite nest from southern Argentina and its paleoclimatological implications. *Ichnos*, 1, 73–79.

Bown, T.M. and Ratcliffe, B.C. (1988). The origin of *Chubutholites* Ihering, ichnofossils from the Eocene and Oligocene of Chubut Province, Argentina. *Journal of Paleontology*, 62, 163–167.

Boyd, R., Dalrymple, R. and Zaitlin, B.A. (1992). Classification of clastic coastal depositional environments. *Sedimentary Geology*, 80, 139–150.

Boyd, R., Dalrymple, R.W. and Zaitlin, B.A. (2006). Estuarine and incised-valley facies models. In *Facies Models revisited*, ed. H.W. Posamentier and R. Walker, *Society for Sedimentary Geology Special Publication*, 84, 175–240.

Bracken, B. and Picard, M.D. (1984). Trace fossils from Cretaceous/Tertiary North Horn Formation in central Utah. *Journal of Paleontology*, 58, 477–487.

Braddy, S.J. (1995). The Ichnotaxonomy of the invertebrate trackways of the Coconino Sandstone (Lower Permian), Northern Arizona. In *Early Permian footprints and facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 219–224.

Braddy, S.J. (2004). Ichnological evidence for the arthropod invasion of land. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 136–140.

Braddy, S.J. and Almond, J.E. (1999). Eurypterid trackways from the Table Mountain Group (Ordovician) of South Africa. *Journal of African Earth Sciences*, 29, 165–177.

Braddy, S.J. and Briggs, D.E.G. (2002). New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. *Journal of Paleontology*, 76, 546–557.

Bradshaw, M.A. (1981). Palaeoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (Lower Beacon Supergroup), Antarctica. *New Zealand Journal of Geology and Geophysics*, 24, 615–652.

Bradshaw, M. and Harmsen, F. (2007). The paleoenvironmental significance of trace fossils in Devonian sediments (Taylor Group), Darwin Mountains to the Dry Valleys, southern Victoria Land. *US Geological Survey and The National Academies; USGS OF-2007–1047*, 15–19.

Brady, L.F. (1947). Invertebrate tracks from the Coconino Sandstone of northern Arizona. *Journal of Paleontology*, 21, 466–472.

Braithwaite, C.J.R. and Talbot, M.R. (1972). Crustacean burrows in the Seychelles, Indian Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 11, 265–285.

Brand, L.R. (1992). Reply to "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin". *Geology*, 20, 668–670.

Brand, L.R. and Kramer, J. (1996). Underprints of vertebrate and invertebrate trackways in the Permian Coconino Sandstone in Arizona. *Ichnos*, 4, 225–230.

Brand, L.R. and Tang, T. (1991). Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin. *Geology*, 19, 1201–1204.

Brandt, D.S., Meyer, D.L. and Lask, P.B. (1995). *Isotelus* (Trilobita) "hunting burrow" from Upper Ordovician strata, Ohio. *Journal of Paleontology*, 69, 1079–1083.

Brandt, D.S., Seitz, M., McCoy, V., Csonka, J., Barringer, J., Holmquist, E., Kraig, S., Morgan, R., Myers, J. and Paquette, L. (2010). A new ichnospecies of *Arthrophycus* from the Late Carboniferous (Pennsylvanian) of Michigan, USA. *Ichnos*, 17, 12–19.

Brasier, M.D., Cowe, J.W. and Taylor, M.E. (1994). Decision on the Precambrian–Cambrian boundary. *Episodes*, 17, 3–8.

Brenchley, P.J. and Harper, D.A.T. (1998). *Palaeoecology: Ecosystems, Environments and Evolution*. London: Chapman & Hall.

Brenchley, P.J., Pickerill, R.K. and Stromberg, S.G. (1993). The role of wave reworking on the architecture of storm sandstone facies, Bell Island Group (Lower Ordovician), eastern Newfoundland. *Sedimentology*, 40, 359–38.

Brenchley, P.J., Marshall, J.D. and Underwood, C.J. (2001). Do all mass extinctions represent an ecological crisis? Evidence from the Late Ordovician. *Geological Journal*, 36, 329–340.

Brett, C.E. (1990). Obrution Deposits. In *Palaeobiology: A Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 239–243.

Bridges, P.H. and Leeder, M.R. (1976). Sedimentary model for intertidal mudflat channels, with examples from the Solway Firth, Scotland. *Sedimentology*, 23, 533–552.

Briggs, D.E.G. and Clarkson, E.N.K. (1990). The late Palaeozoic radiation of malacostracan crustaceans. In *Major Evolutionary Radiations*, ed. P.D. Taylor and G.P. Larwood, *Systematics Association Special Volume*, 42, 165–186.

Briggs, D.E.G. and Fortey, R.A. (1989). The Early radiation and relationships of the major arthropod groups. *Science*, 246, 241–243.

Briggs, D.E.G., Fortey, R.A. and Wills, M.A. (1992). Morphologic disparity in the Cambrian. *Science*, 256, 1670–1673.

Bromham, L. (2006). Molecular dates for the Cambrian Explosion: is the light at the end of the tunnel an oncoming train? *Palaeontologia Electronica*, 9, 1–3.

Bromley, R.G. (1967). Some observations on burrows of thalassinidean Crustacea in chalk hardgrounds. *Quarterly Journal Geological Society of London*, 123, 157–182.

Bromley, R.G. (1970). Borings as trace fossils and *Entobia cretacea* Portlock, as an example. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 49–90.

Bromley, R.G. (1975). Trace fossils at omission surfaces. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 399–428.

Bromley, R.G. (1978). Bioerosion of Bermuda reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 169–197.

Bromley, R.G. (1979). Chalk and Bryozoan limestone: facies, sediments and depositional environments. In *Cretaceous–Tertiary Boundary Events Symposium, I: The Maastrichtian and Danian of Denmark*, ed. T. Birkelund and R.G. Bromley, Copenhagen: University of Copenhagen, pp. 16–32.

Bromley, R.G. (1981). Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispánica*, 16, 55–64.

Bromley, R.G. (1990). *Trace Fossils. Biology and Taphonomy*. London: Unwin Hyman.

Bromley, R.G. (1991). *Zoophycos*: Strip mine, refuse dump, cache or sewage farm? *Lethaia*, 24, 460–462.

Bromley, R.G. (1992). Bioerosion: eating rocks for fun and profit. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 121–129.

Bromley, R.G. (1993). Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis. Bulletin of the Geological Society of Denmark*, 40, 167–173.

Bromley, R.G. (1994). The palaeoecology of bioerosion. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 134–154.

Bromley, R.G. (1996). *Trace fossils. Biology, Taphonomy and Applications*. London: Chapman & Hall.

Bromley, R.G. (2001). Tetrapod tracks deeply set in unsuitable substrates; recent musk oxen in fluid earth (East Greenland) and Pleistocene caprines in aeolian sand (Mallorca). *Bulletin of the Geological Society of Denmark*, 48, 209–215.

Bromley, R.G. (2004). A stratigraphy of marine bioerosion. In *The application of Ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 455–479.

Bromley, R.G. (2005). Preliminary study of bioerosion in the deep-water coral *Lophelia*, Pleistocene, Rhodes, Greece. In *Cold-water Corals and Ecosystems*, ed. A. Freiwald, and J.M. Roberts, Berlin: Springer-Verlag, pp. 895–914.

Bromley, R.G. and Allouc, J. (1992). Trace fossils in bathyal hardgrounds, Mediterranean Sea. *Ichnos*, 2, 43–54.

Bromley, R.G. and Asgaard, U. (1972a). The burrows and microcoprolites of *Glyphea rosenkrantzi*, a Lower Jurassic palinuran crustacean from Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse Rapport*, 49, 15–21.

Bromley, R.G. and Asgaard, U. (1972b). Freshwater *Cruziana* from the Upper Triassic of Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse Rapport*, 49, 15–21.

Bromley, R.G. and Asgaard, U. (1975). Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bulletin of the Geological Society of Denmark*, 24, 261–281.

Bromley, R.G. and Asgaard, U. (1979). Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 28, 39–80.

Bromley, R.G. and Asgaard, U. (1991). Ichnofacies: a mixture of taphofacies and biofacies. *Lethaia*, 24, 153–163.

Bromley, R.G. and Asgaard, U. (1993a). Two bioerosion ichnofacies produced by early and late burial associated with sea-level change. *Geologische Rundschau*, 82, 276–280.

Bromley, R.G. and Asgaard, U. (1993b). Endolithic community replacement on a Pliocene rocky coast. *Ichnos*, 2, 93–116.

Bromley, R.G. and D'Alessandro, A. (1983). Bioerosion in the Pleistocene of Southern Italy: Ichnogenera *Caulostrepsis* and *Maeandropolydora*. *Rivista Italiana di Paleontologia e Stratigrafia*, 89, 283–309.

Bromley, R.G. and D'Alessandro, A. (1990). Comparative analysis of bioerosion in deep and shallow water, Pliocene to recent, Mediterranean Sea. *Ichnos*, 1, 43–49.

Bromley, R.G. and Ekdale, A.A. (1984a). Trace fossil preservation in flint in the European chalk. *Journal of Paleontology*, 58, 298–311.

Bromley, R.G. and Ekdale, A.A. (1984b). *Chondrites*: a trace fossil indicator of anoxia in sediments. *Science*, 224, 872–874.

Bromley, R.G. and Ekdale, A.A. (1986). Composite ichnofabrics and tiering of burrows. *Geological Magazine*, 123, 59–65.

Bromley, R.G. and Frey, R.W. (1974). Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. *Bulletin of the Geological Society of Denmark*, 23, 311–335.

Bromley, R.G. and Fürsich, F.T. (1980). Comments on the proposed amendments to the international Code of zoological nomenclature regarding ichnotaxa. Z.N.(S.) 1973. *Bulletin of Zoological Nomenclature*, 37, 6–10.

Bromley, R.G. and Hanken, N.M. (1991). The growth vector in trace fossils: examples from the Lower Cambrian of Norway. *Ichnos*, 1, 261–276.

Bromley, R.G. and Hanken, N.M. (2003). Structure and function of large, lobed *Zoophycos*, Pliocene of Rhodes, Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 79–100.

Bromley, R.G., Pemberton, S.G. and Rahmani, R.A. (1984). A Cretaceous woodground: the *Teredolites* ichnofacies. *Journal of Paleontology*, 58, 488–498.

Bromley, R.G., Jensen, M. and Asgaard, U. (1995). Spatangoid echinoids: deep-tier trace fossils and chemosymbiosis. *Neues Jahrbuch fr Geologie und Palontologie, Abhandlungen*, 195, 25–35.

Bromley, R.G., Ekdale A.A. and Asgaard, U. (1999). *Zoophycos* in the Upper Cretaceous chalk of Denmark and Sweden. *Greifswalder Geowissenschaftliche Beiträge*, 6, 133–142.

Bromley, R.G., Uchman, A. Gregory, M.R. and Martin, A.J. (2003). *Hillichnus lobosensis* igen. et isp. nov., a complex trace fossil produced by tellinacean bivalves, Paleocene, Monterey, California, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 157–186.

Bromley, R.G., Buatois, L.A., Genise, J.F., Labandeira, C.C., Mángano, M.G., Melchor, R.N., Schlirf, M. and Uchman, A. (2007). Comments on the paper "Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis. *Sedimentary Geology*, 200, 141–150.

Bromley R.G., Kedzierski, M., Kolodziej, B. and Uchman, A. (2009a). Large chambered sponge borings on a Late Cretaceous abrasion platform at Cracow, Poland. *Cretaceous Research*, 30, 149–160.

Bromley, R.G., Uchman, A., Milàn, J., and Hansen, K.S. (2009b). Rheotactic *Macaronichnus*, and human and cattle trackways in Holocene beachrock, Greece: Reconstruction of paleo- shoreline orientation. *Ichnos*, 16, 103–117.

Brown, A.C. and McLachlan, A. (1990). *Ecology of Sandy Shores*, Amsterdam: Elsevier.

Brown, D.E., Lowe, C.H. and Pase, C.P. (1979). A digitized classification system for the biotic communities of North America, with community (Series) and association examples for the Southwest. *Journal of the Arizona-Nevada Academy of Science*, 14, 1–16.

Bruck, P.M., Forbes, W.H., Nance, D. and Pickerill, R.K. (1985). *Beaconites antarcticus* in the (?Middle) Late Devonian McAras Brook Formation, Cape George, Nova Scotia. *Maritime Sediments and Atlantic Geology*, 21, 87–96.

Buatois, L.A. (1995). A new ichnospecies of *Fuersichnus* from the Cretaceous of Antarctica and its paleoecologic and stratigraphic implications. *Ichnos*, 3, 259–263.

Buatois, L.A. and Encinas, A. (2006). La icnofacies de *Glossifungites* en el contacto entre las formaciones Navidad (Miembro Rapel) y La cueva, Plioceno de la Cordillera de la Costa, Chile: su significado estratigráfico-secuencial. *Ameghiniana*, 43, 3–9.

Buatois, L.A. and Encinas, A. (2011). Ichnology, sequence stratigraphy and depositional evolution of an Upper Cretaceous rocky shoreline in central Chile: bioerosion structures in a transgressed metamorphic basement. *Cretaceous Research*, 32, 203–212.

Buatois, L.A. and López Angriman, A.O. (1992a). Trazas fósiles y sistemas deposicionales, Grupo Gustav, Cretácico de la isla James Ross, Antártida. In *Geología de la isla James Ross*, ed. C.A. Rinaldi, Buenos Aires: Publicación del Instituto Antártico Argentino, pp. 239–262.

Buatois, L.A. and López Angriman, A.O. (1992b). The ichnology of a submarine braided channel complex: The Whisky Bay Formation, Cretaceous, James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 94, 119–140.

Buatois, L.A. and Mángano, M.G. (1992). La oxigenación como factor de control en la distribución de asociaciones de trazas fósiles, Formacion Kotick Point, Cretácico de Antártida. *Ameghiniana*, 29, 69–84.

Buatois, L.A. and Mángano, M.G. (1993a). Trace fossils from a Carboniferous turbiditic lake: Implications for the recognition of additional nonmarine ichnofacies. *Ichnos*, 2, 237–258.

Buatois, L.A. and Mángano, M.G. (1993b). Ecospace utilization, paleoenvironmental trends and the evolution of early nonmarine biotas. *Geology*, 21, 595–598.

Buatois, L.A. and Mángano, M.G. (1995a). Postglacial lacustrine event sedimentation in an ancient high mountain setting: the Carboniferous Lake Malanzán from western Argentina. *Journal of Paleolimnology*, 12, 1–22.

Buatois, L.A. and Mángano, M.G. (1995b). The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. *Ichnos*, 4, 151–161.

Buatois, L.A. and Mángano, M.G. (1995c). Sedimentary dynamics and evolutionary history of a Late Carboniferous Gondwanic lake at Northwestern Argentina. *Sedimentology*, 42, 415–436.

Buatois, L.A. and Mángano, M.G. (1996). Icnología de ambientes continentales: Problemas y perspectivas. *Asociación Paleontológica Argentina, Publicación Especial*, 4, 5–30.

Buatois, L.A. and Mángano, M.G. (1998). Trace fossil analysis of lacustrine facies and basins. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 140, 367–382.

Buatois, L.A. and Mángano, M.G. (2000). Icnología: Aplicaciones de la icnología en prospección de hidrocarburos y caracterización de reservorios en la geología sedimentaria y la industria petrolera. *Boletín de Informaciones Petroleras*, 62, 64–85.

Buatois, L.A. and Mángano, M.G. (2002). Trace fossils from Carboniferous floodplain deposits in western Argentina: implications for ichnofacies models of continental environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183, 71–86.

Buatois, L.A. and Mángano, M.G. (2003a). Early colonization of the deep sea: Ichnologic evidence of deep-marine benthic ecology from the Early Cambrian of northwest Argentina. *Palaios*, 18, 572–581.

Buatois, L.A. and Mángano, M.G. (2003b). Caracterización icnológica y paleoambiental de la localidad tipo de *Orchesteropus atavus*, Huerta de Huachi, provincia de San Juán, Argentina: Implicancias en el debate sobre los ambientes de sedimentación en el Carbonífero de Precordillera. *Ameghiniana*, 40, 53–70.

Buatois, L.A. and Mángano, M.G. (2003c). Sedimentary facies and depositional evolution of the Upper Cambrian to Lower Ordovician Santa Rosita Formation in northwest Argentina. *Journal of South American Earth Sciences*, 16, 343–363.

Buatois, L.A. and Mángano, M.G. (2004a). Animal–substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 311–333.

Buatois, L.A. and Mángano, M.G. (2004b). Terminal Proterozoic–Early Cambrian ecosystems: ichnology of the Puncoviscana Formation, Northwest Argentina. In *Trace* Fossils in Evolutionary Palaeoecology, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils & Strata*, 51, 1–16.

Buatois, L.A. and Mángano, M.G. (2007). Invertebrate Ichnology of Continental Freshwater Environments. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 285–323.

Buatois, L.A. and Mángano, M.G. (2008a). Trazas fósiles de invertebrados. In *Invertebrados Fósiles*, ed. H. Camacho, Buenos Aires: Vázquez Manzzini Editores, pp. 751–785.

Buatois, L.A. and Mángano, M.G. (2008b). Continental ichnology and the marine–nonmarine transition. Ichnia 2008, 2nd International Congress on Ichnology, Craków, Poland, p. 22.

Buatois, L.A. and Mángano, M.G. (2009a). Applications of ichnology in lacustrine sequence stratigraphy: potential and limitations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 127–142.

Buatois, L.A. and Mángano, M.G. (2009b). The invertebrate trace fossil record of Mesozoic continental ecosystems. 10th International Symposium on Mesozoic Terrestrial Ecosystems, Abstract Volume, p. 41–42.

Buatois, L.A. and Mángano, M.G. (2010). The trace fossils record of organism-matground interactions in space and time. *Society for Sedimentary Geology Field Conference Abstracts, Microbial Mats in Siliciclastic Deposits (Archean to Today), Denver*, 14.

Buatois, L.A., Martinioni, D. and Lirio, J.M. (1993). Trazas fósiles en una plataforma dominada por tormentas, Formación Rabot (Cretácico superior – Punta Rabot, Isla James Ross, Antártida). *Segundas Reuniones de Comunicaciones Antárticas*, 163–166.

Buatois, L.A., Mángano, M.G. and Aceñolaza, F.G. (1996a). Icnofaunas paleozoicas en sustratos firmes no marinos: Evidencias del Pérmico de la cuenca Paganzo. *Ameghiniana*, 33, 265–270.

Buatois, L.A., Mángano, M.G., Wu X. and Zhang G. (1996b). Trace fossils from Jurassic lacustrine turbidites of the Anyao Formation (Central China) and their environmental and evolutionary significance. *Ichnos*, 4, 287–303.

Buatois, L.A., Jalfin, G. and Aceñolaza, F.G. (1997a). Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina: Ichnologic signatures of substrate consolidation and colonization sequences. *Journal of Paleontology*, 71, 324–336.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1997b). The paradox of nonmarine ichnofaunas in tidal rhythmites: Integrating sedimentologic and ichnologic data from the Late Carboniferous of eastern Kansas, USA. *Palaios*, 12, 467–481.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1998a). Ichnology of an Upper Carboniferous fluvio–estuarine paleovalley: the Tonganoxie Sandstone, Buildex Quarry, eastern Kansas. *Journal of Paleontology*, 71, 152–180.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1998b). Taxonomic reassessment of the ichnogenus *Beaconichnus* and additional examples from the Carboniferous of Kansas, USA. *Ichnos*, 5, 287–302.

Buatois, L.A., Mángano, M.G., Genise, J.F. and Taylor, T.N. (1998c). The ichnologic record of the invertebrate invasion of nonmarine ecosystems: evolutionary trends in ecospace utilization, environmental expansion, and behavioral complexity. *Palaios*, 13, 217–240.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1998d). Allostratigraphic and sedimentologic applications of trace fossils to the study of incised estuarine valleys: An example from the Virgilian Tonganoxie sandstone of eastern Kansas. *Current Research in Earth Sciences*, 241, 1–27.

Buatois, L.A., Mángano, M.G. and Carr, T.R. (1999). Sedimentology and ichnology of Paleozoic estuarine and shoreface reservoirs, Morrow Sandstone, Lower Pennsylvanian of Southwest Kansas, USA. *Current Research in Earth Sciences*, 241, 1–27.

Buatois, L.A., Mángano, M.G., Fregenal-Martinez, M.A. and Gibert, J.M. de (2000). Short-term colonization trace-fossil assemblages in a carbonate lacustrine konservat–lagerstätte (Las Hoyas fossil site, Lower Cretaceous, Cuenca, central Spain). Facies, 43, 145–156.

Buatois, L.A., Mángano, M.G. and Sylvester, Z. (2001). A diverse deep marine ichnofauna from the Eocene Tarcau Sandstone of the Eastern Carpathians, Romania. *Ichnos*, 8, 23–62.

Buatois, L.A., Mángano, M.G. and Aceñolaza, F.G. (2002a). *Trazas fósiles: Señales de comportamiento en el registro estratigráfico*. Trelew, Argentina: Museo Paleontológico Egidio Feruglio.

Buatois, L.A., Mángano, M.G., Alissa, A. and Carr, T.R. (2002b). Sequence stratigraphic and sedimentologic significance of biogenic structures from a late Paleozoic marginal to open-marine reservior, Morrow Sandstone, subsurface of southwest Kansas, USA. *Sedimentary Geology*, 152, 99–132.

Buatois, L.A., Bromley, R.G., Mángano, M.G., Bellosi, E. and Carmona, N.B. (2003). Ichnology of shallow marine deposits in the Miocene Chenque Formation of Patagonia: Complex ecologic structure and niche partitioning in Neogene ecosystems. *In Icnología: Hacia una convergencia entre geología y biología*, ed. L.A. Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 85–95.

Buatois, L.A., Gingras, M.K., MacEachern, J., Mángano, M.G., Zonneveld, J.-P, Pemberton, S.G., Netto, R.G. and Martin, A.J. (2005). Colonization of brackish-water systems through time: Evidence from the trace-fossil record. *Palaios*, 20, 321–347.

Buatois, L.A., Netto, R.G., Mángano, M.G., Balistieri, P. (2006a). Extreme freshwater release during the late Paleozoic Gondwana deglaciation and its impact on coastal ecosystems. *Geology*, 34, 1021–1024.

Buatois, L.A., Zeballo, F.J., Albanesi, G.L., Ortega, G., Vaccari, N.E. and Mángano, M.G. (2006b). Depositional environments and stratigraphy of the upper Cambrian-Lower Ordovician Santa Rosita Formation at the Alfarcito area, Cordillera Oriental, Argentina: Integration of Bioestratigraphy data within a sequence stratigraphic framework. *Latin American Journal of Sedimentology and Basin Analysis*, 13, 1–29.

Buatois, L.A., Uba, C.E., Mángano, M.G. and Hulka, C. (2007a). Deep bioturbation in continental environments: Evidence from Miocene fluvial deposits of Bolivia. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 123–136.

Buatois, L.A., Netto, R.G. and Mángano, M.G. (2007b). Ichnology of Permian marginal-marine to shallow-marine coal-bearing successions: Rio Bonito and Palermo Formations, Parana basin, Brazil. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 167–177.

Buatois, L.A., Almond, J., Gresse, P. and Germs, G. (2007c). The Elusive Proterozoic-Cambrian boundary: Ichnologic data from Vanrynsdorp Group of South Africa. In *IX International Ichnofabric Workshop*, *Abstracts with Program*, ed. J.P. Zonneveld and M.K. Gingras, Calgary, 8–9.

Buatois, L.A., Santiago, N., Parra, K. and Steel, R. (2008). Animal–substrate interactions in an Early Miocene wave-dominated tropical delta: delineating environmental stresses and depositional dynamics (Tácata field, eastern Venezuela). *Journal of Sedimentary Research*, 78, 458–479.

Buatois, L.A., Macsotay, O. and Quiroz, L. (2009a). The trace fossil *Sinusichnus* in Antarctica and Venezuela: expanding the dataset of crustacean burrows. *Lethaia*, 42, 511–518.

Buatois, L.A., Mángano, M.G., Brussa, E., Benedetto, J.L. and Pompei, J. (2009b). The changing face of the deep: Colonization of the Early Ordovician deep-sea floor, Puna, northwest Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 280, 291–299.

Buatois, L.A., Netto, R. and Mángano, M.G (2010a). Ichnology of late Paleozoic post-glacial transgressive deposits in Gondwana: reconstructing salinity conditions in coastal ecosystems affected by strong meltwater discharge. In *Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana*, ed. O. Lopez Gamundi and L.A. Buatois, *Geological Society of America Special Paper*, 468, 149–173.

Buatois, L.A., Mángano, M.G. and Pattison, S. (2010b). Trace fossils from a prodeltaic channel and lobe complex, Aberdeen and Kenilworth members, Upper Cretaceous, Book Cliffs, Utah: Ichnologic signatures of turbidites and hyperpycnites in deltaic systems. *18th International Sedimentological Congress, Sedimentology at the Foot of the Andes, Abstracts*.

Buatois, L.A. Saccavino, L.L. and Zavala, C. (2011). Ichnologic signatures of hyperpycnal-flow deposits in Cretaceous river-dominated deltas, Austral Basin, southern Argentina. In *Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology*, 61, in press.

Buck, S.G. and Goldring, R. (2003). Conical sedimentary structures, trace fossils or not? Observations experiments and review. *Journal of Sedimentary Research*, 73, 338–353.

Buckman, J.O. (1994). *Archaeonassa* Fenton and Fenton 1937 reviewed. *Ichnos*, 3, 185–192.

Buckman, J.O. (1996). *Heimdallia* from the Lower Carboniferous of Ireland: *H. mullaghmori* a new ichnospecies, and re-evaluation of the three-dimensional format of the ichnogenus. *Ichnos*, 5, 43–51.

Budd, G.E. (2003). The Cambrian fossil record and the origin of phyla. *Integrative and Comparative Biology*, 43,157–165.

Budd, G.E. and Jensen, S. (2000). A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Review* 75, 253–295.

Budd, G.E. and Jensen, S. (2004). The limitations of the fossil record and the dating of the origin of the Bilateria. In *Telling the Evolutionary Time: Molecular Clocks and the Fossils Record*, ed. P.C.I. Donoghue and M.P. Smith, London: Taylor and Francis, pp. 166–189.

Bujok, A., Sadlok, G. and Pieńkowski, G. (2008). Stop 4, Baranów, Lower Triassic, Upper Spathian. In *Second International Congress on ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Moiuntains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 54–59.

Bull, W.B. (1977). The alluvial-fan environment. *Progress in Physical Geography*, 1, 222–270.

Burzin, M.B., Debrenne, F. and Zhuravlev, A.Y. (2000). Evolution of shallow-water level-bottom communities. In *The Ecology of the Cambrian Radiation*, ed. A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, pp. 217–237.

Buscombe, D. and Masselink, G. (2006). Concepts in gravel beach dynamics. *Earth Science Reviews*, 79, 33–52.

Bush, A.M., Bambach, R.K. and Daley, G.M. (2007). Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology*, 33, 76–97.

Butterfield, N.J. (2001). Ecology and evolution of Cambrian plankton. In *The Ecology of the Cambrian Radiation*, A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, pp. 217–237.

Byers, C.W. (1977). Biofacies patterns in euxinic basins: A general model. In *Deep-Water Carbonate Environments*, ed. H.E. Cook and P. Enos, *Society for Sedimentary Geology Special Publication*, 25, 5–17.

Cadée, G.C. (1998). Influence of benthic fauna and microflora. In *Intertidal Deposits: River Mouths, Tidal Flats, and Lagoons*, ed. D. Eisma, Boca Raton: CRC Press, pp. 383–402.

Cadée, G.C. and Goldring, R. (2007). The Wadden Sea, cradle of invertebrate ichnology. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 3–13.

Calafat, F., Fornós, J.J., Marzo, M., Ramos-Guerrero, E. and Rodríguez-Perea, A. (1986). Icnología de vertebrados de la facies Buntsandstein de Mallorca. *Acta Geológica Hispánica*, 21, 515–520.

Campbell, K.A., Nesbitt, E.A. and Bourgeois, J. (2006). Signatures of storms, oceanic floods and forearc tectonism in marine shelf strata of the Quinault Formation (Pliocene), Washington, USA. *Sedimentology*, 53, 945–969.

Cañas, F. (1995). Early Ordovician carbonate platform facies of the Argentine Precordillera: Restricted shelf to open platform evolution. In *Ordovician Odyssey*, ed. J.D. Cooper, M.L. Droser and S.C. Finney, *Society for Sedimentary Geology Pacific Section*, 77, 221–224.

Carew, J.L. and Mylroie, J.E. (2001). Quaternary carbonate eolianites of the Bahamas: useful analogs for the interpretation of ancient rocks? In *Modern and Ancient Carbonate Eolianites: Sedimentology, Sequence Stratigraphy, and Diagenesis*, ed. F.E. Abegg, D.B. Loope and P.M. Harris, *Society for Sedimentary Geology Special Publications*, 71, 33–45.

Carmona, N.B. and Buatois, L.A. (2003). Estructuras de crustáceos en el Mioceno de la Cuenca del Golfo San Jorge: Implicancias Paleobiológicas y Evolutivas. In *Icnología: Hacia una convergencia entre geología y biología,* ed. L.A. Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 97–108.

Carmona, N.B. and Ponce, J.J. (2011). Ichnology and Sedimentology of the foreland Austral Basin (Tierra del Fuego, Argentina): Trace-fossil distribution and paleoecological implications. In *Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology*, 61, in press.

Carmona, N.B., Buatois, L.A. and Mángano, M.G. (2004). The trace fossil record of burrowing decapods crustaceans: evaluating evolutionary radiations and behavioural convergence. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 141–153.

Carmona, N.B., Ponce, J.J., Mángano, M.G. and Buatois, L.A. (2006). Variabilidad de la icnofacies de *Glossifungites* en el contacto entre las Formaciones Sarmiento (Eoceno medio-Mioceno temprano) y Chenque (Mioceno temprano) en el Golfo San Jorge, Chubut, Argentina. *Ameghiniana*, 43, 413–425.

Carmona, N.B., Mángano, M.G., Buatois, L.A. and Ponce, J.J. (2007). Bivalve trace fossils in an early Miocene discontinuity surface in Patagonia, Argentina: Burrowing behavior and implications for ichnotaxonomy at the firmground–hardground divide. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255, 329–341.

Carmona, N.B., Buatois, L.A., Mángano, M.G., and Bromley, R.G. (2008). Ichnology of the Lower Miocene Chenque Formation, Patagonia, Argentina: Animal–substrate interactions and the Modern Evolutionary Fauna. *Ameghiniana*, 45, 93–122.

Carmona, N.B., Buatois, L.A., Ponce, J.J. and Mángano, M.G. (2009). Ichnology and sedimentology of a tide-influenced delta, Lower Miocene Chenque Formation, Patagonia, Argentina: Trace-fossil distribution and response to environmental stresses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273, 75–86.

Carmona, N.B., Mángano, M.G., Buatois, L.A. and Ponce, J.J. (2010). Taphonomy and paleoecology of the bivalve trace fossil *Protovirgularia* in deltaic heterolithic facies of the Miocene Chenque Formation, Patagonia, Argentina. *Journal of Paleontology*, 84, 730–738.

Carney, R.S. (1981). Bioturbation and Biodeposition. In *Principles of Benthic Marine Paleoecology*, ed. A.J. Boucot, New York: Academic Press, pp. 357–399.

Caron, J.B., Gaines, R.R., Mángano, M.G., Streng, M. and Daley, A.C. (2010). A new Burgess Shale-type assemblage from the thin Stephen Formation of the Southern Canadian Rockies. *Geology*, 38, 811–814.

Carrano, M.T. and Wilson, J.A. (2001). Taxon distributions and the tetrapod track record. *Paleobiology*, 27, 564–582.

Carvalho, I.S. (1996). As pegadas de dinossauros da Bacia de Uiraúna-Brejo das Freiras (Cretáceo Inferior, Estado da Paraíba). *4º Simposio sobre o Cretáceo do Brasil (Aguas de São Pedro), Boletim*, 115–121.

Carvalho, I.S., Viana, M.S.S. and Lima Filho, M.F. (1995). Os icnofósseis de Dinossauros da Bacia do Araripe (Cretáceo Inferior, Ceará-Brasil). *Anais da Academia brasileira de Ciencias*, 67, 433–442.

Cattaneo, A. and Steel, R.J. (2003). Transgressive deposits: a review of their variability. *Earth Science Reviews*, 1277, 1–43.

Catuneanu, O. (2006). *Principles of Sequence Stratigraphy*. Amsterdam: Elsevier.

Caumette, P. (1986). Phototrophic sulfur bacteria and sulfatereducing bacteria causing red waters in a shallow brackish coastal lagoon (Prévost Lagoon, France). *FEMS Microbiology Letters*, 38, 113–124.

Chamberlain, C.K. (1971). Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. *Journal of Paleontology*, 45, 212–246.

Chamberlain, C. K. (1975). Recent lebensspuren in nonmarine aquatic environments. In *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 431–458.

Chamberlain, C.K. (1978). Recognition of trace fossils in cores. In *Trace Fossil Concepts*, ed. P.B. Basan, *Society for Sedimentary Geology Short Course Notes*, 5, 119–166.

Chiappe, L.M., Jackson, F., Coria, R.A. and Dingus, L. (2005). Nesting Titanosaurs from Auca Mahuevo and Adjacent Sites: Understanding Sauropod Reproductive Behaviour and Embryonic Development. In *The Sauropods: Evolution and Paleobiology*, ed. K.A. Curry Rogers and J.A. Wilson, Berkley, CA: University of California Press, pp. 285–302.

Chiappe, L.M., Schmitt, J.G., Jackson, F.D., Garrido, A., Dingus, L. and Grellet-Tinner, G. (2004). Nest Structure for Sauropods: Sedimentary criteria for recognizing dinosaur nesting traces. *Palaios*, 19, 89–95.

Clack, J.A. (2002). *Gaining Ground: The Origin and Evolution of Tetrapods*. Bloomington, IN: Indiana University Press.

Clack, J.A. (2005). Making headway and finding a foothold: tetrapods come ashore. In *Evolving Form and Function: Fossils and Development*, ed. D.E.G. Briggs, *Peabody Museum of Natural History Special Publications*, 223–244.

Clapham, M.E., Narbonne, G.M. and Gehling, J.G. (2003). Paleoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology*, 29, 527–544.

Clarkson, E.N.K. (1992). *Invertebrate Palaeontology and Evolution*. London: Chapman & Hall.

Clemmensen, L.B., Kent, D.V. and Jenkins, F.A. Jr. (1998). A Late Triassic lake system in East Greenland: facies, depositional cycles and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 140, 135–159.

Clemmey, H. (1976). World's oldest animal traces. *Nature*, 261, 576–578.

Clifton, H.E. (2006). A Reexamination of Facies Models for Clastic Shorelines. In: *Facies Models Revisited*, ed. H.W. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 293–337.

Clifton, H.E. and Thompson, J.K. (1978). *Macaronichnus segregatis*: A feeding structure of shallow marine polychaetes. *Journal of Sedimentary Petrology*, 48, 1293–1302.

Clifton, H.E., Hunter, R.E. and Phillips, R.L. (1971). Depositional structures and processes in the non-bar high energy nearshore. *Journal of Sedimentary Petrology*, 41, 651–670.

Cloud, P., Gustafson, L.B. and Watson, J.A. (1980). The works of living social insects as pseudofossils and the age of the oldest known Metazoa. *Science*, 210, 1013–1015.

Cloudsey-Thompson, J.L. (1991). *Ecophysiology of Desert Arthropods and Reptiles*. New York: Springer-Verlag.

Cohen, A.S. (1982). Paleoenvironments of root casts from the Koobi For a Formation, Kenya. *Journal of Sedimentary Petrology*, 52, 401–414.

Cohen, A.S. (2003). *Paleolimnology: The History and Evolution of Lake Systems*. New York: Oxford University Press.

Cohen, A.S., Lockley, M., Halfpenny, J. and Michel, E. (1991). Modern vertebrate track taphonomy at Lake Manyara, Tanzania. *Palaios*, 6, 371–389.

Cohen, A.S., Halfpenny, J., Lockley, M. and Michel, E. (1993). Modern vertebrate tracks from Lake Manyara, Tanzania and their paleobiological implications. *Paleobiology*, 19, 433–458.

Coleman, F.C. and Williams, S.L. (2002). Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution*, 17, 40–44.

Conway Morris, S. (1989). The persistence of Burgess Shale-type faunas: implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 80, 271–283.

Conway Morris, S. (2000). The Cambrian "explosion": Slow-fuse or megatonnage? *Proceedings of the National Academy of Sciences, USA*, 97, 4426–4429.

Conway Morris, S. (2002). Ancient animals or something else entirely? *Science*, 298, 57–58.

Conway Morris, S. and Bengtson, S. (1994). Cambrian predators: possible evidence from boreholes. *Journal of Paleontology*, 68, 1–23.

Conybeare, D.M., Cannon, S., Karaouz, S. and Uygur, E. (2004). Reservoir modelling of the Hamitabat Field, Thrace Basin, Turkey: an example of a sand-rich turbidite system. In *Confined Turbidite Systems*, ed. S.A. Lomas and P. Joseph, *Geological Society Special Publication*, 222, 307–320.

Cook, A.G. and Bann, K. (2000). Trace fossils from the upper Carboniferous Jericho Formation, Central Queensland. *Memoirs of the Queensland Museum*, 45, 235–251.

Corbeanu, R.M., Wizevich, M.C., Bhattacharya, J.P., Zeng, X. and McMechan, G.A. (2004). Three-dimensional architecture of ancient lower delta-plain point bars using ground-penetrating radar, Cretaceous Ferron Sandstone, Utah. In *Regional to Wellbore Analog for Fluvial-Deltaic Reservoir Modeling: The Ferron Sandstone of Utah*, ed. J.T.C. Chidsey, R.D. Adams and T.H. Morris, *American Association of Petroleum Geologists Studies in Geology*, 50, 285–309.

Corner, G.D. and Fjalstad, A. (1993). Spreite trace fossils (*Teichichnus*) in a raised Holocene fjord-delta, Breidvikeidet, Norway. *Ichnos*, 2, 155–164.

Cornish, F. G. (1986). The trace-fossil *Diplocraterion*: evidence of animal–sediment interactions in Cambrian tidal deposits. *Palaios*, 1, 478–491.

Cosarinsky, M.I. (2003). Micromorphology of the nest of *Cornitermes cumulans* Kollar (Isoptera, Termitidae). In *Icnología: Hacia una convergencia entre geología y biología*, ed. L.A. Buatois and M.G. Mángano, *Publicación Especial Asociación Paleontológica Argentina*, 9, 53–64.

Cotton, W.D., Hunt, A.P. and Cotton, J.E. (1995). Paleozoic vertebrate tracksites in eastern North America. *New Mexico Museum of Natural History and Science Bulletin*, 6, 189–211.

Crame, J.A. (1990). Trophic structure. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Boston, MA, and Oxford, UK: Blackwell, pp. 385–390.

Crawford, C.S. (1988). Surface-active arthropods in a desert landscape: Influences of microclimate, vegetation, and soil texture on assemblage structure. *Pedobiologia*, 32, 373–385.

Crimes, T.P. (1969). Trace fossils from the Cambro–Ordovician rocks of North Wales and their stratigraphic significance. *Geological Journal*, 6, 333–337.

Crimes, T.P. (1970a). Trilobite tracks and other trace fosils from the Upper Cambrian of North Wales. *Geological Journal*, 7, 47–68.

Crimes, T.P. (1970b). The significance of trace fossils in sedimentology, stratigraphy and palaeoecology, with examples from Lower Palaeozoic strata. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 101–126.

Crimes, T.P. (1974). Colonisation of the early ocean floor. *Nature*, 248, 328–330.

Crimes, T.P. (1975). The stratigraphical significance of trace fossils. In *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 109–130.

Crimes, T.P. (1977). Trace fossils of an Eocene deep-sea sand fan. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 71–90.

Crimes, T.P. (1987). Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geological Magazine*, 124, 97–119.

Crimes, T.P. (1992). The record of trace fossils across the Proterozoic-Cambrian boundary. In *Origin and Early Evolution of the Metazoa*, ed. J.H. Lipps and P.W. Signor, New York: Plenum Press, pp. 177–199.

Crimes, T.P. (1994). The period of early evolutionary failure and the dawn of evolutionary success. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 105–133.

Crimes, T.P. (2001). Evolution of the deep-water benthic community. In *The Ecology of the Cambrian Radiation*, ed. A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, 275–290.

Crimes, T.P. and Anderson, M.M. (1985). Trace fossils from Late Precambrian–Early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications. *Journal of Paleontology*, 59, 310–343.

Crimes, T.P. and Crossley, J.D. (1991). A diverse ichnofauna from Silurian flysch of the Aberystwyth Grits Formation, Wales. *Geological Journal*, 26, 27–64.

Crimes, T.P. and Fedonkin, M.A. (1994). Evolution and dispersal of deepsea traces. *Palaios*, 9, 74–83.

Crimes, T.P. and Fedonkin, M.A. (1996). Biotic changes in platform communities across the Precambrian-Phanerozoic boundary. *Revista italiana di Paleontologia e Stratigrafia*, 102, 317–332.

Crimes, T.P. and Germs, G.J.B. (1982). Trace fossils from the Nama Group (Precambrian-Cambrian) of southwest Africa (Namibia). *Journal of Paleontology*, 56, 890–907.

Crimes, T.P. and Jiang, Z. (1986). Trace fossils from the Precambrian-Cambrian boundary candidate at Meishucun, Jinning, Yunnan, China. *Geological Magazine*, 36, 633–642.

Crimes, T.P. and McCall, G.J.H. (1995). A diverse ichnofauna from Eocene-Miocene rocks of the Makran Range (S.E. Iran). *Ichnos*, 3, 231–258.

Crimes, T.P. and McIlroy, D. (1999). An Ediacaran biota from lower Cambrian strata on the Digermul Peninsula, Arctic Norway. *Geological Magazine*, 36, 633–642.

Crimes, T.P. and Marcos, A. (1976). Trilobite traces and the age of the lowest part of the Ordovician reference section for NW Spain. *Geological Magazine*, 113, 349–356.

Crimes, T.P., Legg, I., Marcos, A. and Arboleya, M. (1977). Late Precambrian–low Lower Cambrian trace fossils from Spain. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 91–138.

Crimes, T.P., Goldring, R., Homewood, P., Van Stuijvenberg, J. and Winkler, W. (1981). Trace fossil assemblages of deep-sea fan deposits, Gurnigel and Schlieren flysch (Cretaceous–Eocene), Switzerland. *Eclogae Geologicae Helvetiae*, 74, 953–995.

Crimes, T.P., García Hidalgo J.F. and Poiré D.G. (1992). Trace fossils from Arenig flysch sediments of Eire and their bearing on the early colonisation of the deep seas. *Ichnos*, 2, 61–77.

Croghan, P.C. (1983). Osmotic regulation and the evolution of brackish- and fresh-water faunas. *Journal of the Geological Society, London*, 140, 39–46.

Cunningham, K.J., Sukop, M.C., Huang, H., Alvarez, P.F., Curran, H.A., Renken, R.A. and Dixon, J.F. (2009). Prominence of ichnologically influenced macroporosity in the karst Biscayne aquifer: Stratiform 'super-K' zones. *Geological Society of America, Bulletin*, 121, 164–180.

Curran, H.A. (1984). Ichnology of Pleistocene carbonates on San Salvador, Bahamas. *Journal of Paleontology*, 58, 312–321.

Curran, H.A. (1992). Trace fossils in Quaternary, Bahamian-Style Carbonate Environments: the Modern to Fossil transition. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 105–120.

Curran, H.A. (1994). The palaeobiology of ichnocoenoses in Quaternary, Bahamian-Style carbonate environments: The Modern to Fossil transition. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 83–104.

Curran, H.A. (2007). Ichnofacies, ichnocoenoses and ichnofabrics of Quaternary shallow-marine to dunal tropical carbonates: a model and implications. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 232–247.

Curran, H.A. and Harris, L.A. (1996). Bioturbation of carbonate lagoonal sediments by callianassid shrimp: Examples from the Bahamas. *Geological Society of America, Abstracts with Programs*, 28, A-274.

Curran, H.A. and Martin, A.J. (2003). Complex decapod burrows and ecological relationships in Modern and Pleistocene intertidal carbonate environments, San Salvador Island, Bahamas. *Palaeogeography, Palaeoclimatology, Paleoecology*, 192, 229–245.

Curran, H.A. and White, B. (1991). Trace fossils of shallow subtidal to dunal ichnofacies in Bahamian Quaternary carbonates. *Palaios*, 6, 498–510.

Curran, H.A. and White, B. (1997). A *Conichnus conicus*-generated ichnofabric in the late Pleistocene limestones at Clifton Pier, New Providence Island, Bahamas. In *Guide to Bahamian Ichnology: Pleistocene, Holocene and Modern Environments*, ed. H.A. Curran, San Salvador: Bahamian Field Station, pp. 55–61.

Curran, H.A. and White, B. (2001). Ichnology of Holocene carbonate eolianites of the Bahamas. In *Modern and Ancient Carbonate Eolianites: Sedimentology, Sequence Stratigraphy and Diagenesis*, ed. F.E. Abegg, P.M. Harris and D.B. Loope, *Society for Sedimentary Geology Special Publication*, 71, 47–56.

Currie, P.J., Badamgarav, D. and Koppelhu, E.B. (2003). The first Late Cretaceous footprints from the Nemegt locality in the Gobi of Mongolia. *Ichnos*, 10, 1–12.

Cushing, C.E. and Allan, D. (2001). *Streams: Their Ecology and Life.* San Diego, CA: Academic Press.

D'Alessandro, A. (1980). Prime osservazioni sulla ichnofauna Miocenica della formazione di Gorgoglione' (Castelmezzano, Potenza). *Rivista Italiana di Paleontologia*, 86, 357–398.

D'Alessandro, A. and Bromley, R.G. (1987). Meniscate trace fossils and the *Muensteria–Taenidium* problem. *Palaeontology*, 30, 743–763.

D`Alessandro, A., Ekdale, A.A. and Sonnino, M. (1986). Sedimentologic significance of turbidite ichnofacies in the Saraceno Formation (Eocene), Southern Italy. *Journal of Sedimentary Petrology*, 56, 294–206.

D'Alessandro, A., Ekdale, A.A. and Picard, M.D. (1987). Trace fossils in fluvial deposits of the Duchesne River Formation (Eocene), Uinta Basin, Utah. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 61, 285–301.

Dale, J.E., Aitken, A.E., Gilbert, R. and Risk, M.J. (1989). Macrofauna of Canadian arctic fjords. *Marine Geology*, 85, 331–358.

Daley, B. (1968). Sedimentary structures from a non-marine horizon in the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire, England. *Journal of Paleontology*, 38, 114–127.

Dalrymple, R.W. (1992). Tidal depositional systems. In *Facies Models and Sea Level Changes*, ed. R.G. Walker and N.P. James, St. John's, Canada: Geological Association of Canada, 195–218.

Dalrymple, R.W. (2006). Incised-valleys in time and space: An introduction to the volume and an examination of the controls on valley formation and filling. In *Incised Valleys in Time and Space* ed. R.W. Dalrymple, D.A. Leckie and R.W. Tillman, *Society for Sedimentary Geology Special Publications*, 85, 5–12.

Dalrymple, R.W. and Choi, K. (2007). Morphologic facies trends through the fluvial-marine transition in tide-dominated depositional systems: A schematic framework for environmental and sequence-stratigraphic interpretation. *Earth Science Reviews*, 81, 135–174.

Dalrymple, R.W. and Rhodes, R.N. (1995). Estuarine dunes and bars. *Geomorphology and Sedimentology of Estuaries, Developments in Sedimentology*, 53, 359–406.

Dalrymple, R.W., Knight, R.J., Zaitlin, B.A. and Middleton, G.V. (1990). Dynamics and facies model of a macrotidal sand-bar complex, Cobequid Bay-Salmon River estuary, (Bay of Fundy). *Sedimentology*, 37, 577–612.

Dalrymple, R.W., Zaitlin, B.A. and Boyd, R. (1992). Estuarine facies models: conceptual basis and stratigraphic implications. *Journal of Sedimentary Petrology*, 62, 1130–1146.

Dalrymple, R.W., Baker, E.K., Harris, P.T. and Hughes, M.G. (2003). Sedimentology and stratigraphy of a tide-dominated foreland-basin delta (Fly River, Papua New Guinea). In *Tropical Deltas of Southeast Asia: Sedimentology, Stratigraphy and Petroleum Geology*, ed. F.H. Sidi, D. Nummedal, P. Imbert, H. Darman and H.W. Posamentier, *Society for Sedimentary Geology Special Publication*, 76, 147–173.

Dam, G. (1990). Paleoenvironmental significance of trace fossils from the shallow marine Lower Jurassic Neill Klinter Formation, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 79, 221–248.

Dam, G. and Stemmerik, L. (1994). East Greenland lacustrine complexes. In *Global Geological Record of Lake Basins 1*, ed. E. Gierlowski-Kordesch and K. Kelts, Cambridge, UK: Cambridge University Press, 19–27.

Damiani, R., Modesto, S., Yates, A. and Neveling, J. (2003). Earliest evidence of cynodont burrowing, *Proceedings of the Royal Society B: Biological Sciences*, 270, 1747–1751.

Darwin, C. (1881). *The Formation of Vegetable Mould, Through the Action of Worms*. London: John Murray.

Dashtgard, S.E. and Gingras, M.K. (2005). Facies architecture and ichnology of recent salt-marsh deposits: Waterside Marsh, New Brunswick, Canada. *Journal of Sedimentary Research*, 75, 596–607.

Dashtgard, S.E., Gingras, M.K. and MacEachern, J.A. (2009). Tidally modulated shorefaces. *Journal of Sedimentary Research*, 79, 793–807.

Dashtgard, S.E., MacEachern, J.A., Frey, S.E. and Gingras, M.K. (2011). Tidal effects on the shoreface: Towards a conceptual framework. *Sedimentary Geology*, in press.

Davies, N.S. and Gibling, M.R. (2009). Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. *Earth Science Reviews*, 98, 171–200.

Davies, N.S., Sansom, I.J. and Turner, P. (2006). Trace fossils and paleoenvironments of a Late Silurian marginal-marine/alluvial system: the Ringerike Group (Lower Old Red Sandstone), Oslo region, Norway. *Palaios*, 21, 46–62.

Davies, N.S., Rygel, M.C. and Gibling, M.R. (2010). Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): Implications for the history of life on land. *Palaios*, 25, 527–539.

Davis, R.B., Minter, N. and Braddy, S. (2007). The neoichnology of terrestrial arthropods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255, 284–307.

Debriette, P. and Gand, G. (1990). Stratigraphic and paleoenvironmental results from new paleontological observations made in the Permian of the western part of the Lodève basin (South Massif Central). *Géologie de la France*, 19–32.

de Boer, P.L. (1998). Intertidal sediments: composition and structure. In *Intertidal Deposits: River Mouths, Tidal Flats and Coastal Lagoons*, ed. D. Eisma, *Marine Science Series*, 912–921.

de Mowbray, T. (1983). The genesis of lateral accretion deposits in recent intertidal mudflat channels, Solway Firth, Scotland. *Sedimentology*, 30, 425–435.

Delgado, M., Kabbabe, T., Sampson, E. and Chacartegui, F. (2001). Ichnofossils as a tool for environmental interpretation, Pauji and Misoa formations, Barúa and Motatán fields, Zulia and Trujillo states, Venezuela. *VI International Ichnofabric Workshop Abstarcts, Isla Margarita & Puerto La Cruz*, 27.

Demathieu, G. (1977). La palichnologie de vertebras. Developpement recent et role dans la stratigraphie du Trias. *Bulletin du Bureau Recherches Geologiques et Minires*, 3, 269–278.

Demathieu, G. (1984). Une ichnofaune du Trias moyen du basin de Lodve (Hrault, France). *Annales de Palontologie*, 70, 247–273.

Demathieu, G. (1989). Appearance of the first dinosaur tracks in the French Middle Triassic and their probable significance. In *Dinosaur tracks and traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 201–207.

Demathieu, G. (1994). Synthèse géologique du Sud-Est de la France: Donées bistratigraphiques. *Mémoire du Bureau de Recherches Géologiques et Minières*, 125, 63–64.

Demathieu, G. and Demathieu, P. (2004). *Chirotheria* and other ichnotaxa of the European Triassic. *Ichnos*, 11, 79–88.

Demathieu, G., Gand, G. and Toutin-Morin, N. (1992). La palichnofaune des basins permiens provencaux. *Geobios*, 25, 19–54.

Demircan, H. and Toker, V. (2003). Trace fossils in the western fan of the Cingoz Formation in the northern Adana Basin (Southern Turkey). *Mineral Research and Exploration Bulletin*, 127, 15–32.

Desjardins, P.R., Mángano, M.G., Buatois, L.A. and Pratt, B.R. (2010a). *Skolithos* pipe rock and associated ichnofabrics from the southern Rocky Mountains, Canada: colonization trends and environmental controls in an early Cambrian sand-sheet complex. *Lethaia*, 214, 507–528.

Desjardins, P.R., Buatois, L.A., Mángano, M.G. and Limarino, C.O. (2010b). Ichnology of the latest Carboniferous – earliest Permian transgression in the Paganzo Basin of western Argentina: The changing ecology of sea-level rise during postglacial times in Gondwana. In *Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana*, ed. O. Lopez Gamundi, and L.A. Buatois, *Geological Society of America Special Paper*, 468, 175–192.

Dewitt, T.H., D'Andrea, A.F., Brown, C.A., Griffin, B.D. and Eldridge, P.M. (2004). Impact of burrowing shrimp populations on nitrogen cycling and water quality in western North American temperate estuaries. In *Proceedings of the Symposium on "Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments-from Individual Behaviour to their Role as Ecosystem Engineers*, ed. A. Tamaki, Nagasaki University, Nagasaki, pp. 107–118.

DiMichele, W.A. and Aronson, R.B. (1992). The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore–offshore hypothesis. *Evolution*, 46, 807–824.

Domènech, R., Gibert, J.M. de and Martinell, J. (2001). Ichnological features of a marine transgression: Middle Miocene rocky shores of Tarragona, Spain. *Geobios*, 34, 99–107.

Donovan, S.K. (1994) (ed.). *The Palaeobiology of Trace Fossils*. Chichester, UK: John Wiley & Sons.

Dornbos, S.Q., Bottjer, D.J. and Chen, J.Y. (2004). Evidence for seafloor microbial mats and associated metazoan lifestyles in Lower Cambrian phosphorites of Southwest China. *Lethaia*, 37, 127–137.

Dornbos, S.Q., Bottjer, D.J. and Chen, J.Y. (2005). Paleoecology of benthic metazoans in the Early Cambrian Maotianshan Shale biota and the Middle Cambrian Burgess Shale biota: Evidence for the Cambrian substrate revolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 220, 47–67.

Dornbos, S.Q., Bottjer, D.J. Chen, J.-Y., Gao, F., Oliveri, P. and Li, C.-W. (2006). Environmental controls on the taphonomy of phosphatized animals and animal embryos from the Neoproterozoic Doushantuo Formation, Southwest China. *Palaios*, 21, 3–14.

Dornbos, S.Q., Plotnick, R.E. and Chen, J.Y. (2009). Movement paleoecology of the early Cambrian Chengjiang biota. *Geological Society of America Annual Meeting, Abstracts with Programs*, 41, 163.

Downing, K.P. and Walker, R.G. (1988). Viking Formation, Joffre Field, Alberta: shoreface origin of long, narrow sand body encased in marine mudstones. *American Association of Petroleum Geologists, Bulletin*, 72, 1212–1228.

Draganits, E., Braddy, S.J. and Briggs, D.E.G. (2001). A Gondwanan coastal arthropod ichnofauna from the Muth Formation (Lower Devonian, Northern India): Paleoenvironment and tracemaker behavior. *Palaios*, 16, 126–147.

Draper, J.J. (1980). *Rusophycus* (Early Ordovician ichnofossil) from the Mithaka Formation, Georgina Basin. *Journal of Australian Geology and Geophysics*, 5, 57–61.

Driese, S.G. and Foreman, J.L. (1991). Traces and related chemical changes in a Late Ordovician paleosol *Glossifungites* ichnofacies, southern Appalachians, USA. *Ichnos*, 1, 207–219.

Droser, M.L. (1991). Ichnofabric of the Paleozoic *Skolithos* ichnofacies and the nature and distribution of the *Skolithos* piperock. *Palaios*, 6, 316–325.

Droser, M.L. and Bottjer, D.J. (1986). A semiquantitative field classification of ichnofabric. *Journal of Sedimentary Petrology*, 56, 558–559.

Droser, M.L. and Bottjer, D.J. (1989). Ichnofabric of sandstones deposited in high-energy nearshore environments: Measurement and utilization. *Palaios*, 4, 598–604.

Droser, M.L. and Bottjer, D.J. (1993). Trends and patterns of Phanerozoic ichnofabrics. *Annual Reviews of Earth and Planetary Sciences*, 21, 205–225.

Droser, M.L. and Finnegan, S. (2003). The Ordovician radiation: A follow-up to the Cambrian explosion. *Integrative and Comparative Biology*, 43, 178–184.

Droser, M.L. and Li, X. (2001). The Cambrian radiation and the diversification of sedimentary fabrics. In *The Ecology of the Cambrian Radiation*, ed. A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, pp. 137–164.

Droser, M.L., Bottjer, D.J. and Sheehan, P.M. (1997). Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life. *Geology*, 25, 167–170.

Droser, M.L., Jensen, S., Gehling, J.G., Myrow, P.M. and Narbonne, G.M. (2002). Lowermost Cambrian ichnofabrics from the Chapel Island Formation, Newfoundland: Implications for Cambrian substrates. *Palaios*, 17, 3–15.

Droser, M.L., Jensen, S. and Gehling, J.G. (2004). Development of early Palaeozoic ichnofabrics: evidence from shallow marine siliciclastics. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, *ed.* D. McIlroy, *Geological Society Special Publication*, 228, 383–396.

Droser, M.L., Gehling, J.G. and Jensen, S. (2005). Ediacaran Trace Fossils: True and False. In *Evolving Form and Function: Fossils and Development*, ed. D.E.G. Briggs, *A Special Publication of the Peabody Museum of Natural History, Yale University*, pp. 125–138.

Droser, M.L., Gehling, J.G. and Jensen, S. (2006). Assemblage palaeoecology of the Ediacara biota: The unabridged edition? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232, 131–147.

Durand, J. (1985). Le grès armoricain. Sédimentologie: Traces fossiles. Milieux de dépôt. *Memoires et Documents du Centre Armoricain d'estude Structurale des Socles*, 3–6, 1–119.

Duringer, P., Schuster, M., Genise, J.F., Andossa, L., Machaye, H.T., Vignaud, P. and Brunet, M. (2006). The first fossil fungus gardens of Isoptera: Oldest evidence of symbiotic termite fungiculture (Miocene, Chad basin). *Naturwissenschaften*, 93, 610–615.

Duringer, P., Schuster, M., Genise, J.F., Mackaye, H.T., Vignaud, P. and Brunet, M. (2007). New termite trace fossils: Galleries, nests and fungus combs from the Chad basin of Africa (upper Miocene-Lower Pliocene). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 251, 323–353.

Dworschak, P. and Ott, J.A. (1993). Decapod burrows in mangrove-channel and back-reef environments at the Atlantic Barrier Reef, Belize. *Ichnos*, 2, 277–290.

Dzik, J. (2005). Behavioral and anatomical unity of the earliest burrowing animals and the cause of the "Cambrian explosion". *Paleobiology*, 31, 503–521.

Eagar, R.M.C., Baines, J.G., Collinson, J.D., Hardy, P.G., Okolo, S.A. and Pollard, J.E. (1985). Trace fossil assemblages and their occurrence in Silesian (Mid-Carboniferous) deltaic sediments of the Central Pennine Basin, England. In *Biogenic Structures: Their Use in Interpreting Depositional Environments*, ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 99–149.

Eberth, D.A., Berman, D.S., Sumida, S.S. and Hopf, H. (2000). Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, central Germany): the Upland Holy Grail. *Palaios*, 15, 293–313.

Edwards, D., Selden, P.A., Richardson, J.B. and Axe, L. (1995). Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature*, 377, 329–331.

Edwards, D., Yi, W., Bassett, M.G. and Sen, L.C. (2007). The Earliest vascular plants or a later rooting system? *Pinnatiramosus qianensis* from the marine Lower Silurian Xiushan Formation, Guizhou province, China. *Palaios*, 22, 155–165.

Edwards, J.M. and Frey, R.W. (1977). Substrate Characteristics within a Holocene Salt Marsh, Sapelo Island, Georgia. *Senckenbergiana maritima*, 9, 215–259.

Egenhoff, S.O., Weber, B., Lehnret, O. and Maletz, J. (2007). Biostratigraphic precision of the *Cruziana rugosa* group: a study from the Ordovician succession of southern and central Bolivia. *Geological Magazine*, 144, 289–303.

Eisma, D.E. (1998). *Intertidal Deposits: River Mouths, Tidal Flats, and Coastal Lagoons*. Boca Raton, FL: CRC Press.

Ekdale, A.A. (1977). Abyssal trace fossils in worldwide Deep Sea Drilling Project cores. In, *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 163–182.

Ekdale, A.A. (1978). Trace fossils in Leg 42A cores. *Initial Reports Deep Sea Drilling Project*, 42, 821–827.

Ekdale, A.A. (1979). Trace-fossil evidence for deep-water sedimentation in Cretaceous arc-trench gap, South-central Alaska. *American Association of Petroleum Geologists, Bulletin*, 63, 443.

Ekdale, A.A. (1980). Graphoglyptid burrows in modern deep-sea sediment. *Science*, 207, 304–306.

Ekdale, A.A. (1985). Paleoecology of the marine endobenthos. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 50, 63–81.

Ekdale, A.A. (1988). Pitfalls of paleobathymetric interpretations based on trace fossil assemblages. *Palaios*, 3, 464–472.

Ekdale, A.A. (1992). Muckraking and mudslinging: the joys of deposit feeding. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 145–171.

Ekdale, A.A. and Berger, W.H. (1978). Deep-sea ichnofacies: modern organism traces on and in pelagic carbonates of the western equatorial Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 263–278.

Ekdale, A.A. and Bromley, R.G. (1984a). Comparative ichnology of shelf-sea and deep-sea chalk. *Journal of Paleontology*, 58, 323–332.

Ekdale, A.A. and Bromley, R.G. (1984b). Sedimentology and ichnology of the Cretaceous–Tertiary boundary in Denmark; implications for the causes of the terminal Cretaceous extinction. *Journal of Sedimentary Research*, 54, 681–703.

Ekdale, A.A. and Bromley, R.G. (1991). Analysis of composite ichnofabrics: an example in uppermost Cretaceous chalk of Denmark. *Palaios*, 6, 232–249.

Ekdale, A.A. and Bromley, R.G. (2001a). A day and a night in the life of a cleft-foot clam: *Protovirgularia–Lockeia–Lophoctenium. Lethaia*, 34, 119–124.

Ekdale, A.A. and Bromley, R.G. (2001b). Bioerosional innovation in the Early Ordovician of Sweden: A revolutionary adaptation for living in carbonate hardgrounds. *Lethaia*, 34, 1–12.

Ekdale, A.A. and Gibert, J.M. de. (2010). Paleoethologic significance of bioglyphs: fingerprints of the subterraneans. *Palaios*, 25(8), 540–545.

Ekdale, A.A. and Lewis, D.W. (1991a). The New Zealand *Zoophycos* revisited: morphology, ethology, and paleoecology. *Ichnos*, 1, 183–194.

Ekdale, A.A. and Lewis, D.W. (1991b). Trace fossils and paleoenvironmental control of ichnofacies in a late Quaternary gravel and loess fan delta complex, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 81, 253–279.

Ekdale, A.A. and Lewis, D.W. (1993). Sabellariid reefs in Ruby Bay, New Zealand: A modern analogue of *Skolithos* "piperock" that is not produced by burrowing activity. *Palaios*, 8, 614–620.

Ekdale, A.A. and Mason, T.R. (1988). Characteristic trace-fossil associations in oxygen-poor sedimentary environments. *Geology*, 16, 720–723.

Ekdale, A.A. and Picard, M.D. (1985). Trace fossils in a Jurassic eolianite, Entrada Sandstone, Utah, USA. *Society for Sedimentary Geology, Special Publication*, 35, 3–12.

Ekdale, A.A. and Stinnesbeck, W. (1998). Trace fossils in Cretaceous-Tertiary (KT) boundary beds in northeastern Mexico: implications for sedimentation during the KT boundary event. *Palaios*, 13, 593–602.

Ekdale, A.A. and Warme, J.E. (1975). Trace fossil facies in the Jurassic High Atlas Trough, Morocco. *American Association of Petroleum Geologists, Annual Meeting Abstracts*, 21.

Ekdale, A.A., Bromley, R.G. and Pemberton, S.G. (1984). *Ichnology, Trace Fossils in Sedimentology and Stratigraphy*. *Society for Sedimentary Geology Short Course Notes*, 15.

Ekdale, A.A., Brown, F.H. and Feibel, C.S. (1989). Non-marine macroborings in early Pleistocene algal biolithites (Stromatolites) of the Turkana Basin, northern Kenya. *Palaios*, 4, 389–396.

Ekdale, A.A., Benner, J.S., Bromley, R.G. and Gibert, J.M. de (2002). Bioerosion of Lower Ordovician hardgrounds in southern Scandinavia and western North America. *Acta Geologica Hispanica*, 37, 9–13.

Ekdale, A.A., Bromley, R.G., and Loope, D.B. (2007). Ichnofacies of an Ancient Erg: A Climatically Influenced Trace Fossil Association in the Jurassic Navajo Sandstone, Southern Utah, USA. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 562–564.

Eldredge, N. (1970). Observations on burrowing behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites. *American Museum of Natural History, New York, American Museum Novitates*, 2436, 17.

El Khayal, A.A. and Romano, M. (1988). A revision of the upper part of the Saq Formation and Hanadir Shale (lower Ordovician) of Saudi Arabia. *Geological Magazine*, 125, 161–174.

Eliade, M. (1959). *The Sacred and the Profane: The Nature of Religion*. San Diego, CA: Harvest Books.

Elliott, D.K. and Nations, J. D. (1998). Bee burrows in the Late Cretaceous (Late Cenomanian) Dakota Formation, Northeastern Arizona. *Ichnos*, 5, 243–253.

Emig, C.C., Gall, J.-C., Pajaud, D. and Plaziat, J.-C. (1978). Réfexions critiques sur l'écologie et la systématique des lingules actuelles et fossiles. *Géobios*, 11, 573–609.

Encinas, A., Buatois, L.A. and Finger, K.L. (2008). Paleoecological and paleoenvironmental implications of a high-density *Chondrites* association in slope deposits of the Neogene Santo Domingo Formation, Valdivia, south-central Chile. *Ameghiniana*, 45, 225–231.

Engel, M.S. (2001). A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 1–192.

English, A.M. and Babcock, L.E. (2007). Feeding behaviour of two Ordovician trilobites inferred from trace fossils and non-biomineralised anatomy, Ohio and Kentucky, USA. *Memoirs of the Association of Australasian Palaeontologists*, 34, 537–544.

Ernst, G. and Gierlowski-Kordesch, E. (1989). Epeiric sea deposits and graphoglyptid burrows in upper Cretaceous of Tanzania. *International Geological Congress Abstracts*, 28, 1460.

Erwin, D.H. (2001). Metazoan origins and early evolution. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Publishing Company, pp. 25–31.

Erwin, D.H. (2006). *Extinction*. Princeton, NJ: Princeton University Press.

Erwin, D.H. (2007). Disparity: morphological pattern and developmental context. *Paleontology*, 50, 57–73.

Ettema, C.H. and Wardle, D.A. (2002). Spatial soil ecology. *Trends in Ecology and Evolution*, 17, 177–183.

Ewing, M. and Davis, R.A. (1967). Lebensspuren photographed on the ocean floor. In *Deep Sea Photography*, ed. J.B. Hersey, Baltimore, MD: The John Hopkins University Press, pp. 259–294.

Eyles, N., Vossler, S.M. and Lagoe, M.B. (1992). Ichnology of a glacially-influenced continental shelf and slope; the late Cenozoic Gulf of Alaska (Yakataga Formation). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 94, 193–221.

Falcon-Lang, H.J., Benton, M.J. and Stimson, M. (2007). Ecology of earliest reptiles inferred from basal Pennsylvanian trackways. *Journal of the Geological Society*, 164, 1113–1118.

Falkingham, P.L., Margetts, L., Smith, I.M. and Manning, P.L. (2009). Reinterpretation of palmate and semi-palmate (webbed) fossil tracks: Insights from finite element modeling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 271, 69–76.

Farlow, J.O. (1992). Sauropod Tracks and Trackmakers: Integrating the Ichnological and Skeletal Records. Logrono, Spain. *Zubia, Instituto de Estudios Riojanos*, 10, 89–138.

Farlow, J.O. and Galton, P.M. (2003). Dinosaur trackways of Dinosaur State Park, Rocky Hill, Connecticut. In *The Great Rift Valleys of Pangea in Eastern North America*, Vol. 2, ed. P.M. Letourneau and P.E. Olsen, New York: Columbia University Press, pp. 248–263.

Farrow, G.E. (1971). Back-reef and lagoonal environments of Aldabra Atoll distinguished by their crustacean burrows. *Zoological Society of London, Symposia*, 28, 455–500.

Farrow. G.E., Syvitski, J.P.M. and Tunnicliffe, V. (1983). Suspended particulate loading on the macrobenthos in a highly turbid fjord: Knight Inlet, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 273–288.

Fauchald, K. and Jumars, P. (1979). The diet of worms: a study of polychaetes feeding guilds. *Oceanography and Marine Biology: An Annual Review*, 17, 193–284.

Faugères, J.-C. and Stow, D.A.V. (2008) contourite drifts: Nature, Evolution and Controls. In *Contourites*, ed. M. Rebesco and A. Carmerlenghi, Developments in Sedimentology, Elsevier, 60, 259–288.

Fayers, S.R., Trewin, N.H. and Morrissey, L. (2010). A large arthropod from the Lower Old Red Sandstone (Early Devonian) of Tredomen Quarry, South Wales. *Palaeontology*, 53, 627–643.

Feder, H.M. and Keiser, G.E. (1980). Intertidal biology. In *Port Valdez, Alaska: Environmental studies 1976–1979*, ed. J.M. Colonell, *Institute of Marine Science, University of Alaska, Occasional Publication*, 5, 143–233.

Feder, H.M. and Matheke, G.E.M. (1980). Subtidal benthos. In: *Port Valdez, Alaska: Environmental Studies 1976–1979*, ed. J.M. Colonell and H. Stockholm, Fairbanks, Alaska: Institute of Marine Science, University of Alaska, pp. 235–318.

Fedonkin, M.A. (1985). Paleoichnology of Vendian Metazoa. In *The Vendian System 1: Historic-Geological and Palaeontological Basis*, ed. B.S. Sokolov and A.B. Ivanovskiy, Moscow: Nauka, pp. 112–116.

Fedonkin, M.A. (2003). Origin of the Metazoa in the light of Proterozoic fossil records. *Paleontological Research*, 7, 9–41.

Fedonkin, M.A. and Waggoner, B.M. (1997). The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature*, 388, 868–871.

Fedonkin, M.A., Simonetta, A. and Ivantsov, A.Y. (2007). New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): Palaeoecological and evolutionary implications. *Geological Society of London Special Publication*, 286, 157–179.

Fell, H.B. (1966). The ecology of ophiuroids. In *Physiology of Echinodermata*, ed. R.A. Boolootian, New York: Interscience, pp. 129–143.

Ferguson, R.L., Thayer, G.W. and Rice, T.R. (1981). Marine primary producers. In *Functional Adaptations of Marine Organisms*, ed. F.J. Vernberg and W.B. Vernberg, New York: Academic Press, pp. 9–69.

Fernandes, A.C.S., Carvalho, I.S. and Netto, R.G. (1990). Icnofósseis de invertebrados da Formacao Botucatu, Sao Paulo (Brasil). *Anais da Academia brasileira de Ciencias*, 62, 45–49.

Fey, M. (2010). *Soils of South Africa*. Singapore: Cambridge University Press.

Fillion, D. and Pickerill, R.K. (1990). Ichnology of the Lower Ordovician Bell Island and Wabana Groups of eastern Newfoundland. *Palaeontographica Canadiana*, 7, 1–119.

Fillion, D., Pickerill, R.K. and Harland, T.L. (1990). Influence de la diagènese sur la production, la préservation et l'échantillonnage des ichnofossiles au sein des séries carbonatées: L'exemple du bassin intracratonique ordovicien du lac-St-Jean et de Chicoutimi (Québec). *Geobios*, 23, 485–511.

Fitzgerald, P.G. and Barret, P.J. (1986). *Skolithos* in a Permian braided river deposit, southern Victoria Land, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52, 237–247.

Flint, S.S. and Hodgson, D.M. (2005). Submarine slope systems: processes and products. *Geological Society of London, Special Publication*, 244, 1–6.

Föllmi, K.B. and Grimm, K.A. (1990). Doomed pioneers: gravity-flow deposition and bioturbation in marine oxygen-deficient environments. *Geology*, 18, 1069–1072.

Foote, M. (1993). Contributions of individual taxa to overall morphological disparity. *Paleobiology*, 19, 403–419.

Foote, M. (1997). The evolution of morphological diversity. *Annual Review of Ecology and Systematics*, 28, 129–152.

Fordyce, R.W. (1980). Trace fossils from Ohika Formation (Pororari Group, Lower Cretaceous), lower Buller Gorge, Buller, New Zealand. *New Zealand Journal of Geology and Geophysics*, 23, 121–124.

Fornós, J.J., Bromley, R.G., Clemmensen, L.B. and Rodriguez-Perea, A. (2002). Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic islands, western Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 180, 277–313.

Forster C.A., Arcucci A.B., Marsicano C.A., Abdala, F. and May C.L. (1995). New vertebrate material from the Los Rastros Formation (Middle Triassic), La Rioja Province, northwestern Argentina. *Journal of Vertebrate Paleontolology*, 15, 29A.

Fortes, M.D. (2002). Natural biological processes and controls. In *Muddy Coasts of the World: Processes, Deposits and Function*, ed. T. Healy, Y. Wang and J.-A. Healy, *Proceedings in Marine Science*, 4, 229–244.

Fortey, R.A. and Owens, R.M. (1999). Feeding habits in trilobites. *Palaeontology*, 42, 429–465.

Fortey, R.A. and Seilacher, A. (1997). The trace fossil *Cruziana semiplicata* and the trilobite that made it. *Lethaia*, 30, 105–112.

Fortey, R.A., Briggs, D.E.G. and Wills, M.A. (1996). The Cambrian evolutionary 'explosion': Decoupling cladogenesis from morphological disparity. *Biological Journal of the Linnean Society*, 57, 13–33.

Foster, J. and Lockley, M.G. (2006). Preservation and abundance patterns in the ichnological record of the Morrison Formation (Upper Jurassic, North America). In *Paleontology and Geology of the Upper Jurassic Morrison Formation*, ed. J.R. Foster and S.G. Lucas, *New Mexico Museum of Natural History and Science Bulletin*, 36, 203–216.

Fraaye, R.H.B. and Werver, O.P. (1990). Trace fossils and their environmental significance in Dinantian carbonates of Belgium. *Paläontologische Zeitschrift*, 64, 367–377.

Fraiser, M.L. and D.J. Bottjer. (2009). Opportunistic behaviour of invertebrate marine tracemakers during the Early Triassic aftermath of the end-Permian mass extinction. *Australian Journal of Earth Sciences*, 56, 841–857.

Francois, F., Poggiale, J-C., Durbec, J-P. and Stora, G. (1997). A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheoretica*, 45, 295–319.

Frey, R.W. (1970). Trace fossils of Fort Hays Limestone Member of Niobrara Chalk (Upper Cretaceous), west-central Kansas. *University of Kansas Paleontological Contributions*, 53, 1–41.

Frey, R.W. (1971). Ichnology: the study of fossil and recent lebenspurren, In *Trace Fossils, A Field Guide to Selected Localities in Pennsylvanian, Permian, Cretaceous and Tertiary Rocks of Texas,* *and Related Papers*, ed. B.F. Perkins, *Louisiana State University School of Geoscience, Miscellaneous Publication*, 71, 91–125.

Frey, R.W. (1972). Paleoecology and depositional environment of Fort Hays Limestone Member, Niobrara Chalk (Upper Cretaceous), west-central Kansas. *University of Kansas Paleontological Contributions*, 58, 1–72.

Frey, R.W. (1973). Concepts in the study of biogenic sedimentary structures. *Journal of Sedimentary Petrology*, 43, 6–19.

Frey, R.W. (1975). The realm of ichnology, its strengths and limitations. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 13–38.

Frey, R.W. (1990). Trace fossils and hummocky cross-stratification, Upper Cretaceous of Utah. *Palaios*, 5, 203–218.

Frey, R. W and Bromley, R.G. (1985). Ichnology of American chalks: the Selma Group (Upper Cretaceous), western Alabama. *Canadian Journal of Earth Sciences*, 22, 801–828.

Frey, R.W. and Cowles, J. (1969). New observations on *Tisoa*, a trace fossil from the Lincoln Creek Formation (Mid-Tertiary) of Washington. *The Compass*, 47, 10–22.

Frey, R.W. and Goldring, R. (1992). Marine event beds and recolonization surfaces as revealed by trace fossil analysis. *Geological Magazine*, 129, 325–335.

Frey, R.W. and Pemberton, S.G. (1984). Trace fossils *Facies Models*. In *Facies Models*, ed. R.G. Walker, *Geoscience Canada Reprint Series*, 189–207.

Frey, R.W. and Pemberton, S.G. (1985). Biogenic structures in outcrops and cores; I, Approaches to ichnology. *Bulletin of Canadian Petroleum Geology*, 33, 72–115.

Frey, R.W. and Pemberton, S.G. (1986). Vertebrate Lebensspuren in Intertidal and Supratidal Environments, Holocene Barrier Islands, Georgia. *Senckenbergiana Maritima*, 18, 45–95.

Frey, R.W. and Pemberton, S.G. (1987). The *Psilonichnus* ichnocoenose, and its relationship to adjacent marine and nonmarine ichnocoenoses along the Georgia coast. *Bulletin of Canadian Petroleum Geology*, 35, 333– 357.

Frey, R.W. and Pemberton, S.G. (1991). Or is it bioturbate texture? *Ichnos*, 1, 327–329.

Frey, R.W. and Seilacher, A. (1980). Uniformity in marine invertebrate ichnology. *Lethaia*, 13, 183–207.

Frey, R.W. and Wheatcroft, R.A. (1989). Organism–substrate relations and their impact on sedimentary petrology. *Journal of Geological Education*, 37, 261–279.

Frey, R.W., Curran, H.A. and Pemberton, S.G. (1984a). Tracemaking activities of crabs and their environmental significance; the ichnogenus *Psilonichnus*. *Journal of Paleontology*, 58, 333–350.

Frey, R.W., Pemberton, S.G. and Fagerstrom, J.A. (1984b). Morphological, ethological and environmental significance of the ichnogenera *Scoyenia* and *Ancorichnus*. *Journal of Paleontology*, 58, 511–528.

Frey, R.W., Hong, J.S., Howard, J.D., Park, B.K. and Han, S.J. (1987a). Zonation of benthos on a macrotidal flat, Inchon, Korea. *Senckenbergiana Maritima*, 19, 295–329.

Frey, R.W., Howard, J.D. and Hong, J.S. (1987b). Prevalent Lebensspuren on a modern macrotidal flat, Inchon, Korea: ethological and environmental significance. *Palaios*, 2, 571–593.

Frey, R.W., Pemberton, S.G. and Saunders, T.D.A. (1990). Ichnofacies and bathymetry: A passive relationship. *Journal of Paleontology*, 64, 155–158.

Fu, S. (1991). Funktion, Verhalten und Einteilung fucoider und lophocteniider Lebensspuren. *Courier Forschung-Institut Senckenberg*, 135, 1–79.

Fu, S. and Werner, F. (1994). Distribution and composition of biogenic structures on the Iceland–Faeroe Ridge: relation to different environments. *Palaios*, 9, 92–101.

Fu, S. and Werner, F. (1995). Is *Zoophycos* a feeding trace? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 195, 37–47.

Fuchs, T. (1895). Studien über Fucoiden und Hyeroglyphen. *Akademie der Wissenschaften zu Wien, mathematisch-naturwissenschaftliche Klasse, Denkschriften*, 62, 369–448.

Fuchs, T. (1909). Über einiger neure Arbeiten zur Aufklärung der Natur der Alectoruriden. *Mitteilungen der Geologischen Gesellschaft in Wien*, 2, 335–350.

Fuglewicz, R., Ptaszyliski, T. and Rdzanek, K. (1990). Lower Triassic footprints from the Swigtokrzyskie (Holy Cross) Mountains, Poland. *Acta Palaeontologica Polonica*, 35, 109–164.

Furnes, H., Banerjee, N.R., Muehlenbachs, K., Staudigel, H. and de Wit, M. (2004). Early life recorded in Archean pillow lavas. *Science*, 304, 578–581.

Fürsich, F.T. (1972). *Thalassinoides* and the origin of nodular limestone in the Corallian beds (Upper Jurassic) of southern England. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 3, 136–156.

Fürsich, F.T. (1973). A revision of the trace fossils *Spongeliomorpha, Ophiomorpha* and *Thalassinoides*. *Neues Jahrbuch für Geologie, und Paläontologie, Monatshefte*, 1973, 719–735.

Fürsich, F.T. (1974). Ichnogenus *Rhizocorallium*. *Palaontologische Zeitschrift*, 48, 16–28.

Fürsich, F.T. (1981). Invertebrate trace fossils from the Upper Jurassic of Portugal. *Comunicações Servicio Geologico de Portugal*, 67, 153–168.

Fürsich, F.T. 1998. Environmental distribution of trace fossils in the Jurassic of Kachch (western India). *Facies*, 39, 46–53.

Fürsich, F.T. and Mayr, H. (1981). Non–marine *Rhizocorallium* (trace fossil) from the Upper Freshwater Molasse (Upper Miocene) of southern Germany. *Neues Jahrbuch für Geologie und Palaontologie, Monashefte*, 321–333.

Fürsich, F.T., Taheri, J. and Wilmsen, M. (2007). New occurrences of the trace fossil *Paleodictyon* in shallow marine environments: Examples from the Triassic-Jurassic of Iran. *Palaios*, 22, 424–432.

Gage, J.D. and Tyler, P.A. (1991). *Deep-sea Biology*. Cambridge, UK: Cambridge University Press.

Gaigalas A. and Uchman, A. (2004). Trace fossils form the Upper Pleistocene varved clays S of Kaunas, Lithuania. *Geologija*, 45, 16–26.

Gaillard, C. (1988). Bioturbation récente au large de la Nouvelle-Calédonie. Premiers résultats de la campagne Biocal. *Oceanologica Acta*, 11, 389–399.

Gaillard, C. (1991). Recent organism traces and ichnofacies on the deep-sea floor off New Caledonia, southwestern Pacific. *Palaios*, 6, 302–315.

Gaillard, C. and Olivero, D. (1993). Interprétation paléoécologique nouvelle de *Zoophycos* Massalongo, 1855. *Comptes Rendus de l'Académie des Sciences de Paris*, 316, 823–830.

Gaillard, P. B, Gall, J. C, Gruet, Y., Barale, G., Bourseau, J. P, Buffetaut, E. and Wenz, S. (1994). Ichnofabric from the Upper Jurassic Lithographic Limestone of Cerin, Southeast France. *Palaeontology*, 37, 285–304.

Galloway, W.E. (1975). Process framework for describing the morphologic and stratigraphic evolution of deltaic depositional systems. In *Deltas, Models for Exploration*, ed. M.L. Broussard, Houston, TX: Houston Geological Society, pp. 87–89.

Gámez Vintaned, J.A., Liñan, E., Mayoral, E., Dies, M.E., Gozalo, R. and Muñiz, F. (2006). Trace and soft body fossils from the Pedroche Formation (Ovetian, Lower Cambrian of the Sierra de Córdoba, S Spain) and their relation to the Pedroche event. *Geobios*, 39, 443–468.

Gand, G. (1975). Sur quelques empreintes de pas de vertbrs rcoltes dans le Stphanien moyen de Montceau-les-Mines (Sane-et-Loire-France). *Bulletin de la Socit d'Historie Naturelle d'Autun*, 74, 9–31.

Gand, G., Kerp, H., Parsons, C. and Martínez García, E. (1997). Palaeoenvironmental and stratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Peña Sagra, Cantabrian Mountains, Spain). *Geobios*, 30, 295–318.

Gandini, R., Netto, R.G. and Souza, P.A. (2007). Paleoicnologia e a Palinologia dos ritmitos do Grupo Itararé na pedreira de Águas Claras (Santa Catarina, Brasil). *Gaea*, 3, 47–59.

Gangloff, R.A., May, K.C. and Storer, J.E. (2004). An early Late Cretaceous dinosaur tracksite in central Yukon Territory, Canada. *Ichnos*, 11, 299–309.

García-Ramos, J.C. and Valenzuela, M. (1979). Estudio e interpretación de la icnofauna (vertebrados e invertebrados) en el Jurásico de la costa asturiana. *Cuadernos Geológicos*, 10, 13–22.

Garrison, J.R. Jr. and van den Bergh, T.C.V. (2004). The high-resolution depositional sequence stratigraphy of the Upper Ferron Sandstone, Last Chance Delta: An application of coal zone stratigraphy. In *Regional to Wellbore Analog for Fluvial–Deltaic Reservoir Modeling: The Ferron Sandstone of Utah*, ed. T.C. Chidsey Jr., R.D. Adams and T.H. Morris, *American Association of Petroleum Geologists Studies in Geology*, 50, 125–192.

Gehling, J.G. (1999). Microbial mats in terminal Proterozoic siliciclastic Ediacaran masks. *Palaios*, 14, 40–57.

Gehling, J. (2002). *Terminal Proterozoic–Cambrian of the Flinders Ranges, South Australia. 1st International Palaeontological Congress, Field Trip Pre-3 Guide Book*.

Gehling, J.G., Droser, M., Jensen, S. and Runnegar, B. (1998). Similar cycles – different strokes: Closing a taphonomic window across the Precambrian-Cambrian boundary. *Inaugural Sprigg Symposium: The Ediacaran Revolution, Abstracts & Programme*, 20–21.

Gehling, J.G., Narbonne, G.M. and Anderson, M. (2000). The first named Ediacaran body fossil, *Aspidella terranovica*. *Palaeontology*, 43, 427–456.

Gehling, J.G., Jensen, S., Droser, M.L., Myrow, P.M. and Narbonne, G.M. (2001). Burrowing below the basal Cambrian GSSP, Fortune Head, Newfoundland. *Geological Magazine*, 138, 213–218.

Gehling, J.G., Droser, M., Jensen, S. and Runnegar, B. (2005). Ediacara organisms: relating form to function. In *Evolving Form and Function: Fossils and Development. A Special Publication of the Peabody Museum of Natural History*, ed. D.E.G. Briggs, New Haven, CT: Yale University Press, pp. 43–66.

Genise, J.F. (1995). Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos*, 3, 287–299.

Genise, J.F. (1997). A fossil termite nest from the Marplatan stage (Late Pliocene) of Argentina: paleoclimatic indicator. *Palaeogeography, Paleoclimatology, Palaeoecology*, 136, 139–144.

Genise, J.F. (1999). Insect paleoichnology. *Revista de la Sociedad Entomologica Argentina*, 58, 104–116.

Genise, J.F. (2000). The ichnofamily Celliformidae for *Celliforma* and allied ichnogenera. *Ichnos*, 7, 267–284.

Genise, J.F. (2004). Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, ants and termites. In *The application of ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 419–453.

Genise, J.F. and Bown, T.M. (1990). The constructor of the ichnofossil *Chubutolithes*. *Journal of Paleontology*, 64, 482–483.

Genise, J.F. and Bown, T.M. (1994a). New Miocene scarabeid and hymenopterous nests and Early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos*, 3, 107–117.

Genise, J.F. and Bown, T. M. (1994b). New trace fossils of termites (Insecta: Isoptera) from the Late Eocene–Early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. *Ichnos*, 3, 155–183.

Genise, J.F. and Cladera, G. (2004). *Chubutolithes gaimanensis* and other wasp trace fossils: breaking through the taphonomic barrier. *Journal of the Kansas Entomological Society*, 77, 626–638.

Genise, J.F. and Edwards, N. (2003). Ichnotaxonomy, Origin, and palaeoenvironment of Quaternary insect cells from Fuerteventura, Canary Islands, Spain. *Journal of the Kansas Entomological Society*, 76, 320–327.

Genise, J.F. and Hazeldine, P.L. (1995). A new insect trace fossil in Jurassic wood from Patagonia, Argentina. *Ichnos*, 4, 1–5.

Genise, J.F. and Hazeldine, P.L. (1998). 3D-reconstruction of insect trace fossils: *Ellipsoideichnus meyeri* Roselli. *Ichnos*, 5, 167–175.

Genise, J.F. and Laza, J.H. (1998). *Monesichnus ameghinoi* Roselli: A complex insect trace fossil produced by two distinct trace makers. *Ichnos*, 5, 213–223.

Genise, J.F. and Verde, M. (2000). *Corimbatichnus fernandezi*: A cluster of fossil bee cells from the Late Cretaceous-Early Tertiary of Uruguay. *Ichnos*, 7, 115–125.

Genise, J.F., Mángano, M.G., Buatois, L.A., Laza, J. and Verde, M. (2000). Insect trace fossil associations in paleosols: The *Coprinisphaera* ichnofacies. *Palaios*, 15, 33–48.

Genise, J.F., Sciutto, J.C., Laza, J.H., Gonzalez, M.G. and Bellosi, E.S. (2002). Fossil bee nests, coleopteran pupal chambers and tuffaceous Paleosol from the Late Cretaceous Laguna Palacios Formation, central Patagonia (Argentina). *Paleogeography, Paleoclimatology, Paleoecology*, 177, 215–235.

Genise, J.F., Mángano, M.G. and Buatois, L.A. (2004a). Ichnology moving out of the water: a model for terrestrial ichnofacies. In *First International Congress on Ichnology, Trelew, Argentina*, ed. L.A. Buatois and M.G. Mángano, *Museo Paleontologico Egidio Feruglio, Abstract Book*, 38.

Genise, J.F., Bellosi, E.S. and Gonzalez, M.G. (2004b). An approach to the description and interpretation of ichnofabrics in palaeosols. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 355–382.

Genise, J.F., Melchor, R.N., Bellosi, E.S., Gonzalez, M.G. and Krause, M. (2007). New insect pupation chambers (Pupichnia) from the Upper Cretaceous of Patagonia, Argentina. *Cretaceous Research*, 28, 545–559.

Genise, J.F., Bedatou, E. and Melchor, R.N. (2008). Terrestrial crustacean breeding trace fossils from the Cretaceous of Patagonia (Argentina): palaeobiological and evolutionary significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 264, 128–139.

Genise J.F., Melchor R.N., Archangelsky M., Bala L.O., Straneck R. and de Valais S. (2009). Application of neoichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: the Late Triassic–Early Jurassic? Santo Domingo Formation, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 143–161.

Genise, J.F., Melchor R.N., Bellosi, E.S. and Verde. (2010a). Invertebrate and Vertebrate Trace Fossils from Continental Carbonates. In *Carbonates in Continental Settings: Facies, Environments, and Processes*, ed. A.M. Alonso-Zarza and L. Tanner, *Developments in Sedimentology*, 61, 319–369.

Genise, J.F., Alonso-Zarza, A.M., Krause, J.M., Sánchez, M.V., Sarzetti, L., Farina, J.F., González, M.G., Cosarinsky, M. and Bellosi, E.S. (2010b). Rhizolith balls from the Lower Cretaceous of Patagonia: Just roots or the oldest evidence of insect agriculture? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 287, 128–142.

Gérard, J. and Bromley, R. (2008) *Ichnofabrics in Clastic Sediments. Applications to Sedimentological Core Studies. A Practical Guide*. Madrid: J. Gérard.

Gerdes, G., Krumbein, W.E. and Reineck, H.E. (1985). The depositional record of sandy, versicolored tidal flats (Mellum Island, southern North Sea). *Journal of Sedimentary Petrology*, 55, 265–278.

Gerdes, G., Krumbein, W.E., and Reineck, H.E. (1994). Microbial mats as architects of sedimentary surface structures. In *Biostabilization of Sediments*, ed. W.E. Krumbein, D.M. Peterson and L.J. Stal, Oldenburg, Germany: BIS, pp. 165–182.

Gerdes, G., Klenke, T. and Noffke, N. (2000). Microbial signatures in peritidal siliciclastic sediments: A catalogue. *Sedimentology*, 47, 279–308.

Getty, P.R. (2005). Excavated and *in situ* dinosaur footprints from the Murray Quarry (Early Jurassic East Berlin Formation), Holyoke, Massachusetts, USA. *Ichnos*, 12, 163–178.

Getty, P.R. and Hagadorn, J.W. (2008). Reinterpretation of *Climactichnites* Logan 1860 to include subsurface burrows, and erection of *Musculopodus* for resting traces of the trailmaker. *Journal of Paleontology*, 82, 1161–1172.

Getty, P.R. and Hagadorn, J.W. (2009). Palaeobiology of the *Climactichnites* tracemaker. *Palaeontology*, 52, 753–778.

Gevers, T.W. and Twomey, A. (1982). Trace fossils and their environment in Devonian (Silurian?) Lower Beacon strata in the Asgaard Range, Victoria Land, Antarctica. In *Antarctic Geoscience*, ed. C. Craddock, J.K. Loveless, T.L. Vierima and K.A. Crawford, Madison, WI: University of Wisconsin Press, pp. 639–647.

Gevers, T.W., Frakes, L.A., Edwards, L.N. and Marzolff, J.E. (1971). Trace fossils in the Lower Beacon sediments (Devonian), Darwin Mountains, southern Victoria Land, Antarctica. *Journal of Paleontology*, 45, 81–94.

Geyer, G. and Uchman, A. (1995). Ichnofossil assemblages from the Nama Group (Neoproterozoic–Lower Cambrian) in Namibia and the Proterozoic–Cambrian boundary problem revisited. *Beringeria Special Issue*, 2, 175–202.

Ghare, M.A. and Badve, R.M. (1984). Observations on ichnoactivity from the intertidal environment, West Coast of Raigad District, Maharashtra. *Biovigyanam*, 10, 173–178.

Ghibaudo, G., Grandesso, P., Massari, F. and Uchman, A. (1996). Use of trace fossils in delineating sequence stratigraphic surfaces (Tertiary Venetian Basin, northeastern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 120, 261–279.

Gibbard, P.L. (1977). Fossil tracks from varved sediments near Lammi, south Finland. *Bulletin Geological Society of Finland*, 49, 53–57.

Gibbard, P.L. and Dreimanis, A. (1978). Trace fossils from late Pleistocene glacial lake sediments in southwestern Ontario, Canada. *Canadian Journal of Earth Sciences*, 15, 1967–1976.

Gibbard, P.L. and Stuart, A.J. (1974). Trace fossils from proglacial lake sediments. *Boreas*, 3, 69–74.

Gibert, J.M. de (1996). A new decapod burrow system from the NW Mediterranean Pliocene. *Revista Española de Paleontología*, 11, 251–254.

Gibert, J.M. de, and Ekdale, A.A. (1999). Trace fossil assemblages reflecting stressed environments in the Middle Jurassic Carmel Seaway of central Utah. *Journal of Paleontology*, 73, 711–720.

Gibert, J.M. de and Martinell, J. (1992). Principales estructuras biogénicas en el Plioceno marino de la Cuenca del Baix Llobregat (Catalunya). *Geogaceta*, 12, 104–106.

Gibert, J.M. de and Martinell, J. (1993). Controles paleoambientales sobre la distribución de las paleoicnocenosis en el estuario plioceno del Baix Llobregat (Barcelona, Catalunya). *Revista Española de Paleontología*, 8, 140–146.

Gibert, J.M. de and Martinell, J. (1996). Trace fossil assemblages and their palaeoenvironmental significance in the Pliocene marine deposits of the Baix Ebre (Catalonia, NE Spain). *Géologie Méditerranéenne*, 23, 211–225.

Gibert, J.M. de and Sáez A. (2009). Paleohydrological significance of trace fossil distribution in Oligocene fluvial-fan-to-lacustrine systems of the Ebro Basin, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 162–175.

Gibert, J.M. de, Martinell, J. and Domenech, R. (1996). El Mioceno marino entre las playas de L'Arrabassada y El Miracle (Tarragona): aspectos paleontológicos e implicaciones sedimentológicas. *Acta Geologica Hispanica*, 29, 133–148.

Gibert, J.M. de, Martinell, J. and Domènech, R. (1998). *Entobia* ichnofacies in fossil rocky shores, Lower Pliocene, Northwestern Mediterranean. *Palaios*, 13, 476–487.

Gibert, J.M. de, Buatois, L.A., Fregenal-Martinez, M.A., Mángano, M.G., Ortega, F., Poyato-Ariza, F.J. and Wenz, S. (1999). The fish trace fossil *Undichna* from the Cretaceous of Spain: Taphonomic and palaeoenvironmental implications for the ichnogenus. *Palaeontology*, 42, 409–427.

Gibert, J.M. de, Fregenal-Martínez, M.A., Buatois, L.A and Mángano, M.G. (2000). Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. *Paleogeography, Paleoclimatology, Palaeoecology*, 156, 89–101.

Gibert, J.M. de, Arbués, P., Puig, M., and Marzo, M. (2001a). Ichnological signatures of turbidite channels from the Eocene Ainsa slope complex (Spanish Pyrenees). *American Association of Petroleum Geologists Annual Meeting 2001: An Energy Odyssey, Expanded Abstracts*, 71.

Gibert, J.M. de, Arbués, P., Puig, M., and Marzo, M. (2001b). Implicaciones sedimentológicas de *Diplocraterion* en canales turbidíticos de talud (Eoceno, Ainsa, NE de España). *IV Reunión de icnología y segunda reunion de icnología del Mercosur, Tucuman, Resumenes*, 48.

Gibert, J.M. de, Domènech, R. and Martinell, J. (2004). An ethological framework for animal bioerosion trace fossils upon mineral substrates with a proposal for a new class, Fixichnia. *Lethaia*, 37, 429–437.

Gibert, J.M. de, Domènech, R. and Martinell, J. (2007). Bioerosion in shell beds from the Pliocene Roussillon Basin, France: implications for the (macro) bioerosion ichnofacies model. *Acta Palaeontologica Polonica*, 52, 783–798.

Gierliński, G., Pieńkowski, G. and Niedźwiecki, G. (2004). Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. *Ichnos*, 11, 195–213.

Gierlowski-Kordesch, E. (1991). Ichnology of an ephemeral lacustrine/alluvial plain system: Jurassic East Berlin formation, Hartford Basin, USA. *Ichnos*, 1, 221–232.

Gierlowski-Kordesch, E. and Ernst, F. (1987). A flysch trace fossil assemblage from the Upper Cretaceous shelf of Tanzania. In *Current Research in African Earth Sciences*, ed. G. Mathies and H. Schandelmeir, *14th Coloquium on African Geology (Berlin), Extended Abstracts*, 217–221.

Gierlowski-Kordesch, E. and Park, L.E. (2004). Comparing species diversity in the modern and fossil record of lakes. *The Journal of Geology*, 112, 703–717.

Gili, J.M. and Coma, R. (1998). Benthic suspension Feeders: Their paramount role in littoral marine; food webs. *Trends in Ecology and Evolution*, 13, 316–321.

Giller, P.S. and Malmquist, B. (1998). *The Biology of Streams and Rivers.* Oxford, UK: Oxford University Press.

Gilmore, C.W. (1926). Fossil footprints from the Grand Canyon. *Smithsonian Miscellanea Collection*, 77, 1–41.

Gilmore, C.W. (1927). Fossil footprints from the Grand Canyon. *Smithsonian Miscellanea Collection*, 80, 1–78.

Ginsburg, R.N. (1953). Intertidal erosion on the Florida Keys. *Bulletin of Marine Science*, *Gulf Caribbean*, 3, 1–14.

Gingras, M.K. (2008). Revisiting Willapa Bay: facies templates for estuary deposits modelled from Pleistocene outcrops. *Back to Exploration, CSPG CSEG CWLS Convention*, 562–563.

Gingras, M.K. and Pemberton, S.G. (2000). A field method for determining the firmness of colonized sediment subtrates. *Journal of Sedimentary Research*, 70, 1341–1344.

Gingras, M.K., MacEachern, J.A. and Pemberton, S.G. (1998). A comparative analysis of the ichnology of wave- and river-dominated allomembers of the Upper Cretaceous Dunvegan Formation. *Bulletin of Canadian Petroleum Geology*, 46, 51–73.

Gingras, M.K., Pemberton, S.G., Mendoza, C.A. and Henk, F. (1999). Assessing the anisotropic permeability of *Glossifungites surfaces. Petroleum Geoscience*, 5, 349–357.

Gingras, M.K., Pemberton, S.G., Saunders, T.D.A. and Clifton, H.E. (1999). The ichnology of Modern and Pleistocene brackish-water deposits at Willapa Bay, Washington: Variability in estuarine settings. *Palaios*, 14, 352–374.

Gingras, M.K., Pemberton, S.G. and Saunders, T.D.A. (2000). Firmness Profiles associated with tidal creek deposits: the temporal significance of *Glossifungites* assemblages. *Journal of Sedimentary Research*, 70, 1017–1025.

Gingras, M.K., Pemberton, S.G., Saunders, T.D.A. (2001). Bathymetry, sediment texture, and substrate cohesiveness; their impact on *Glossifungites* Ichnofacies at Willapa Bay, Washington. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 169, 1–21.

Gingras, M.K., MacMillan, B., Balcom, B.J. and Saunders, T. (2002). Using magnetic resonance imaging and petrographic techniques to understand the textural attributes and porosity distribution in *Macaronichnus*-burrowed sandstone. *Journal of Sedimentary Research*, 72, 552–558.

Gingras, M.K., MacEachern, J.A., and Pickerill, R.K. (2004). Modern Perspectives on the *Teredolites* Ichnofacies: Observations from Willapa bay, Washington. *Palaios*, 19, 79–88.

Gingras, M.K., Dashtgard, S.E. and Pemberton, S.G. (2006). Latitudinal (climatic) controls on neoichnological assemblages of modern marginal-marine depositional environments. *American Association of Petroleum Geologists 2006 Annual Convention (Houston)*, Abstract, 38.

Gingras, M.K., Lalonde, S.V., Amskold, L. and Konhauser, K.O. (2007). Wintering chironomids mine oxygen. *Palaios*, 22, 433–438.

Gingras, M.K., Dashtgard, S.E., MacEachern, J.A. and Pemberton, S.G. (2008a). Biology of shallow marine ichnology: a modern perspective. *Aquatic Biology*, 2, 255–268.

Gingras, M.K., Pemberton, S.G., Dashtgard, S. and Dafoe, L. (2008b). How fast do marine invertebrates burrow? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 280–286.

Giosan, L. and Bhattacharya, J.P. (2005) (eds.). *River Deltas: Concepts, Models and Examples*. *Society for Sedimentary Geology Special Publication*, 83.

Giosan, L., Vespremeanu, E., Donnelly, J.P., Bhattacharya, J.P. and Buonaiuto, F. (2005). Morphodynamics and evolution of Danube delta. In *River Deltas: Concepts, Models and Examples*, ed. L. Giosan and J.P. Bhattacharya, *Society for Sedimentary Geology Special Publication*, 83, 391–410.

Glaessner, M.F. (1984). *The Dawn of Animal Life. A Biohistorical Study*. Cambridge, UK: Cambridge University Press.

Glaub, I. (1994). Mikrobohrspuren in ausgewählten Ablagerungsräumen des europäischen Jura und der Unterkreide. *Courier Forschungsinstitut Senckenberg*, 174, 1–324.

Glaub, I. (2004). Recent and sub-recent microborings from the upwelling area off Mauritania (West Africa) and their implications for palaeoecology. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 63–76.

Glaub, I. and Vogel, K. (2004). The stratigraphic record of microborings. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 126–135.

Glaub, I., Vogel, K. and Gektidis, M. (2001). The role of modern and fossil cyanobacterial borings in bioerosion and bathymetry. *Ichnos*, 8, 185–196.

Glaub, I., Gektidis, M., and Vogel, K. (2002). Microborings from different North Atlantic shelf areas- variability of the euphotic zone extension and implications for paleodepth reconstructions. *Courier Forschungsinstitut Senckenberg*, 237, 25–37.

Glaub, I., Golubic, S., Gektidis, M., Radtke, G. and Vogel, K. (2007). Microborings and microbial endoliths: Geological implications. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 368–381.

Głuszek, A. (1995). Invertebrate trace fossils in the continental deposits of an Upper Carboniferous coal-bearing succession, Upper Silesia, Poland. *Studia Geologica Polonica*, 108, 171–202.

Groenewald, G.H., Welman, J. and MacEachern, J.A. (2001). Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios*, 16, 148–160.

Gobetz, K.E., Lucas, S.G. and Lerner, A.J. (2006). Lungfish burrows of varying morphology from the Upper Triassic Redonda Formation, Chinle Group, eastern New Mexico. In *The Triassic–Jurassic Terrestrial Transition*, ed. J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 140–147.

Goldring, R. (1962). The trace fossils of the Baggy Beds (Upper Devonian) of North Devon, England. *Paläontologische Zeitschrift*, 36, 232–251.

Goldring, R. (1964). Trace fossils and the sedimentary surface in shallow water marine sediments. *Developments in Sedimentology*, 1, 136–143.

Goldring, R. (1991). *Fossils in the Field. Information Potential and Analysis*. Singapore: Longman Scientific & Technical.

Goldring, R. (1993). Ichnofacies and facies interpretation. *Palaios*, 8, 403–405.

Goldring, R. (1995). Organisms and the substrate: Response and effect. In *Marine Palaeoenvironmental Analysis from Fossils*, ed. D.W.J. Bosence and P.A. Allison, *Geological Society Special Publication*, 83, 151–180.

Goldring, R. (1996). The sedimentological significance of concentrically laminated burrows from Lower Cretaceous Ca-bentonites, Oxfordshire. *Journal of the Geological Society, London*, 153, 255–263.

Goldring, R. and Kaźmierczak, J. (1974). Ecological succession in intraformational hardground formation. *Palaeontology*, 17, 949–962.

Goldring, R. and Seilacher, A. (1971). Limulid undertracks and their sedimentological implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 137, 422–442.

Goldring, R., Pollard, J.E. and Taylor, A.M. (1991). *Anconichnus horizontalis*: a pervasive ichnofabric-forming trace fossil in post-Paleozoic offshore siliciclastic facies. *Palaios*, 6, 250–263.

Goldring, R., Pollard, J.E. and Taylor, A.M. (1997). Naming trace fossils. *Geological Magazine*, 134, 265–268.

Goldring, R., Cadée, G.C., D'Alessandro, A., Gibert, J.M. de, Jenkins, R. and Pollard, J.E. (2004). Climatic Control of Trace Fossil Distribution in the Marine Realm. In *The application of Ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 77–92.

Gordon, E.A. (1988). Body and trace fossils from the Middle–Upper Devonian Catskill magnafacies, southeastern New York, USA. In *The Devonian of the World*, ed. N.J. McMillan, A.F. Embry and D.J. Glass, *Canadian Society of Petroleum Geologists Memoir*, 14, 139–155.

Gore, P.J.W. (1989). Toward a model for open– and closed–basin deposition in ancient lacustrine sequences: the Newark Supergroup (Triassic–Jurassic), eastern North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 70, 29–51.

Gould, S.J. (1987). *Time's Arrow, Time's Cycle*. Cambridge, MA: Harvard University Press.

Gould, S.J. (1989). *Wonderful life: The Burgess Shale and the Nature of History*. New York: Norton.

Gould, S.J. (1991). The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology*, 17, 411–423.

Gowland, A.S. (1996). Facies characteristics and depositional models of highly bioturbated shallow marine siliciclastic strata: an example from the Fulmar Formation (Late Jurasic), UK Central Graben. In *Geology of the Humber Group: Central Graben and Moray Firth, UKCS*, ed. A. Hurst, *Geological Society Special Publication*, 114, 185–214.

Gradzinski, R. and Uchman, A. (1994). Trace fossil from interdune deposits: An example from the Lower Triassic aeolian Tumlin Sandstone, central Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108, 121–138.

Graham, J.R. and Pollard, J.E. (1982). Occurrence of the trace fossil *Beaconites antarcticus* in the Lower Carboniferous fluviatile rocks of County Mayo, Ireland. Palaeogeography, *Palaeoclimatology, Palaeoecology*, 38, 257–268.

Grassé, P.P. (1984). *Termitologia, Tome II*. Paris: Masson.

Grassé, P.P. (1986). Evolution as seen through insects. *Bulletin of the Society of Entomology of France*, 91, 5–18.

Grassle, J.F. (1985). Hydrothermal vent animals: distribution and biology. *Science*, 229, 713–717.

Grazhdankin, D. (2004). Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology*, 30, 179–221.

Green, R.H. and Hobson, K.D. (1970). Spatial and temporal structure in a temperate intertidal community with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). *Ecology*, 51, 999–1011.

Grimaldi, D.A. (1999). Co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Gardens*, 86, 373–406.

Grimaldi, D.A. and Engel, M.S. (2005). *Evolution of the Insects*. Cambridge, UK: Cambridge University Press.

Grimm, K.A. and Föllmi, K.B. (1994). Doomed pioneers: Allochthonous Crustacean tracemakers in anaerobic basinal strata, Oligo-Miocene San Gregorio Formation, Baja California Sur, Mexico. *Palaios*, 9, 313–334.

Grotzinger, J.P., Bowring, S.A., Saylor, B.Z. and Kaufman, A.J. (1995). Biostratigraphic and geochronologic constraints on early animal evolution. *Science*, 270, 598–604.

Gruszczynski, M. (1979). Ecological succession in Upper Jurassic hardgrounds from central Poland. *Acta Palaeontologica Polonica*, 24, 429–450.

Haberland, W. and Grebe, W.H. (1957). Prehistoric footprints from El Salvador. *American Antiquity*, 22, 282–285.

Habersetzer, J., Richter, G., and Storch, G. (1994). Paleoecology of early middle Eocene bats from Messel, FRG; aspects of flight, feeding and echolocation. In *Fifth International Theriological Congress; Symposium on Mammalian Evolutionary Paleoecology*, ed. S. Legendre and R.K. Stucky, Amsterdam: Harwood Academic Publishers, pp. 235–260.

Habgood, K.S., Hass, H. and and Kerp, H. (2003). Evidence for an early terrestrial food web: coprolites from the Early Devonian Rhynie chert. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 94, 371–389.

Hagadorn, J.W. and Belt, E.S. (2008). Stranded in upstate New York: Cambrian medusae from the Potsdam Sandstone. *Palaios*, 23, 424–441.

Hagadorn, J.W., Fedo, C.M., Waggoner, B.M. (2000). Early Cambrian Ediacaran-type fossils from California. *Journal of Paleontology*, 74, 731–740.

Hagadorn, J.W., Dott, R.H. and Damrow, D. (2002). Stranded on an Upper Cambrian shoreline: Medusae from Central Wisconsin. *Geology*, 30, 147–150.

Haines, P.W. (2000). Problematic fossils in the late Neoproterozoic Wonoka Formation, South Australia. *Precambrian Research*, 100, 97–108.

Hakes, W.G. (1976). Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *The University of Kansas Paleontological Contributions*, 63, 1–46.

Hakes, W.G. (1985). Trace fossils from brackish-marine shales, Upper Pennsylvanian of Kansas, U.S.A. In *Biogenic Structures: their use in interpreting depositional environments* ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 21–35.

Halffter, G. and Edmonds, W.D. (1982). The nesting behaviour of dung-beetles. An Ecological and Evolutive Approach. *Publicaciones del instituto de Ecología de México*, 10, 1–176.

Hallam, A., (1970). *Gyrochorte* and other trace fossils in the Forest Marble (Bathonian) of Dorset, England. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 189–200.

Hallam, A. (1975). Preservation of trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 55–63.

Hallam, A. and Wignall, P.B. (1997). *Mass Extinctions and their Aftermath*. Oxford, UK: Oxford University Press.

Hammer, Ø. (1998). Computer simulation of the evolution of foraging strategies: application to the ichnological record. *Palaeontologia Electronica*, 1, 21.

Hanken, N.M., Bromley, R.G. and Miller, J. (1996). Plio-Pleistocene sedimentation in coastal grabens, north-east Rhodes, Greece. *Geological Journal*, 31, 271–298.

Hanken, N.M., Bromley, R.G. and Thomsen, E. (2001). Trace fossils of the bivalve *Panopea faujasi*, Pliocene, Rhodes, Greece. *Ichnos*, 8, 117–130.

Hanor, J.S. and Marshall, N.F. (1971). Mixing of sediment by organisms. *School of Geoscience Miscellaneous Publications, Lousiana State University*, 71, 127–135.

Hansen, C.D. and MacEachern, J.A. (2007). Application of the asymmetric delta model to along-strike facies variations in a mixed wave- and river-influenced delta lobe, Upper Cretaceous Basal Belly River Formation, Central Alberta. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 1–16.

Häntzschel, W. (1975). Trace fossils and Problemática. In *Treatise on Invertebrate Paleontology, Part W, Miscellanea*, *Supplement* 1, ed. C. Teichert, Lawrence, KS: Geological Society of America and University of Kansas Press, 1–269.

Häntzschel, W. and Frey, R.W. (1978). Bioturbation. In *The Encyclopedia of Sedimentology*, ed. R.W. Fairdbridge amd J. Bourgeois, Stroudsburg, Dowden: Hutchinson & Ross, pp. 68–71.

Harada, T. and Noto, T. (1984). Volcanic calamity season. *Bulletin of the Gunma Prefecture Museum of History*, 5, 1–21.

Harper, E.M., Forsythe, G.T.W. and Palmer, T.J. (1999). A fossil record full of holes: The Phanerozoic history of drilling predation: Comment and Reply. *Geology*, 27, 959–960.

Harrison, B. (1977). The effect of sand ripples on the small-scale distribution of the interstitial meiobenthos with particular reference to the harpacticoid copepods. *Proceedings 3rd International Meiofauna Conference*, Abstract.

Harvey, A.M., Mather, A.E. and Stokes, M. (2005). Alluvial fans: geomorphology, sedimentology, dynamics – introduction. A review of alluvial-fan research. *Geological Society, London, Special Publications*, 251, 1–7.

Hasiotis ST. (2002). *Continental trace fossils*. Society for Sedimentary Geology Short Course Notes, 51.

Hasiotis, S.T. (2003). Complex ichnofossils of solitary to social organisms: Understanding their evolution and roles in terrestrial paleoecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 259–320.

Hasiotis, S.T. (2004). Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. *Sedimentary Geology*, 167, 177–268.

Hasiotis, S.T. and Bown, T.M. (1992). Invertebrate trace fossils: the backbone of continental ichnology. In *Trace Fossils: Their Paleobiological Aspects*, ed. C. Maples, and R. West, R., *Paleontological Society Short Course Notes*, 5, 64–104.

Hasiotis, S.T. and Dubiel, R.F. (1993). Continental trace fossils of the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. In *The Nonmarine Triassic*, ed. S.G. Lucas and M. Morales, *Bulletin of the New Mexico Museum of Natural History and Science*, 3, 175–178.

Hasiotis, S.T. and Dubiel, R.F. (1995). Termite (Insecta: Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos*, 4, 119–130.

Hasiotis, S.T. and Honey, J.G. (2000). Paleohydrologic and stratigraphic significance of crayfish burrows in Continental deposits: examples from several Paleocene laramide basins in the Rocky Mountains. *Journal of Sedimentary Research*, 70, 127–139.

Hasiotis, S.T. and Mitchell, C.E. (1993). A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures. *Ichnos*, 2, 291–314.

Hasiotis, S.T., Mitchell, C.E. and Dubiel, R.F. (1993a). Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish? *Ichnos*, 2, 315–333.

Hasiotis, S.T., Aslan, A. and Bown, T.M. (1993b). Origin, architecture, and paleoecology of the early Eocene continental ichnofossil *Scaphichnium hamatum*: integration of ichnology and paleopedology. *Ichnos*, 3, 1–9.

Hasiotis, S.T., Kirkland, J.I. and Callison, G. (1998). Crayfish fossils and burrows, Upper Jurassic Morrison Formation, western Colorado: evolutionary and paleohydrologic implications. *Modern Geology*, Part 1, 22, 481–491.

Hasiotis, S.T., Kraus, M.J. and Demko, T.M. (2007). Climatic Controls on Continental Trace Fossils. In *Trace Fossils: Concepts, Prolems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 172–195.

Haubold, H.H. (1986). Archosaur footprints at the terrestrial Triassic-Jurassic transition. In *The Beginning of the Age of Dinosaurs*, ed. K. Padian, Cambridge, UK: Cambridge University Press, pp. 189–201.

Haubold, H. (1996). Ichnotaxonomie und Klassifikation von Tetrapodenfahrten aus dem Perm. *Hallesches Jahrbuch Geowissenshaft B*, 18, 28–86.

Haubold, H. (1999). Tracks of the Dinosauromorpha from the Early Triassic. *Zentralblatt fr Geologie und Palontologie Teil I*, 1998, 783–795.

Haubold, H. and Katzung, G. (1978) Paleoecology and paleoenvironments of tetrapod footprints from the Rotliegend (Lower Permian) of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 307–323.

Haubold, H. and Klein, H. (2000). Die dinosauroiden Fährten *Parachirotherium–Atreipus–Grallator* aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn, ?Nor) in Franken. *Hallesches Jahrbuch für Geowissenschaften B*, 22, 59–85.

Haubold, H. and Klein, H. (2002). Chirotherien und Grallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria. *Hallesches Jahrbuch für Geowissenschaften B*, 24, 1–22.

Haubold, H. and Lucas, S. G. (2001) Early Permian tetrapod tracks: Preservation, taxonomy, and Euramerican distribution. *Natura Bresciana*, 25, 347–354.

Haubold, H. and Lucas, S.G. (2003). Tetrapod footprints of the Lower Permian Choza Formation at Castle Peak, Texas. *Paläontologische Zeitschrift*, 77, 247–261.

Haubold, H. and Sarjeant, W.A.S. (1973). Tetrapodenfa Èhrten aus den Keele und Enville Groups (Permokarbon: Stefan und Autun) von Shropshireund South Staffordshire, Groûitannien. *Zeitschrift Geologische Wissenschaften*, 8, 895–933.

Haubold, H., Buta, R.J., Rindsberg, A.K. and Kopaska-Merkel, D.C. (2005). Atlas of Union Chapel Mine vertebrate trackways and swimming traces. *Alabama Paleontological Society, Monographs*, 1, 207–276.

Hauck, T.E., Dashtgard, S.E. and Gingras, M.K. (2008). Relationships between organic carbon and Fodinichnia morphology. *Palaios*, 23, 336–343.

Hay, R.L. and Leakey, M.D. (1982). The fossil footprints of Laetoli. *Scientific American*, 246, 38–45.

Hayes, B. (2003). In search of the optimal scumsucking bottomfeeder. *American Scientist*, 91, 392–396.

Hayward, B.W. (1976). Lower Miocene bathyal and submarine canyon ichnocoenoses from Northland, New Zealand. *Lethaia*, 9, 149–162.

Heard, T.G. and Pickering, K.T. (2008). Trace fossils as diagnostic indicators of deep-marine environments, middle EoceneAinsa-Jaca basin, Spanish Pyrenees. *Sedimentology*, 55, 809–844.

Heddle, D. (1967). Versatility of movement and the origin of the asteroids. In *Echinoderm Biology*, ed. N. Millott, *Symposia of the Zoological Society of London*, 20, 125–141.

Heer, O. (1865). *Die Urwelt der Schweiz*. Zurich: Friedrich Schultze.

Heezen, B.C. and Hollister, C.D. (1971). *The Face of the Deep*. New York: Oxford University Press.

Hein, F.J. and Risk, M.J. (1975). Bioerosion of coral heads: inner patch reefs, Florida Reef Tract. *Bulletin of Marine Science*, 25, 133–138.

Hembree, D.I. (2009). Neoichnology of burrowing millipedes: understanding the relationships between ichnofossil morphology, behavior, and sediment properties. *Palaios*, 24, 425–439.

Hembree, D.I. and Hasiotis, S.T. (2007). Biogenic structures produced by the Kenyan sand boa *Eryx colubrinus* (Reptilia: Ophidia: Boidae): modern analog for interpreting continental trace fossils. *Journal of Sedimentary Research*, 77, 389–397.

Hembree, D.I., Martin, L.D. and Hasiotis, S.T. (2004). Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 203, 127–152.

Henbest, L.G. (1960). Fossil spoor and their environmental significance in Morrow and Atoka series, Pennsylvanian, Washington County, Arkansas. *US Geological Survey, Professional Paper*, 400B, 383–385.

Herringshaw, L.G. and Davies, N.S. (2008). Bioturbation levels during the end-Ordovician extinction event: a case study of shallow marine strata from the Welsh Basin. *Aquatic Biology*, 2, 279–287.

Hester, P.M. and Lucas, S.G. (2001). Lacustrine depositional environments of the Upper Triassic Redonda Formation, east-central New Mexico. *New Mexico Geological Society, Guidebook*, 52, 153–16.

Hickman, C.S. (1993). Theoretical design space; a new program for the analysis of structural diversity; Progress in constructional morphology. *Neues Jahrbuch fuer Geologie und Palaeontologie Abhandlugen*, 190, 169–182.

Higgs, R. (1988). Fish trails in the Upper Carboniferous of south-west England. *Palaeontology*, 31, 55–272.

Higgs, W. (2001). *Ichnology in archaeology*. Thesis. York University.

Hirsch, K.E. (1994). The fossil record of vertebrate eggs. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 269–294.

Hobbs, H.H. Jr. (1981). The Crayfishes of Georgia. *Smithsonian Contributions to Zoology*, 318.

Hobday, D.K. and Tavener-Smith, R. (1975). Trace fossils in the Ecca of northern Natal and their *palaeoenvironmental significance*. *Palaeontologia Africana*, 18, 47–52.

Hofmann, H.J. (1967). Precambrian fossils near Elliot Lake, Ontario. *Science*, 156, 500–504

Hofmann, H.J. (1971). Precambrian fossils, pseudofossils, and problemática in Canada. *Geological Survey of Canada, Bulletin*, 189, 1–146.

Hofmann, H.J. (1990). Computer simulation of trace fossils with random patterns, and the use of goniograms. *Ichnos*, 1, 15–22.

Hofman, H.J. (2005). Palaeoproterozoic dubiofossils from India revisited: Vindhyan triploblastic animal burrows or pseudopfossils. *Journal of the Palaeontological Society of India, Golden Jubilee*, 50, 113–120.

Hogue, E.W. and Miller, C.B. (1981). Effects of sediment microtopography on small-scale spatial distribution of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology*, 53, 181–191.

Hölldobler, B. and Wilson, E.O. (1990). *The Ants*. Cambridge, MA: Harvard University Press.

Hollister, C.D., Heezen, B.C. and Nafe, K.E. (1975). Animal traces on the deep-sea floor. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 493–510.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences, USA*, 105, 19060–19065.

Horodyski, R.J. and Knauth, L.P. (1994). Life on land in the Precambrian. *Science*, 263, 494–498.

Hovikoski, J., Lemiski, R., Gingras, M., Pemberton, G. and MacEachern, J.A. (2008). Ichnology and Sedimentology of a Mud-Dominated Deltaic Coast: Upper Cretaceous Alderson Member (Lea Park Fm), Western Canada. *Journal of Sedimentary Research*, 78, 803–824.

Howard, J.D. (1975). The sedimentological significance of trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 131–145.

Howard, J.D. (1978). Sedimentology and trace fossils. In *Trace fossil concepts*, ed. P.B. Basan, *Society for Sedimentary Geology Short Course Notes*, 5, 11–42.

Howard, J.D. and Dörjes, J. (1972). Animal–sediment relationships in two beach-related tidal flats: Sapelo Island, Georgia. *Journal of Sedimentary Petrology*, 42, 608–623.

Howard, J.D. and Frey, R.W. (1975). Regional animal–sediment characteristics of Georgia estuaries. *Senckenbergiana Maritima*, 7, 33–103.

Howard, J.D. and Frey, R.W. (1984). Characteristic trace fossils in near-shore to offshore sequences, Upper Cretaceous of east-central Utah. *Canadian Journal of Earth Sciences*, 21, 200–219.

Howard, J.D. and Reineck, H. (1981). Depositional facies of high-energy beach-to-offshore sequence with low-energy sequence. *American Association of Petroleum Geologists, Bulletin*, 65, 807–830.

Howard, J.D., Elders, C.A. and Heinbokel, J.F. (1975). Estuaries of the Georgia coast, USA. Sedimentology and Biology V. Animal–sediment relationships in estuarine point bar deposits, Ogeechee River, Ossabaw Sound. *Senckenbergiana Maritima*, 7, 181–203.

Howell, C.D. Jr., Bhattacharya, J.P. and MacEachern, J.A. (2007). Bedset sedimentation rates in a Turonian Greenhouse delta front, Wall Creek Member, Frontier Formation, Powder Reiver Basin, Wyoming. In *Ichnological Application to Sedimentological and Sequence Stratigraphic Problems*, ed. J.A. MacEachern, M.K. Gingras, K.L. Bann and S.G. Pemberton, Society for Sedimentary Geology Research Conference, Price, pp. 81–84.

Howell, J.A. and Flint, S.F. (2003). Sequences and systems tracts in the Book Cliffs. In *Sedimentary Record of Sea-Level Change*, ed. A.L. Coe, Cambridge, UK: Cambridge University Press and Open University, pp. 179–197.

Hu, B., Wang, G. and Goldring, R. (1998). *Nereites* (or *Neonereites*) from Lower Jurassic lacustrine turbidites of Henan, central China. *Ichnos*, 6, 203–209.

Hua, H., Pratt, B.R. and Zhang, L.Y. (2003). Borings in *Cloudina* shells: Complex predatory-prey dynamics in the Terminal Neoproterozoic. *Palaios*, 18, 454–459.

Hubbard, S.M. and Shultz, M.R. (2008). Deep burrows in submarine fan-channel deposits of the Cerro Toro Formation (Cretaceous), Chilean Patagonia: Implications for firmground development and colonization in the deep-sea. *Palaios*, 23, 223–232.

Hudson, J.D. (1990). Salinity from faunal analysis and geochemistry. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 406–410.

Hunt, A.P. and Lucas, S.G. (2006a). Permian tetrapod ichnofacies. In *Non-marine Permian biostratigraphy and Biocronology*, ed. S.G. Lucas, G. Cassinis and J.W. Schneider, *Geological Society Special Publication*, 265, 137–156.

Hunt, A.P. and Lucas, S.G. (2006b). The taphonomy of the Cleveland-Lloyd Dinosaur Quarry, Upper Jurassic Morrison Formation, Utah: a re-evaluation. In *Paleontology and Geology of the Upper Jurassic Morrison Formation*, ed. J.R. Foster and S.G. Lucas, *New Mexico Museum of Natural History and Science Bulletin*, 36, 57–65.

Hunt, A.P. and Lucas, S.G. (2006c). Triassic-Jurassic tetrapod ichnofacies. In *The Triassic–Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 12–22.

Hunt, A.P. and Lucas, S.G. (2007). Tetrapod ichnofacies: a new paradigm. *Ichnos*, 14, 59–68.

Hunt, A.P., Chin, K. and Lockley, M.G. (1994). The paleobiology of coprolites. In *The Paleobiology of Trace Fossils*, ed. S.K. Donovan, London: John Wiley, pp. 221–240.

Hunt, A.P., Lucas, S.G. and Lockley, M.G. (1998). Taxonomy, stratigraphic and facies significance of vertebrate coprolites of the Upper Triassic Chinle Group, western United States. *Ichnos*, 5, 225–234.

Hunt, A.P., Lucas, S.G. and Lockley, M.G. (2004a). Large pelycosaur footprints from the Lower Pennsylvanian of Alabama, USA. *Ichnos*, 11, 39–44.

Hunt, A.P., Lucas, S.G., Calder, J.H., van Allen, H.E.K., George, E., Gibling, M.R., Herbert, B.L., Mansky, C. and Reid, D.R. (2004b). Tetrapod footprints from Nova Scotia; the Rosetta Stone for Carboniferous tetrapod ichnology. *Geological Society of America, Abstracts with Programs*, 36, 66.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A. (2005). Early Permian tetrapod tracksites in New Mexico. In: *The Permian of Central New Mexico*, ed. S.G. Lucas, K.E. Zeigler and J.A. Spielmann, *New Mexico Museum of Natural History and Science Bulletin*, 31, 46–48.

Hunter, M.A. and Lomas, S.A. (2003). Reconstructing the Siluro-Devonian coastline of Gondwana: insights from the sedimentology of the Port Stephens Formation, Falkland Islands. *Journal of the Geological Society, London*, 160, 459–476.

Ingle, J.C. (1980). Cenozoic paleobathymetry and depositional history of selected sequences within the Southern California Continental Borderland. *Cushman Found Special Publication*, 19, 163–195.

Ishigaki, S. (1989). Footprints of swimming sauropods from Morocco. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 83–86.

Ivantsov, A.Y. and Malakhovskaya, Y.E. (2002). Giant traces of Vendian animals. *Doklady Earth Sciences A*, 385, 618–622.

Jablonski, D. (1995). Extinction in the fossil record. In *Extinction Rates*, ed. R.M. May and J.H. Lawton, Oxford, UK: Oxford University Press, pp. 25–44.

Jaglarza, P. and Uchman, A. (2010). A hypersaline ichnoassemblage from the Middle Triassic carbonate ramp of the Tatricum domain in the Tatra Mountains, Southern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 71–81.

James, N.P., Kobluk, D.R. and Pemberton, S.G. (1977). The oldest macroborers: Lower Cambrian of Labrador. *Science*, 197, 980–983.

Janicke, V. (1969). Untersuchungen ueber den Biotop der Solnhofener Plattenkalke. Investigations of the biotope of the Solnhofen limestones. *Mitteilungen der Bayerischen Staatssammlung fuer Palaeontologie und Historische Geologie*, 9, 117–180.

Jansson, A.M. (1967). Food-web of Cladophora-belt Fauna. *Helgolander Wissenschaftliche Meeresuntersuchungen*, 15, 574–578.

Jenkins, R.J.F. (1995). The problems and potential of using animal fossils and trace fossils in terminal Proterozoic biostratigraphy. *Precambrian Research*, 73, 51–69.

Jensen, S. (1990). Predation by early Cambrian trilobites on infaunal worms – evidence from the Swedish Mickwitzia Sandstone. *Lethaia*, 23, 29–42.

Jensen, S. (1997). Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. *Fossils and Strata*, 42, 1–111.

Jensen, S. (2003). The Proterozoic and earliest trace fossil record; Patterns, problems and perspectives. *Integrative and Comparative Biology*, 43, 219–228.

Jensen, S. and Bergström, J. (2000). *Cheiichnus gothicus* igen. et. isp. n., a new *Bergaueria*-like arthropod trace fossil from the lower Cambrian of Vastergotland, Sweden. *Geologiska Föreningens I Stockholm Förhandlingar*, 122, 293–296.

Jensen, S. and Mens, K. (1999). Lower Cambrian shallow-water occurrence of the branching "deep-water" type of trace fossil *Dendrorhaphe* from the Lontova Formation, eastern Latvia. *Paläontologische Zeitschrift*, 73, 187–193.

Jensen, S. and Runnegar, B.N. (2005). A complex trace fossil from the Spitskop Member (terminal Ediacaran–? Lower Cambrian) of southern Namibia. *Geological Magazine*, 142, 561–569.

Jensen, S., Gehling, J.G. and Droser, M.L. (1998). Ediacara-type fossils in Cambrian sediments. *Nature*, 393, 567–569.

Jensen, S., Saylor, B.Z., Gehling, J.G. and Germs, G.J.B. (2000). Complex trace fossils from the terminal Proterozoic of Namibia. *Geology*, 28, 143–146.

Jensen, S., Gehling, J.G., Droser, M.L. and Grant, S.W.F. (2002). A scratch circle origin for the medusoid fossil *Kullingia*. *Lethaia*, 35, 291–299.

Jensen, S., Droser, M.L. and Gehling, J.G. (2005). Trace fossil preservation and the early evolution of animals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 220, 19–29.

Jensen, S., Droser, M.L. and Gehling, J.G. (2006). A critical look at the Ediacaran trace fossil record. In *Neoproterozoic Geobiology and Paleobiology*, ed. J. Kaufman and S. Xiao, Topics in Geobiology, 27, 115–157.

Johnson, E.W., Briggs, D.E.G., Suthren, R.J. Wright, J.L. and Tunncliff, S.P. (1994). Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake district. *Geological Magazine*, 131, 395–406.

Johnson, M.E. (1988). Why are ancient rocky shores so uncommon? *Journal of Geology*, 96, 469–480.

Johnson, M.E. (2006). Uniformitarianism as a guide to rocky-shore ecosystems in the geological record. *Canadian Journal of Earth Sciences*, 43, 1119–1147.

Johnson, R.G. (1967). Salinity of interstitial water in a sandy beach. *Limnology and Oceanography*, 12, 1–7.

Johnston, P.A., Eberth, D.A., and Anderson, P.K. (1996). Alleged vertebrate eggs from Upper Cretaceous red beds, Gobi Desert, are fossil insect (Coleoptera) pupal chambers: *Fictovichnus* new ichnogenus. *Canadian Journal of Earth Sciences*, 33, 511–525.

Johnstone, P.D., Mustard, P.S. and MacEachern, J.A. (2006). The basal unconformity of the Nanaimo Group, southwestern British Columbia: a Late Cretaceous storm-swept rocky shoreline. *Canadian Journal of Earth Sciences*, 43, 1165–1181.

Jones, S.E. and Jago, C.F. (1993). In situ assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology*, 115, 133–142.

Jones, B. and Pemberton, S.G. (1989). Sedimentology and ichnology of a Pleistocene unconformity-bounded, shallowing-upward carbonate sequence: the Ironshore Formation, Salt Creek, Grand Cayman. *Palaios*, 4, 343–355.

Jones, C.G., Lawton, J.H. and Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.

Jorgensen, B.B. (1996). Bacteria and marine biogeochemistry. In *Marine Geochemistry, 2nd edn*, ed. H.D. Schulz and M. Zabel, Berlin: Springer, pp. 169–206.

Kanazawa, K. (1992). Adaptation of test shape for burrowing and locomotion in spatangoid echinoids. *Palaeontology*, 35, 733–750.

Kanazawa, K. (1995). How spatangoids produce their traces: relationship between burrowing mechanism and trace structure. *Lethaia*, 28, 211–219.

Kauffman, E.G. and Hart, M.B. (1996). Cretaceous bio-events. In *Global Events and Event Stratigraphy*, ed. O.H. Walliser, Berlin: Springer, pp. 285–312.

Keighley, D.G. and Pickerill, R.K. (1994). The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology*, 37, 305–337.

Keighley, D.G. and Pickerill, R.K. (1997). Systematic ichnology of the Mabou and Cumberland Groups (Carboniferous) of western Cape Breton Island, eastern Canada, 1: burrows, pits, trails, and coprolites. *Atlantic Geology*, 33, 181–215.

Keighley, D.G. and Pickerill, R.K. (2003). Ichnocoenoses from the Carboniferous of eastern Canada and their implications for the recognition of ichnofacies in nonmarine strata. *Atlantic Geology*, 39, 1–22.

Keller, G. (2001). The end-Cretaceous mass extinction in the marine realm: Year 2000 assessment. *Planetary and Space Science*, 49, 817–830.

Keller, G. (2003). Biotic effects of impacts and volcanism. *Earth and Planetary Science Letters*, 215, 249–264.

Kelley, P.H. and Hansen, T.A. (2001). The Mesozoic marine revolution. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 94–97.

Kelly, S.R.A. and Bromley, R.G. (1984). Ichnological nomenclature of clavate borings. *Palaeontology*, 27, 793–807.

Kennedy, W.J. (1967). Burrows and surface traces from the Lower Chalk of southern England. *British Museum (Natural History), Geology Bulletin*, 15, 127–167.

Kennedy, W.J. (1970). Trace fossils in chalk environments. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 263–282.

Kennedy, W.J. (1975). Trace fossils in carbonate rocks. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, Berlin: Springer-Verlag, pp. 377–398.

Kennedy, W.J. and Garrison, R.E. (1974). Morphology and genesis of nodular chalks and hardgrounds in the Upper Cretaceous of southern England. *Sedimentology*, 22, 311–386.

Kern, J. P. (1980). Origin of trace fossils in Polish Carpathian flysch. *Lethaia*, 13, 347–372.

Kern, J.P. and Warme, J.E. (1974). Trace fossils and bathymetry of the Upper Cretaceous Point Loma Formation, San Diego, California. *Geological Society of America, Bulletin*, 85, 893–900.

Kidwell, S.M. and Brenchley, P.J. (1994). Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction? *Geology*, 22, 1139–1143.

Kim, J.Y. and Paik, I.S. (1997). Nonmarine *Diplocraterion luniforme* (Blanckenhorn 1916) from the Hasandong Formation (Cretaceous) of the Jinju area, Korea. *Ichnos*, 5, 131–138.

Kim, J.Y., Keighley, D.G., Pickerill, R.K., Hwang, W. and Kim, K.-S. (2005). Trace fossils from marginal lacustrine deposits of the Cretaceous Jinju Formation, southern coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 218, 105–124.

Kim, J.Y., Kim, S.H., Kim, K.S. and Lockley, M.G. (2006). The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): more evidence of high avian diversity in East Asia. *Cretaceous Research*, 27, 56–69.

Kim, J.Y., Kim, K.S. and Lockley, M.G. (2008a). Hominid ichnology: tracking our own origins. *Ichnos*, 15, 103–105.

Kim, J.Y., Kim, K.S., Lockley, M.G. and Matthews, N. (2008b). Hominid ichnotaxonomy: An exploration of a neglected discipline. *Ichnos*, 15, 126–139.

Kim, S.K., Kim, J.Y., Kim, S.H., Lee, C.Z. and Lim, J.D. (2009). Preliminary Report on Hominid and Other Vertebrate Footprints from the Late Quaternary Strata of Jeju Island, Korea. *Ichnos*, 16, 1–11.

Kineke, G.C., Sternberg, R.W., Trowbridge, J.H. and Rockwell, G.W. (1996). Fluid-mud processes on the Amazon continental shelf. *Continental Shelf Research*, 16, 667–696.

King, M.J. and Benton, M.J. (1996). Dinosaurs in the Early and Mid Triassic? The footprint evidence from Britain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 122, 213–225.

King, M.J., Sarjeant, W.A.S., Thompson, D.B. and Tresise, G. (2005). A revised systematic ichnotaxonimy and review of the vertebrate footprint ichnofamily Chirotheriidae from the British Triassic. *Ichnos*, 12, 241–299.

Kinne, O. (1964). Non-genetic adaptation to temperature and salinity. *Helgolander wissenschaftliche Meeresuntersuchungen*, 9, 443–458.

Kitchell, J.A. (1979). Deep-sea foraging pathways: an analysis of randomness and resource exploitation. *Paleobiology*, 5, 107–125.

Kitchell, J.A., Kitchell, J. F., Clark, D.L. and Dangeard, L. (1978a). Deep-sea foraging behavior: its bathymetric potential in the fossil record. *Science*, 200, 1289–1291.

Kitchell, J.A., Kitchell, J.F., Johnson, G.L. and Hunkins, K.L. (1978b). Abyssal traces and megafauna: comparison of productivity, diversity, and density in the Arctic and Antarctic. *Paleobiology*, 4, 171–180.

Klein, G. de V. (1971). A sedimentary model for determining paleotidal range. *Geological Society of America Bulletin*, 82, 2585–2592.

Klein, G. de V. (1977). *Clastic Tidal Facies*. Champaign, IL: CEPCO.

Klein, R., Mokady, O. and Loya, Y. (1991). Bioerosion in ancient and contempary coral of the genus *Porites*: patterns and palaeoenvironmental implications. *Marine Ecology Progress Series (Halsten- bek)*, 77, 245–251.

Knaust, D. (1997). Die Karbonatrampe am SE-Rand des Persischen Golfes (Vereinigte Arabische Emirate): Resentes Analogon für den Unteren Muschelkalk der Germanischen Trias? *Greifswalder Geowissenschaftliche Beiträge*, 5, 101–123.

Knaust, D. (2004a). The oldest Mesozoic nearshore *Zoophycos*: evidence from the German Triassic. *Lethaia*, 37, 297–306.

Knaust, D. (2004b). Cambro-Ordovician trace fossils from the SW-Norwegian Caledonides. *Geological Journal*, 39, 1–24.

Knaust, D. (2007). Invertebrate trace fossils and ichnodiversity in shallow-marine carbonates of the German Middle Triassic (Muschelkalk). In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publications*, 88, 223–240.

Knaust, D. (2008). Complex behavioural pattern as an aid to identify the producer of *Zoophycos* from the Middle Permian of Oman. *Lethaia*, 42, 146–154.

Knaust, D. (2009). Characterisation of a Campanian deep-sea fan system in the Norwegian Sea by means of ichnofabrics. *Marine and Petroleum Geology*, 26, 1199–1211.

Knecht, R.J., Benner, J.S., Rogers, D.C. and Ridge, J.C. (2009). *Surculichnus bifurcauda* n. igen., n. isp., a trace fossil from Late Pleistocene glaciolacustrine varves of the Connecticut River Valley, USA, attributed to notostracan crustaceans based on neoichnological experimentation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 232–239.

Kneer, D., Asmus, H., Ahnelt, H. and Vonk, J.A. (2008). Records of *Austrolethops wardi* Whitley (Teleostei: Gobiidae) as an inhabitant of burrows of the thalassinid shrimp *Neaxius acanthus* in tropical seagrass beds of the Spermonde Archipelago, Sulawesi, Indonesia. *Journal of Fish Biology*, 72, 1095–1099.

Knoll, A.H., Golubic, S., Green, J. y Swett, K. (1986). Organically preserved microbial endoliths from the late Proterozoic of East Greenland. *Nature*, 321, 856–857.

Knoll, A., Walter, M., Narbonne, G. and Chirstie-Blick, N. (2006). The Ediacaran Period: a new addition to the geologic time scale. *Lethaia*, 39, 13–30.

Knox, G.A. (1986). *Estuarine Ecosystems: A Systems Approach*. Boca Raton, FL: CRC Press.

Knox, L.W. and Miller, M.F. (1985). Environmental control of trace fossil morphology. In *Biogenic Structures: Their Use in Interpreting Depositional Environments*, ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 167–176.

Kobluk, D.R., James, N.P. and Pemberton, S.G. (1978). Initial diversification of macroboring ichnofossils and exploitation of macroboring niche in the lower Paleozoic. *Paleobiology*, 4, 163–170.

Komar, P.D. (1976). *Beach Processes and Sedimentation: Englewood Cliffs*. Upper Saddle River, NJ: Prentice Hall.

Kotake, N. (1989). Paleoecology of the *Zoophycos* producers. *Lethaia*, 22, 327–341.

Kotake, N. (1991). Non-selective surface deposit feeding by the *Zoophycos* producers. *Lethaia*, 24, 379–385.

Kotake, N. (1992). Deep sea echiurans: possible producers of *Zoophycos*. *Lethaia*, 25, 311–316.

Kotake, N. (1994). Population paleoecology of the *Zoophycos* producing animal. *Palaios*, 9, 84–91.

Kotake, N. (1997). Ethological interpretation of the trace fossil *Zoophycos* in the Hikoroichi Formation (Lower Carboniferous), southern Kitakami Mountains, Northeast Japan. *Paleontological Research*, 1, 15–28.

Kotake, N. (2007). *Macaronichnus* isp. associated with *Piscichnus waitemata* in the Miocene of Yonaguni-jima Island, southwest Japan. In *Trace Fossils, Concepts, Problems, Prospects*, ed. W. Miller, III, Amsterdam: Elsevier, pp. 492–500.

Kowalewski, M., Dulai, A. and Fürsich, F.T. (1998). A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology*, 26, 1091–1094.

Kowalewski, M., Dulai, A. and Fürsich, F.T. (1999). A fossil record full of holes: the Phanerozoic history of drilling predation – Reply to comment. *Geology*, 27, 959–960.

Koy, K. and Plotnick, R.E. (2007). Theoretical and experimental ichnology of mobile foraging. In *Trace Fossils: Concepts, Problems and Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 428–441.

Koy, K. and Plotnick, R.E. (2010). Ichnofossil morphology as a response to resource distribution: insights from modern invertebrate foraging. *Palaeogeography Palaeoclimatology Palaeoecology*, 292, 272–281.

Kozur, H.W. and Lemone, D.V. (1995). New terrestrial arthropod trackways from the Abo Member (Sterlitamakian, late Sakmarian, late Wolfcampian) of the Shalem Colony section, Robledo Mountains, New Mexico. In *Early Permian Footprints and Facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 107–113.

Kozur, H.W., Krainer, K. and Mostler, H. (1996). Ichnology and Sedimentology of the Early Permian deep-water deposits from the Lercara-Roccapalumba Area (Western Sicily, Italy). *Facies*, 34, 123–150.

Kramer, J.M., Erickson, B.R., Lockley, M.G., Hunt, A.P. and Braddy, S.J. (1995). Pelycosaur predation in the Permian: Evidence from *Laoporus* trackways from the Coconino Sandstone with a description of a new ichnospecies of *Permichnium*. In *Early Permian footprints and facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 245–249.

Krapovickas, V. (2010). El Rol de las trazas fósiles de tetrápodos en los modelos de icnofacies continentales en ambientes de climas áridos – semiáridos. PhD dissertation, Universidad de Buenos Aires, Buenos Aires.

Krapovickas, V., Mángano, M.G., Mancuso, A., Marsicano, C.A. and Volkheimer, W. (2008). Icnofaunas triásicas en abanicos aluviales distales: evidencias de la Formación Cerro Puntudo, Cuenca Cuyana, Argentina. *Ameghiniana*, 45, 463–472.

Krapovickas, V., Ciccioli, P.L., Mángano, M.G., Marsicano, C.A. and Limarino, C.O. (2009). Paleobiology and paleoecology of an arid–semiarid Miocene South American ichnofauna in anastomosed fluvial deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 284, 129–152.

Kraus, M.J. and Hasiotis, S.T. (2006). Significance of different modes of rhizolith preservation to interpreting paleoenvironmental and paleohydrologic settings: examples from Paleogene paleosols, Bighorn Basin, Wyoming, USA. *Journal of Sedimentary Research*, 76, 633–646.

Książkiewicz, M. (1970). Observations on the ichnofauna of the Polish Carpathians. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 283–322.

Książkiewicz, M. (1977). Trace fossils in the flysch of the Polish Carpathians. *Paleontologica Polonica*, 36, 1–200.

Kuban, G.J. (1989). Elongate dinosaur tracks. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 57–82.

Kumar, A., Gopolan, K. and Rajagopalan, G. (2000). Mesoproterozoic Age of the Vindhyan Sediments, Central India from Glauconite Rb-Sr Systematics. *Journal of Conference Abstracts*, 5, 608.

Labandeira, C.C. (1997). Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences*, 26, 329–377.

Labandeira, C.C. (1998). Plant–insect associations from the fossil record. *Geotimes*, 43, 18–24.

Labandeira, C.C. (2000). The paleobiology of pollination and its precursors. In *Phanerozoic Terrestrial Ecosystems*, ed. R.A. Gastaldo and W.A. DiMichele, *Paleontological Society Papers*, 6, 233–269.

Labandeira, C.C. (2002). The history of associations between plants and animals. In *History of Plant–Animal Interactions*, ed. C. Herrera and O. Pellmyr, Oxford, UK: Blackwell Science, pp. 26–74.

Labandeira, C.C. (2006). The four phases of plant–arthropod associations in deep time. *Geologica Acta*, 4, 409–438.

Labandeira, C.C. (2007). The origin of herbivory on land: The initial pattern of live tissue consumption by arthropods. *Insect Science*, 14, 259–274.

Labandeira, C.C., Phillips, T.L. and Norton, R.A. (1997). Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. *Palaios*, 12, 319–353.

Labandeira, C.C., Johnson, K.R. and Wilf, P. (2002a). Impact of the terminal Cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences, USA*, 99, 2061–2066.

Labandeira, C.C., Johnson, K.R. and Lang, P. (2002b). A preliminary assessment of insect herbivory across the Cretaceous/Tertiary boundary: extinction and minimal rebound. In *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains-An Integrated Continental Record at the End of the Cretaceous*, ed. J.H. Hartman, K.D. Johnson and D.T. Nichols, Boulder, CO: Geological Society of America, pp. 297–327.

Lamond, R.E., and Tapanila, L. (2003). Embedment cavities in lacustrine stromatolites: Evidence of animal interactions from Cenozoic carbonates in USA and Kenya. *Palaios*, 18, 445–453.

Landing, E. (1994). Precambrian-Cambrian boundary global stratotyperatified and a new perspective of Cambrian time. *Geology*, 22, 179–182.

Landing, E. and Brett, C.E. (1987). Trace fossils and regional significance of a Middle Devonian (Givetian) discomformity in southwestern Ontario. *Journal of Paleontology*, 61, 205–230.

Lanes, S., Manceñido, M. and Damborenea, S. (2007). *Lapispira*: a double helicoidal burrow from Jurassic marine nearshore environments. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, MG. Mángano, J.F. Genise and N.G. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 59–77.

Lanier, W.P., Feldman, H.R. and Archer, A.W. (1993): Tidal sedimentation from a fluvial to estuarine transition, Douglas Group, Missourian-Virgilian, Kansas. *Journal of Sedimentray Petrology*, 63, 860–873.

Larson, D.W. and Rhoads, D.C. (1983). The evolution of infaunal communities and sedimentary fabrics. In *Biotic Interactions in Recent and Fossil Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenum Press, pp. 627–648.

Larsonneur, C. (1994). The Bay of Mont-Saint-Michel: a sedimentation model in a temperate macrotidal environment. *Senckenbergiana Maritima*, 24, 3–63.

Laza, J.H. (2006). Dung-beetle fossil brood balls: The ichnogenera *Coprinisphaera*, Sauer and *Quirogaichnus* (Coprinisphaeridae). *Ichnos*, 13, 217–235.

Leakey, M.D. (1981). Tracks and tools. *Philosophical Transactions Royal Society London B*, 292, 95–102.

Leakey, M.D. (1987). Animals prints and trails. In *Laetoli: a Pliocene site in northern Tanzania*, ed. M. D. Leakey and J.M. Harris, Oxford, UK: Clarendon Press, pp. 451–489.

Leakey, M.D. and Harris, J.M. (1987). *Laetoli: A Pliocene Site in Northern Tanzania*. Oxford, UK: Clarendon Press.

Leakey, M.D. and Hay, R.L. (1979). Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature*, 278, 317–323.

Legarreta, L., Uliana, M.A., Larotonda, C.A. and Meconi, G.R. (1993). Approaches to nonmarine sequence stratigraphy: theoretical models and examples from Argentine basins. In *Subsurface Reservoir Characterisation from Outcrop Observations*, ed. R. Eschard and B. Doliez, Editions Technip, *Collection Colloques et Seminaires*, 51, 125–145.

Legg, I.C. (1985). Trace fossils from a Middle Cambrian deltaic sequence, North Spain. *Society for Sedimentary Geology Special Publication*, 35, 151–165.

Leithold, E.L. and Dean, W.E. (1998). Depositional processes and carbon burial on a Turonian prodelta at the margin of the western interior Seaway. In *Stratigraphy and Palaeoenvironments of the Cretaceous Western Interior seaway, USA*, ed. W.E. Dean and M.A. Arthur, *Society for Sedimentary Geology Concepts in Sedimentology and Palaeontology*, 6, 189–200.

Leonardi, G. (1981). *Brasilichnium elusivum* gen. et sp. nov.: pistas de tetrapodes do Mesozoico guardadas nas colecoes de Museu Nacional de Rio de Janeiro. *Anais Academia Brasileira de Ciencias*, 53, 793–805.

Leonardi, G. (1989). Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 165–178.

Leszczyński, S. (1991a). Oxygen-related controls on predepositional ichnofacies in turbidites, Guipúzcoan Flysch (Albian-Lower Eocene), Northern Spain. *Palaios*, 6, 271–280.

Leszczyński, S. (1991b). Trace Fossil tiering in flysch sediments: examples form the Guipzcoan flysch (Cretaceous-Paleogene), northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 88, 167–184.

Leszczyński, S. (1992a). Controls on trace fossil distribution in flysch deposits. *Nakladem Uniwersytetu Jagiellonskiego, Rozprawy Habilitacyjne*, 236, 1–120.

Leszczyński, S. (1992b). A generalized model for the development of ichnocoenoses in flysch deposits. *Ichnos*, 2, 137–146.

Leszczyński, S. (1993). A generalized model for the development of ichnocoenoses in flysch deposits. *Ichnos*, 2, 137–146.

Leszczyński, S. and Seilacher, A. (1991). Ichnocoenoses of a turbidite sole. *Ichnos*, 1, 293–303.

Lettley, C.D., Gingras, M.K., Pearson, N.J. and Pemberton, S.G. (2007a). Burrowed stiffgrounds on estuarine point bars: Modern and ancient examples, and criteria for their discrimination from firmgrounds developed along omission surfaces. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentray Geology Short Course Notes*, 52, 325–333.

Lettley, C.D., Pemberton, S.G., Gingras, M.K., Ranger, M.J. and Blakney, B.J. (2007b). Integrating sedimentology and ichnology to shed light on the system dynamics and paleogeography of an ancient riverine estuary. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentray Geology Short Course Notes*, 52, 147–165.

Levin, L.A., Blair, N.E., DeMaster, D.J., Plaia, G., Fornes, W., Martin, C.M. and Thomas, C.J. (1997). Rapid subduction of organic matter by maldanid polychaetes on the North Carolina Slope. *Journal of Marine Research*, 55, 595–611.

Levin, L.A., Blair, N.E., Martin, C.M., DeMaster, D.J., Plaia, G. and Thomas, C.J. (1999). Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *In situ* experiments using 13C-labeled diatom. *Marine Ecology Progress Series*, 182, 37–54.

Levin, L.A., Rathburn, A.E., Gutierrez, D., Munoz, P. And Shankle, A. (2003). Bioturbation by symbiont-bearing annelids in near-anoxic sediments; implications for biofacies models and paleo-oxygen assessments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199, 129–140.

Levi-Setti, R. (1993). *Trilobites*. 2nd edn. Chicago, IL: University of Chicago Press.

Lewis, D.W. and Ekdale, A.A. (1991). Lithofacies relationships in a Late Quaternary gravel and loess fan delta complex, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 81, 229–251.

Lewis, D.W. and Ekdale, A.A. (1992). Composite ichnofabric of a Mid-Tertiary unconformity on a pelagic limestone. *Palaios*, 7, 222–235.

Lewis, J.R. (1961). The littoral zone on a rocky shore. A biological or physical entity. *Oikos*, 12, 280–301.

Lewis, J.R. (1964). *The Ecology of Rocky Shore*. London: English Universities Press.

Li, X. and Droser, M.L. (1999). Lower and Middle Ordovician shell beds from the Basin and Range province of western United States (California, Nevada, and Utah.). *Palaios*, 14, 215–233.

Liebau, A. (1984). Grundlagen der Okobathymetrie. In *Palaobathymetrie*, ed. H. Luterbacher, *Palaontologische Kursbucher*, 2, 149–184.

Lillie, M.C. (1998). Cranial surgery dates back to Mesolithic. *Nature*, 391, 854.

Lim, S.K., Yang, S.Y. and Lockley, M.G (1989). Large dinosaur footprint assemblages from the Cretaceous Jindong Formation of southern Korea. In *Dinosaurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 333–336.

Lin, J.P., Zhao, Y.L., Rahman, I.A., Xiao, S. and Wang, Y. (2010). Bioturbation in Burgess Shale-type *Lagerstätten*. Case study of trace fossil–body fossil association from the Kaili Biota (Cambrian Series 3), Guizhou, China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291, 245–256.

Lindholm, R.M. and Casey, J.F. (1990). The distribution and possible biostratigraphic significance of the ichnogenus *Oldhamia* in the shales of the Blow Me Down Brook Formation, western Newfoundland. *Canadian Journal of Earth Sciences*, 27, 1270–1287.

Little, C. (2000). *The Biology of Soft Shores and Estuaries*. New York: Oxford University Press.

Liu, A.G., Mcllroy, D. and Brasier, M.D. (2010). First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology*, 38, 123–126.

Liu, H.T.H., Kneer, D., Asmus, H. and Ahnelt, H. (2008). The feeding habits of *Austrolethops wardi*, a gobiid fish inhabiting burrows of the thalassinidean shrimp *Neaxius acanthus*. *Estuatine, Coastal and Shelf Science*, 79, 764–767.

Lobza, V. and Schieber, J. (1999). Biogenic sedimentary structures produced by worms in soupy, soft muds: Observations from the Chattanooga Shale (Upper Devonian) and experiments. *Journal of Sedimentary Research*, 69, 1041–1049.

Locklair, R.E. and Savrda, C.E. (1998a). Ichnofossil tiering analysis of a rhythmically bedded chalk-marl sequence in the Upper Cretaceous of Alabama. *Lethaia*, 31, 311–322.

Locklair, R.E. and Savrda, C.E. (1998b). Ichnology of rhytmically bedded Demopolis Chalk (Upper Cretaceous, Alabama): Implication for paleoenvironment, depositional cycle origins, and tracemaker behavior. *Palaios*, 13, 423–438.

Lockley, M.G. (1986). The Paleobiological and paleoenvironmental importance of dinosaur footprints. *Palaios*, 1, 37–47.

Lockley, M.G. (1987). Dinosaur footprints from the Dakota Group of eastern Colorado. *The Mountain Geologist*, 24, 107–122.

Lockley, M.G. (1989). Summary and prospectus. In *Dinosurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 441–447.

Lockley, M.G. (1991). *Tracking Dinosaurs. A New Look at an Ancient World*. Cambridge, UK: Cambridge University Press.

Lockley, M.G. (1992). Comment on "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin". *Geology*, 20, 666–667.

Lockley, M.G. (1993). *Siguiendo las huellas de los dinosaurios*. Madrid: McGraw Hill.

Lockley, M.G. (1998). The vertebrate track record. *Nature*, 396, 429–432.

Lockley, M.G. (2001). A decade of dinosaur tracking at Dinosaur Ridge. *Mountain Geologist*, 38, 119–135.

Lockley, M.G. (2003). *A Guide to the Fossil Footprints of the Dinosaur Ridge and Fossil Trace Areas*. Morrison, CO: Friends of Dinosaur Ridge.

Lockley, M.G. (2007). A tale of two ichnologies: The different goals and potentials of Invertebrate and Vertebrate (Tetrapod) Ichnotaxonomy and how they relate to Ichnofacies analysis. *Ichnos*, 14, 39–58.

Lockley, M.G. and Conrad, K. (1989). The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the western USA. In *Dinosurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 121–134.

Lockley, M.G. and Foster, J.R. (2006). Dinosaur and turtle tracks from the Morrison Formation (upper Jurassic) of Colorado National Monument, with observations on the taxonomy of vertebrate swim tracks. In *Geology and Paleontology of the Morrison Formation*, ed. J.R. Foster and S.G. Lucas, *New Mexico Museum of Natural History and Science Bulletin*, 36, 193–198.

Lockley, M.G. and Hunt, A.P. (1994). A review of vertebrate ichnofaunas of the Western Interior United States: evidence and implications. In *Mesozoic Systems of the Rocky Mountain Region, United States*, ed. M.V. Caputo, J.A. Peterson, K.J. Franczyk, Denver, CO: RMS-SEPM, 95–108.

Lockley, M.G. and Hunt, A.P. (1995). *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. New York: Columbia University Press.

Lockley, M.G. and Meyer, C.A. (2000). *Dinosaur Tracks and Other Fossil Footprints of Europe.* New York: Columbia University Press.

Lockley, M.G. and Rainforth. E.C. (2002). The track record of Mesozoic birds and pterosaurs: an ichnological and paleoecological perspective. In *Mesozoic Birds: Above the Heads of Dinosaurs*, ed. L.M. Chiappe and L.M. Witmer, Berkley, CA: University of California Press, pp. 405–418.

Lockley, M.G., Houck, K.J. and Prince, N.K. (1986). North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. *Geological Society of America Bulletin*, 97, 1163–1176.

Lockley, M.G., Rindsberg, A.K. and Zeiler, R.M. (1987). The paleoenvironmental significance of the nearshore *Curvolithus* ichnofacies. *Palaios*, 2, 255–262.

Lockley, M.G., Holbrook, J., Hunt, AP., Matsukawa, M. and Meyer, C. (1992). The Dinosaur Freeway: a Preliminary Report on the Cretaceous Megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico. In *Mesozoic of the Western Interior*, ed. R. Flores, *Society for Sedimentary Geology Midyear Meeting, Fieldtrip Guidebook*, 39–54.

Lockley, M.G., Hunt, A.P. and Meyer, C.A. (1994). Vertebrate tracks and the ichnofacies concept: Implications for palaeoecology and palichnostratigraphy. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 241–268.

Lockley, M.G., Hunt, A.P., Haubold, H. and Lucas, S.G. (1995). Fossil footprints in the DeChelly Sandstone of Arizona: with paleoecological observations on the ichnology of dune facies. *Bulletin of New Mexico Museum of Natural History and Science*, 6, 225–233.

Lockley, M.G., Wright, J.L. and Matsukawa, M. (2001). A new look at *Magnoavipes* and so-called big bird tracks from Dinosaur Ridge (Cretaceous, Colorado). *The Mountain Geologist*, 38. 137–146.

Lockley, M.G., Matsukawa, M. and Jianjun, L. (2003). Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. *Ichnos*, 10, 169–177.

Lockley, M.G., Lucas, S.G., Hunt, A.P. and Gaston, R. (2004). Ichnofaunas from the Triassic–Jurassic boundary sequences of the Gateway area, western Colorado: implications for faunal composition and correlation with other areas. *Ichnos*, 11, 89–102.

Lockley, M.G., Matsukawa, M., Ohira, H., Li, J., Wright, J., White, D. and Chen, P. (2006). Bird track from Liaoning Province, China: New insights into avian Evolution during the Jurassic-Cretaceous transition. *Cretaceous Research*, 27, 33–43.

Lockley, M.G., Roberts, G. and Kim, J.Y. (2008a). In the footprints of our ancestors: an overview of the hominid track record. *Ichnos*, 15, 106–125.

Lockley, M.G., Garcia-Vasquez, R., Espinoza, E. and Lucas, S.G. (2008b). America's most famous hominid footprints: history and context of tracks from Nicaragua. *Ichnos*, 15, 55–69.

Löffler, E. and Margules, C. (1980). Wombats detected from space. *Remote Sensing of Environment*, 9, 47–56.

Lohrer, A.M., Thrush, S.F. and Gibbs, M.M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, 431, 1092–1095.

Loope, D.B. (1992). Comment on "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin". *Geology*, 20, 667–668.

Loope, D.B. (2006). Dry-season tracks in dinosaur-triggered grainflows. *Palaios*, 21, 132–142.

Loope, D.B. (2008). Life beneath the surfaces of active Jurassic dunes: Burrows from the Entrada Sandstone of south-central Utah. *Palaios*, 23, 411–419.

López Cabrera, M.I., Olivero, E.B., Carmona, N.B. and Ponce, J.J (2008). Cenozoic trace fossils of the *Cruziana, Zoophycos* and *Nereites* ichnofacies from the Fuegian Andes, Argentina. *Ameghiniana*, 45, 377–392.

Lord, A.R. (1990). The Pleistocene–Holocene transition in south-western Sweden and the recognition of deglaciation effects in adjacent seas. In Glacimarine Environments: Processes and Sediments, ed. J.A.. Dowdeswell and J.D. Scourse, *Geological Society, London, Special Publications*, 53, 317–328.

Loutit, T.S., Hardenbol, J., Vail, P.R. and Baum, G.R. (1988). Condensed sections: the Key to age determination and correlation of continental margin sequences. In *Sea Level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S.Hastings, C.G.St.C. Kendell, H.W. Posamentier, C.A. Ross and J.C. van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 183–213.

Lovegrove, B.G. and Siegfried, W.R. (1989). Spacing and origins of Mima-like earth mounds in the cape of South Africa. *South African Journal of Science*, 85, 108–112.

Löwemark, L. and Schäfer, P. (2003). Ethological implications from a detailed X-ray radiograph and 14C-study of the modern deep-sea Zoophycos. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 101–21.

Löwemark, L., Schönfeld, J., Werner, F. and Schäfer, P. (2004). Trace fossils as a paleoceanographic tool: evidence from late Quaternary sediments of the southwestern Iberian margin. *Marine Geology*, 204, 27–41.

Löwemark, L., Lin, H.L. and Sarnthein, M. (2006). Temporal variations of the trace fossil *Zoophycos* in a 425 ka long sediment record from the South China Sea: implications for the ethology of the *Zoophycos* producer. *Geological Magazine*, 143, 105–114.

Löwemark, L., Lin, I.T, Wang, C.H. and Schönfeld, J. (2007). A test of the Gradening Hypothesis for the trace fossil *Zoophycos*. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R. Bromley, L.A. Buatois, M.G. Mángano, J. Genise and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 79–86.

Lucas, S.G. (2001). Taphotaxon. *Lethaia*, 34, 30.

Lucas, S.G. (2004). A global hiatus in the Middle Permian tetrapod fossil record. *Stratigraphy*, 1, 47–64.

Lucas, S.G. (2007). Tetrapod footprint biostratigraphy and biochronology. *Ichnos*, 14, 5–38.

Lucas, S.G. and Hunt, A.P. (2006). Permian tetrapod footprint: Bioestratigraphy and biocronology. In *Non-marine Permian biostratigraphy and Biocronology*, ed. S.G. Lucas, G. Cassinis and J.W. Schneider, *Society for Sedimentary Geology Special Publication*, 265, 179–200.

Lucas, S.G. and Lerner, A.J. (2005). Lower Pennsylvanian invertebrate ichnofossils from the Union Chapel Mine, Alabama; a preliminary assessment. *Alabama Paleontological Society, Monographs*, 1, 147–152.

Lucas, S.G. and Lerner, A.J. (2006). Invertebrate ichnofossil assemblages of the Upper Triassic Redonda Formation at Mesa Redonda, East-Central New Mexico. In: *The Triassic-Jurassic Terrestrial Transition*, ed. J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 122–136.

Lucas, S.G., Lozovsky, V.R. and Shishkin, M.A. (1999). Tetrapod footprint from Early Permian redbeds of the northern Caucasus, Russia. *Ichnos*, 6, 277–281.

Lucas, S.G., Morgan, G.S., Hawley, J.W., Love, D.W. and Myers, R.G. (2002). Mammal footprints from the upper Pleistocene of the Tularosa Basin, Doña Ana County, New Mexico. In *Geology of White Sands*, ed. V. Lueth, K.A. Giles, S.G. Lucas, B.S. Kues, R.G. Myers and D. Ulmer-Scholle, *New Mexico Geological Society Guide Book*, 53, 285–288.

Lucas, S.G., Hunt, A.P., Mansky, C. and Calder, J.H. (2004a). The oldest tetrapod footprint ichnofaunas, from the Lower Mississippian Horton Bluff Formation, Nova Scotia, Canada. *Geological Society of America, Abstracts with Programs*, 36, 66.

Lucas, S.G, Lerner, A.J. and Hunt, A.P. (2004b). Permian tetrapod footprints from the Lucero Uplift, central New Mexico, and Permian footprint biostratigraphy. In *Carboniferous–Permian Transition at Carrizo Arroyo, Central New Mexico*, ed. S.G. Lucas and K.E. Ziegler, *New Mexico Museum of Natural History and Science Bulletin*, 25, 291–300.

Lucas, S.G., Lerner, A.J., Hannibal. J.T., Hunt, A.P. and Schneider, J.W. (2005). Trackway of a giant *Arthropleura* from the Upper Pennsylvanian of El Cobre Canyon, New Mexico. *New Mexico Geological Society, 56th Field Conference Guidebook, Geology of the Chama Basin*, pp. 279–282.

LucasS.G., LernerA.J., Spielmann, J.A. and Hunt, A.P. (2006a). Invertebrate ichnofossils from the Upper Triassic Bull Canyon Formation, east central New Mexico. In *The Triassic–Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 118–121.

Lucas S.G., Lerner A.J., Milner A.C. and Lockley M.G. (2006b). Lower Jurassic invertebrate ichnofossils from a clastic lake margin, Johnson Farm, Southwestern Utah. In *The Triassic-Jurassic Terrestrial Transition*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 128–136.

Lucas, S.G., Gobetz, K.E., Odier, G.P., McCormick, T. and Egan, C. (2006c). Tetrapod burrows from the Lower Jurassic Navajo Sandstone, southeast Utah. In *The Triassic-Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 147–154.

Lucas, S.G., Spielmann, J.A., Klein, K. and Lerner, A.J. (2010a). Ichnology of the Upper Triassic (Apachean) Redonda Formation, east-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 47, 1–75.

Lucas, S.G., Minter, N. and Hunt, A.P. (2010b). Re-evaluation of alleged bees' nests from the Upper Triassic of Arizona. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 286, 194–201.

Lyell, C. (1830). *Principles of Geology*. London: John Murray.

MacArthur, R.H. and Wilson E.O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

MacEachern, J.A. and Burton, J.A. (2000). Firmground *Zoophycos* in the Lower Cretaceous, Viking Formation Alberta: a distal expression of the *Glossifungites* ichnofacies. *Palaios*, 15, 387–398.

MacEachern, J.A. and Gingras, M. (2007). Recognition of brackish-water trace fossil assemblages in the Cretaceous western interior seaway of Alberta. In *Sediment-Organism Interactions: A Multifaceted Ichnology*, ed. R. Bromley, L.A. Buatois, M.G. Mángano, J. Genise and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 149–194.

MacEachern, J.A. and Pemberton, S.G. (1992). Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton. *Society for Sedimentary Geology Core Workshop*, 17, 57–84.

MacEachern, J.A. and Pemberton, S.G. (1994). Ichnological aspects of incised valley fill systems from the Viking Formation of the Western Canada Sedimentary Basin, Alberta, Canada. In *Incised Valley Systems: Origin and Sedimentary Sequences*, ed. R. Boyd, B.A. Zaitlin and R. Dalrymple, *Society for Sedimentary Geology Special Publication*, 51, 129–157.

MacEachern, J.A. and Pemberton, S.G. (1997). Ichnology: biogenic utility in genetic stratigraphy. *Canadian Society of Petroleum Geologists and Society for Sedimentary Geology Joint Convention (Calgary), Notes Core Conference*, 387–412.

MacEachern, J.A., Raychaudhuri, I. and Pemberton, S.G. (1992). Stratigraphic applications of the *Glossifungites* ichnofacies: delineating discontinuities in the rock record. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 169–198.

MacEachern, J.A., Zaitlin, B.A. and Pemberton, S.G. (1998). High-resolution sequence stratigraphy of early transgressive deposits, Viking Formation, Joffre Field, Alberta, Canada. *American Association of Petroleum Geologists, Bulletin*, 82, 729–756.

MacEachern, J.A., Zaitlin, B.A. and Pemberton, S.G. (1999a). A sharp-based sandstone of the Viking Formation, Joffre Field, Alberta, Canada: criteria for recognition of transgressively incised shoreface complexes. *Journal of Sedimentary Research*, 69, 876–892.

MacEachern, J.A., Stelck, C.R. and Pemberton, S.G. (1999b). Marine and marginal marine mudstone deposition: paleoenvironmental interpretations based on the integration of ichnology, palynology and foraminiferal paleoecology. In *Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic Analysis and Sedimentological Interpretation*, ed. K.M. Bergman and J.W. Snedden, *Society for Sedimentary Geology Special Publication*, 64, 205–225.

MacEachern, J.A., Zaitlin, B.A. and Pemberton, S.G. (1999c). Coarse-grained, shoreline-attached, marginal-marine parasequences of the Viking Formation, Joffre Field, Alberta, Canada. In *Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic Analysis and Sedimentological Interpretation*, ed. K.M. Bergman and J.W. Snedden, *Society for Sedimentary Geology Special Publication*, 64, 273–296.

MacEachern, J.A., Bann, K.L., Bhattacharya, J.P. and Howell, C.D. Jr. (2005). Ichnology of deltas: organism responses to the dynamic interplay of rivers, waves, storms, and tides. In *River Deltas: Concepts, Models, and Examples*, ed. L. Giosan and J.P. Bhattacharya, *Society for Sedimentary Geology Special Publication*, 83, 49–85.

MacEachern, J.A., Bann, K.L., Pemberton, S.G. and Gingras, M.K. (2007a). The Ichnofacies paradigm: High-resolution paleoenvironmental interpretation of the rock record. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 27–64.

MacEachern, J.A., Pemberton, S.G. and Bhattacharya, J.P. (2007b). Ichnological and sedimentological evaluation of the Ferron Sandstone Cycles in Ivie Creek Cores #3 and #11. In *Ichnological Applications to Sedimentological and Sequence Stratigraphic Problems*, ed. J.A. MacEachern, M.K. Gingras, K.L. Bann and S.G. Pemberton, *Society for Sedimentary Geology Research Conference Abstract Volume*, 144–174.

MacEachern, J.A., Pemberton, S.G., Gingras, M.K., Bann, K.L. and Dafoe, L.T. (2007c). Use of trace fossils in genetic stratigraphy. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 110–134.

Mackie, G.L. (2001). *Applied Aquatic Ecosystem Concepts*. Dubuque, IA: Kendall/Hunt.

MacNaughton, R.B. (2007). The application of trace fossils to biostratigraphy. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 135–158.

MacNaughton, R.B. and Narbonne, G.M. (1999). Evolution and ecology of Neoproterozoic-Lower Cambrian trace fossils, NW Canada. *Palaios*, 14, 97–115.

MacNaughton, R.B. and Pickerill, R.K. (1995). Invertebrate ichnology of the nonmarine Lepreau Formation (Triassic), southern New Brunswick, eastern Canada. *Journal of Paleontology*, 69, 160–171.

MacNaughton, R.B. and Pickerill, R.K. (2003). Taphonomy and the taxonomy of trace fossils: a commentary. *Lethaia*, 36, 66–70.

MacNaughton, R.B., Narbonne, G.M., Dalrymple, R.W. (2000). Neoproterozoic slope deposits, Mackenzie Mountains, northwestern Canada: implications for passive-margin development and Ediacaran faunal ecology. *Canadian Journal of Earth Sciences*, 37, 997–1020.

MacNaughton, R.B., Cole, J.M., Dalrymple, R.W., Braddy, S.J., Briggs, D.E.G. and Lukie, T.D. (2002). First steps on land: Arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology*, 5, 391–394.

Macsotay, O. (1967). Huellas problemáticas y su valor paleoecológico en Venezuela. *Geos*, 16, 7–79.

Maerz, R.H. Jr., Kaesler, R.L. and Hakes, W.G. (1976). Trace fossils from the Rock Bluff Limestone (Pennsylvanian, Kansas). *The University of Kansas Paleontological Contributions*, 80, 1–6.

Mafart, B. (2006). Anthropological study of Holocene human footprints of the sebkra El Azrag (Islamic Republic of Mauritania). *Anthropologie*, 110, 766–787.

Magwood, J.P.A. (1992). Ichnotaxonomy: a burrow by any other name? In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Short Courses in Paleontology*, 5, 15–33.

Magwood, J.P.A. and Pemberton, S.G. (1990). Stratigraphic significance of Cruziana: New data concerning the Cambrian–Ordovician ichnostratigraphic paradigm. *Geology*, 18, 729–732.

Main, B.Y. (1982). Adaptations to arid habitats by mygalomorph spiders. In *Evolution of the Flora and Fauna of Arid Australia*, ed. W.R. Barker and P.J.M. Greenslade, Norwood, Australia: Peacock Publications, pp. 273–283.

Malanson, G.P. (1993). *Riparian Lanscapes.* Cambridge, UK: Cambridge University Press.

Mángano, M.G. (2011). Trace-fossil assemblages in a Burgess Shale-type deposit from the Stephen Formation at Stanley Glacier, Canadian Rocky Mountains: Unraveling ecologic and evolutionary controls. In *Proceedings of the International Conference on the Cambrian Explosion*, ed. P.A. Johnston and K.J. Johnston, *Palaeontographica Canadiana*, 31, in press.

Mángano, M.G. and Buatois, L.A. (1991). Discontinuity surfaces in the Lower Cretaceous of the High Andes (Mendoza, Argentina): Trace fossils and environmental implications. *Journal of South American Earth Sciences*, 4, 215–229.

Mángano, M.G. and Buatois, L.A. (1994). Trazas fósiles e icnofábricas en depósitos carbonáticos cretácicos, Las Cuevas, Alta Cordillera de Mendoza. *Ameghiniana*, 31, 55–66.

Mángano, M.G. and Buatois, L.A. (1995a). A conceptual framework for trace fossil lagerstatten. *2nd International Symposium on Lithographic Limestones, Extended Abstracts*, 103–105.

Mángano, M.G. and Buatois, L.A. (1995b). Biotic response to volcanic and sedimentologic processes in a Gondwanic active plate margin basin; the Arenig-Llanvirn Suri Formaiton, Famatina Basin, Northwest Argentina. *Field Trip Guidebook- Pacific section, Society for Sedimentary Geology*, 77, 229–232.

Mángano, M.G. and Buatois, L.A. (1996). Shallow marine event sedimentation in a volcanic arc-related setting: the Ordovician Suri Formation, Famatina Range, northwest Argentina (Famatina System). *Sedimentary Geology*, 105, 63–90.

Mángano, M.G. and Buatois, L.A. (1997). Slope apron deposition in an Ordovician arc-related setting, Chaschuil area, Famatina Basin, Northwest Argentina. *Sedimentary Geology*, 109, 155–180.

Mángano, M.G. and Buatois, L.A. (1999a). Feeding adaptations. In *Encyclopedia of Paleontology, Volume 1*, ed. R. Singer, Chicago: Fitzroy Dearborn Publishers, pp. 458–465.

Mángano, M.G. and Buatois, L.A. (1999b). Ichnofacies models in Early Paleozoic tide-dominated quartzites: onshore–offshore gradients and the classic Seilacherian paradigm. *Acta Universitatis Carolinae*, 43, 151–154.

Mángano, M.G. and Buatois, L.A. (2003a). Trace Fossils. In *Ordovician Fossils of Argentina*, ed. J.L. Benedetto, Cordoba, Spain: Universidad Nacional de Córdoba, Secretaría de Cienciay Tecnología, pp. 507–553.

Mángano, M.G. and Buatois, L.A. (2003b). *Rusophycus leifeiriksssoni* en la Formación Campanario: Implicancias paleobiológicas, paleoecológicas y paleoambientales. In *Icnología: Hacia una convergencia entre geología y biología*, ed. L.A. Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 65–84.

Mángano, M.G. and Buatois, L.A. (2004a). Ichnology of Carboniferous tide-influenced environments and tidal flat variability in the North American Midcontinent. In *The application of ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 157–178.

Mángano, M.G. and Buatois, L.A. (2004b). Reconstructing Early Phanerozoic intertidal ecosystems: Ichnology of the Cambrian Campanario Formation in northwest Argentina. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 17–38.

Mángano, M.G. and Buatois, L.A. (2004c). Decoupling of ichnotaxonomic diversification and mixground ecology during the Early Cambrian. In *First International Congress on ichnology, Trelew, Argentina*, ed. L.A. Buatois and M.G. Mángano, Museo Paleontologico Egidio Fureglio, 50.

Mángano, M.G. and Buatois, L.A. (2006). Nemakit-Daldynian ichnofaunas: Evidence of a phylogenetic fuse to the Cambrian explosion? *Geological Society of America Annual Meeting, Abstracts with Program*, 474.

Mángano, M.G. and Buatois, L.A. (2007). Trace fossils in evolutionary paleoecology. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 391–409.

Mángano, M.G. and Buatois, L.A. (2011). Timing of Infaunalization in shallow-marine Early Paleozoic communities in Gondwanan Settings: Discriminating evolutionary and paleogeographic controls. *Palaeontologica Electronica*, 14, in press.

Mángano, M.G. and Caron, J.B. (2008). What can trace fossils tell us about the Burgess Shale? In *Second International Congress on Ichnology, Cracow*, ed. A. Uchman, *Polish Geological Institute Abstract Book*, pp. 73–75.

Mángano, M.G. and Droser, M.L. (2004). The ichnologic record of the Ordovician radiation. In *The Great Ordovician Biodiversification Event*, ed. B.D. Webby, F. Paris, M.L. Droser and I.G. Percival, New York: Columbia University Press.

Mángano, M.G., Buatois, L.A., Wu, X., Sun, J. and Zhang, G. (1994). Sedimentary facies, depositional processes and climatic controls in a Triassic lake, Tanzhuang Formation, western Henan Province, China. *Journal of Paleolimnology*, 11, 41–65.

Mángano, M.G., Buatois, L.A. and Claps, G. (1996a). Grazing trails formed by soldier fly larvae (Diptera, Stratiomyidae) and their paleoenvironmental and paleoecological implications for the fossil record. *Ichnos*, 4, 163–167.

Mángano, M.G., Buatois, L.A. and Aceñolaza, G.F. (1996b). Trace fossils and sedimentary facies from an Early Ordovician tide-dominated shelf (Santa Rosita Formation, northwest Argentina): Implications for ichnofacies models of shallow marine successions. *Ichnos*, 5, 53–88.

Mángano, M.G., Buatois, L.A. and Aceñolaza, F.G. (1996c). Icnología de ambientes marinos afectados por vulcanismo: La Formación Suri, Ordovícico del extremo norte de la sierra de Narváez, Sistema del Famatina. *Asociación Paleontológica Argentina, Publicación Especial*, 4, 69–88.

Mángano, M.G., Buatois, L.A., Maples, C.G. and Lanier, W.P. (1997). *Tonganoxichnus*, a new insect trace fossil from the Upper Carboniferous of eastern Kansas, USA. *Lethaia*, 30, 113–125.

Mángano, M.G., Buatois, L.A., West, R.R. and Maples, C.G. (1998). Contrasting behavioral and feeding strategies recorded by tidal-flat bivalve trace fossils from the Upper Carboniferous of eastern Kansas. *Palaios*, 13, 335–351.

Mángano, M.G., Buatois, L.A., West, R.R. and Maples, C.G. (1999). The origin and paleoecologic significance of the trace fossil *Asteriacites* in the Pennsylvanian of Kansas and Missouri. *Lethaia*, 32, 17–30.

Mángano, M.G., Buatois, L.A., Maples, C.G. and West, R.R. (2000). A new ichnospecies of *Nereites* from Carboniferous tidal-flat facies of eastern Kansas, USA: Implications for the *Nereites-Neonereites* debate. *Journal of Paleontology*, 74, 149–157.

Mángano, M.G., Labandeira, C., Kvale, E. and Buatois, L.A. (2001a). The insect trace fossil *Tonganoxichnus* from the Middle Pennsylvanian of Indiana: Paleobiologic and paleoenvironmental implications. *Ichnos*, 8, 165–175.

Mángano, M.G., Buatois, L.A. and Moya, M.C. (2001b). Trazas fósiles de trilobites de la Formación Mojotoro (Ordovícico inferior-medio de Salta, Argentina): Implicancias paleoecológicas, paleobiológicas y bioestratigráficas. *Revista Española de Paleontología*, 16, 9–28.

Mángano, M.G., Buatois, L.A., West, R.R. and Maples, C.G. (2002a). Ichnology of a Pennsylvannian Equatorial Tidal Flat: the Stull Shale Member at Waverly, Eastern Kansas. *Kansas Geological Survey*, 245, 1–133.

Mángano, M.G., Buatois, L.A. and Rindsberg, A.K. (2002b). Carboniferous *Psammichnites*: systematic re-evaluation, taphonomy and autecology. *Ichnos*, 9, 1–22.

Mángano, M.G., Buatois, L.A. and Muñiz-Guinea, F. (2002c). *Rusophycus moyensis* n. isp. en la transición Cámbrica-Tremadociana del noroeste Argentino: implicancias paleoambientales y bioestratigráficas. *Revista Brasileira de Paleontologia*, 4, 35–44.

Mángano, M.G., Buatois, L.A. and Muñiz-Guinea, F. (2005a). Ichnology of the Alfarcito Member (Santa Rosita Formaiton) of northwestern Argentina: animal–substrate interactions in a lower Paleozoic wave-dominated shallow sea. *Ameghiniana*, 42, 641–668.

Mángano, M.G., Carmona, N.B., Buatois, L.A. and Muñiz-Guinea, F. (2005b). A new ichnospecies of *Arthrophycus* from the Upper Cambrian-lower Tremadocian of northwest Argentina: Implications for the Arthrophycid lineage and potential in ichnostratigraphy. *Ichnos*, 12, 179–190.

Mángano, M.G., Hofmann, R., Elicki, O. and Shinaq, R. (2007). The aftermath of the agronomic revolution: Trace fossils from Lower to Middle Cambrian marginal-marine environments, Hanneh Member, Burj Formation, southern Dead Sea, Jordan. *Quinta Reunion Argentina de Icnologia y Tercera Reunion de Icnologia del Mercosur*, 23.

Mangum, C.P. (1964). Studies on speciation in maldanid polychaetes of the North American Atlantic coast II. Distribution and competitive interaction of five sympatric species. *Limnology and Oceanography*, 9, 12–26.

Manning, P.L. (2008). *T. rex* speed trap. In *Tyrannosaurs rex: The Tyrant King*, ed. K. Carpenter and P.L. Larson, Bloomington, IN: Indiana University Press, pp. 204–231.

Manning, P.L., Margetts, L., Johnson, M.R., Withers, P., Sellers, W.I., Falkingham, P.L., Mummery, P.M., Barret, P.M. and Raymont, D.R. (2009). Biomechanics of dromaeosaur dinosaur claws: Application of x-ray microtomography, nanoidentation and finite element analysis. *Invited paper, Anatomical Record*, 292, 1397–1405.

Manton, S.M. (1977). The *Arthropoda. Habits, Functional Morphology, and Evolution*. Oxford UK: Clarendon Press.

Maples, C.G. and Archer, A.A. (1986). Shoaling-upward sequences and facies-dependent trace fossils in the Monteagle Limestone (Mississippian) of Alabama. *Southeastern Geology*, 27, 35–43.

Maples, C.G. and Archer, A.A. (1989). The potential of Paleozoic nonmarine trace fossils for paleoecological interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 73, 185–195.

Marshall, C.D. (2006). Explaining the Cambrian "explosion" of animals. *Annual Review of Earth and Planetary Science*, 34, 355–384.

Marintsch, E. J., and Finks, R. M. (1982). Lower Devonian ichnofacies at Highland Mills, New York and their gradual replacement across environmental gradients. *Journal of Paleontology*, 56, 1050–1078.

Marsicano, C.A., Arcucci, A., Mancuso, A.C. and Caselli, A. (2004). Early–Middle Triassic tetrapod footprints of southern South America: a phylogenetic approach. *Ameghiniana*, 41, 171–184.

Marsicano, C.A., Domnanovich, N. and Mancuso, A.C. (2007). Dinosaur origins: evidence from the footprint record. *Historical Biology*, 19, 83–91.

Marsicano, C.A., Mancuso, A.C., Palma, R.M. and Krapovickas, V. (2010). Tetrapod tracks in a marginal lacustrine setting (Middle Triassic, Argentina): taphonomy and significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291, 388–399.

Martin, A.J. (1993). Semiquantitative and statistical analysis of bioturbate textures, Sequatchie Formation (Upper Ordovician), Georgia and Tennessee, USA. *Ichnos*, 2, 117–136.

Martin, A.J. (2006a). Resting traces of *Ocypode qudrata* associated with hydration and respiration: Sapelo Island, Georgia, USA. *Ichnos*, 13, 57–68.

Martin, A.J. (2006b). A composite trace fossil of decapod and hymenopteran origin from the Rice Bay Formation (Holocene), San Salvador, Bahamas. *The 12th Symposium on the Geology of the Bahamas and other Carbonate Regions*, pp. 99–112.

Martin, A.J. and Pyenson, N.D. (2005). Behavioral significance of vertebrate trace fossils from the Union Chapel site. *Alabama Paleontological Society, Monographs*, 1, 59–73.

Martin, A.J., Close, J.C. and Simones, G.C. (1994). Theoretical and practical considerations of integrating subsurface ichnological and geophysical data in Late Cretaceous strata, southeastern Atlantic Coastal Plain, USA. *14th International Sedimentological Congress (Recife), Abstracts of Papers*, S52–S53.

Martin, K.D. (2004). A re-evaluation of the relationship between trace fossils and dysoxia. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 141–156.

Martin, L.D. and Bennett, D.K. (1977). The burrows of the Miocene beaver *Paleocastor*, western Nebraska, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 22, 173–193.

Martin, M.A. and Pollard, J.E. (1996). The role of trace fossil (ichnofabric) analysis in the development of depositional models for the Upper Jurassic Fulmar Formation of the Kittiwake Field (Quadrant 21 UKCS). In *Geology of the Humber Group: Central Graben and Moray Firth, UKCS*, ed. A. Hurst, *Geological Society Special Publication*, 114, 163–183.

Martin, M.W., Grazhdankin, D.V., Bowring, S.A., Evans, D.A.D., Fedonkin, M.A. and Kirschvink, J.L. (2000) Age of Neoproterozoic bilaterian body and trace fossils, White Sea, Russia: implications for metazoan evolution. *Science*, 288, 841–845.

Martin, P., Boes, X., Goddeeris, B. and Fagel, N. (2005). A qualitative assessment of the influence of bioturbation in Lake Baikal sediments. *Global Planet Change*, 46, 87–99.

Martinell, J. and Domènech, R. (1995). Bioerosive structures on the Pliocene rocky shores of Catalonia (Spain). *Revista Española de Paleontología*, 10, 37–44.

Martinius, A.W. and Molenaar, N. (1991). A coral–mollusc (*Goniaraea–Crassatella*) dominated hardground community in a siliciclastic-carbonate sandstone (the Lower Eocene Roda Formation, Southern Pyrenees, Spain). *Palaios*, 6, 142–155.

Martinius, A. W., Kaas, I., Næss, A., Helgesen, G., Kjærefjord, J.M, and Leith, D.A. (2001) Sedimentology of the heterolithic and tide-dominated Tilje Formation (Early Jurassic, Halten Terrace offshore mid-Norway). In *Sedimentary environments Offshore Norway: Palaeozoic to Recent*, ed. O. Martinsen and T. Dreyer, *Norwegian Petroleum Society, Special Publication*, 10, 103–144.

Martinsson, A. (1970). Toponomy of trace fossils. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 323–330.

Mason, T.R. (1980). Formation and diagenesis of Visean trace fossils from Ireland. *Lethaia*, 13, 229–237.

Masselink, G. and Hegge, B.J. (1995). Morphodynamics of meso- and macrotidal beaches. Examples from central Queensland. *Marine Geology*, 129, 1–23.

Masselink, G. and Short, A.D. (1993). The effect of tidal range on beach morphodynamics and morphology: a conceptual beach model. *Journal of Coastal Research*, 9, 785–800.

Mastrolorenzo, G., Petrone, P., Pappalardo, L. and Sheridan, M.F. (2006). The Avellino 3780-yr-B.P. catastrophe as a worst-case scenario for a future eruption at Vesuvius. *Proceedings of the National Academy of Sciences, USA*, 103, 4366–4370.

Matthews, S.C. and Missarzhevsky, V.V. (1975). Small shelly fossils of late Precambrian and Early Cambrian age: a review of recent work. *Journal of the Geological Society, London*, 131, 289–304.

Mata, S.A. and Bottjer, D.J. (2009) The paleoenvironmental distribution of Phanerozoic wrinkle structures. *Earth Science Reviews*, 96, 181–195.

Matz, M.V., Frank, T.M., Marshall, N.J., Widder, E.A. and Johnsen, S. (2008). Giant deep-sea Protist produces bilaterian-like traces. *Current Biology*, 18, 1849–1854.

Mayor, A. and Sarjeant, W.A.S. (2001). The folklore of footprints in stone: From classical antiquity to the present. *Ichnos*, 8, 143–163.

Mayoral, E. and Muñiz, F. (1996). La icnofacies de *Gnathichnus* en el sector suroccidental de la Cuenca del Guadalquivir (Lepe, Huelva, España). *Coloquios de Paleontología*, 48, 71–82.

McCann, T. (1990). Distribution of Ordovician-Silurian ichnofossil assemblages in Wales: Implications for Phanerozoic ichnofaunas. *Lethaia*, 23, 243–255.

McCann, T. (1993). A *Nereites* ichnofacies from the Ordovician–Silurian Welsh basin. *Ichnos*, 3, 39–56.

McCann, T. and Pickerill, R.K. (1988). Flysch trace fossils from the Cretaceous Kodiak Formation of Alaska. *Journal of Paleontology*, 62, 330–348.

McCrea, R.T., Pemberton, S.G. and Currie, P J. (2004). New ichnotaxa of mammal and reptile tracks from the upper Paleocene of Alberta. *Ichnos*, 11, 323–339.

McGhee, G.R. Jr. (1996). *The Late Devonian Mass Extinction*. New York: Columbia University Press.

McGhee, G.R. Jr. (2001). The "multiple impacts hypothesis" for mass extinction: a comparison of the late Devonian and the late Eocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 176, 47–58.

McGhee, G.R. Jr., Sheehan, P.M., Bottjer, D.J. and Droser, M.L. (2004). Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 211, 289–297.

McIlroy, D. (2004a). Some Ichnolgical concepts, methodologies, applications and frontiers. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 3–27.

McIlroy, D. (2004). Ichnofabrics and sedimentary facies of a tide-dominated delta: Jurassic Ile Formation of Kristin Field, Haltenbanken, Offshore Mid-Norway. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, Geological Society Special Publication, 228, 237–272.

McIlroy, D. (2007a). Lateral variability in shallow marine ichnofabrics; implications for the ichnofabric analysis method. *Journal of the Geological Society, London*, 164, 359–369.

McIlroy, D. (2007b). Ichnology of a macrotidal tide-dominated deltaic depositional system: Lajas Formation, Neuquén Province, Argentina. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 195–211.

McIlroy, D. (2008). Ichnological analysis: the common ground between ichnofacies workers and ichnofabric analysts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 332–338.

McIlroy, D. (2010). Biogenic cross-lamination produced by the pistol-shrimp *Alpheus bellulus* in microcosm experiments. *Journal of Sedimentary Research*, 80, 151–154.

McIlroy, D. and Garton, M. (2004). A worm's eye view of the Early Palaeozoic sea floor. *Geology Today*, 20, 224–230.

McIlroy, D. and Logan, G.A. (1999). The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. *Palaios*, 14, 58–72.

McIlroy, D., Worden, R.H. and Needham, S.J. (2003). Faeces, clay minerals and reservoir potential. *Journal of the Geological Society, London*, 160, 489–493.

McIlroy, D., Brasier, M.D. and Lang, A.S. (2009) Smothering of microbial mats by macrobiota: implications for the Ediacara biota. *Journal of the Geological Society*, 166, 1117–1121.

McKeever, P.J. (1991). Trackway preservation in eolian sandstones from the Permian of Scotland. *Geology*, 19, 726–729.

McKeever, P.J. and Haubold, H. (1996). Reclassification of vertebrate trackways from the Permian of Scotland and related forms from Arizona and Germany. *Journal of Paleontology*, 70, 1011–1022.

McLusky, D.S. (1989). *The Estuarine Ecosystem. 2nd edn.* London: Blackie.

Meadows, A., Meadows, P.S. and McLoughlin, P. (1998). Spatial heterogeneity in an intertidal sedimentary environment and it's macrobenthic community. In *Sedimentary Processess in the Intertidal Zone*, ed. K.S. Black, D.M. Patterson and A. Cramp, *Geological Society Special Publication*, 139, 367–388.

Meadow, P.S. and Anderson, J.G. (1968). Micro-organisms attached to marine sand grains. *Journal of the Marine Biology Association of the United Kingdom*, 48, 161–175.

Melchor, R.N. (2001). Icnología y sedimentología de una sucesión lacustre influenciada por tormentas: Formación Los Rastros (Triásico), Talampaya, La Rioja. *Abstracts 4th Reunión Argentina de Icnología and 2nd Reunión de Icnología del Mercosur*, *San Miguel de Tucumán*, 56.

Melchor, R.N. (2004). Trace fossil distribution in lacustrine deltas: examples from the Triassic rift lakes of the Ischigualasto-Villa Union Basin, Argentina. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 335–354.

Melchor, R.N. (2007). Changing lake dynamics and sequence stratigraphy of synrift lacustrine strata in a haf-graben: an example from the Triassic Ischigualasto–Villa Unión Basin, Argentina. *Sedimentology*, 54, 1417–1446.

Melchor, R.N. and Genise, J.F. (2004a). Critical appraisal of vertebrate ichnotaxonomy. *32nd International Geological Congress Italia 2004, Abstracts part 1. International Union of Geological Sciences*, 597.

Melchor, R.N. and Genise, J.F. (2004b). Vertebrate vs. Invertebrate ichnology…or one ichnology. In *First International Congress on Ichnology, Trelew, Argentina*, ed. L.A. Buatois and M.G. Mángano, *Museo Paleontólogico Egidio Feruglio Abstract Book*, 55–56.

Melchor, R.N. and Sarjeant, W.A.S. (2004). Small amphibian and reptile footprints from the Permian Carapacha Basin, Argentina. *Ichnos*, 11, 57–78.

Melchor, R.N., Genise, J.F. and Miquel, S.E. (2002). Ichnology, sedimentology and paleontology of Eocene calcareous paleosols from a palustine sequence, Argentina. *Palaios*, 17, 16–35.

Melchor, R.N., Bellosi, E. and Genise, J.F. (2003). Invertebrate and vertebrate trace fossils from a lacustrine delta: The Los Rastros Formation, Ischigualasto Provincial Park, San Juan, Argentina. In *Icnología: Hacia una Convergencia entre Geología y Biología*, ed. L.A. Buatois and M.G. Mángano, *Asociación Paleontológica Argentina Publicación Especial*, 9, 17–33.

Melchor, R.N., Bedatou, E., Valais, S. de and Genise, J.F. (2006). Lithofacies distribution of invertebrate and vertebrate trace fossil assemblages in an Early Mesozoic ephemeral fluvio- lacustrine system from Argentina: Implications for the *Scoyenia* ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239, 253–285.

Meldrum, D.J., Lockley, M.G., Lucas, S.G. and Mussiba, C. (2011). Ichnotaxonomy of the Laetoli trackways: the earliest hominin footprints. *Journal of African Earth Sciences*, in press.

Mellere, D. and Steel, R.J. (1995). Facies architecture and sequentiality of nearshore and "shelf" sandbodies; Haystack Mountains Formation, Wyoming, USA. *Sedimentology*, 42, 551–574.

Metz, R. (1991). Scratch circles from the Towaco Formation (Lower Jurassic), Riker Hill, Roseland, New Jersey. *Ichnos*, 1, 233–235.

Metz, R. (1993). A new ichnospecies of *Spongeliomorpha* from the Late Triassic of New Jersey. *Ichnos*, 2, 259–262.

Metz, R. (1995). Ichnologic study of the Lockatong Formation (Late Triassic), Newark Basin, southeastern Pennsylvania. *Ichnos*, 4, 43–51.

Metz, R. (1996). Newark Basin ichnology: The Late Triassic Perkasie Member of the Passaic Formation, Sanatoga, Pennsylvania. *Notheastern Geology and Environmental Sciences*, 18, 118–129.

Metz, R. (2000). Triassic Trace Fossils from Lacustrine Shoreline Deposits of the Passaic Formation, Douglassville, Pennsylvania. *Ichnos*, 7, 243–318.

Miall, A.D. (1995). Whither stratigraphy? *Sedimentary Geology*, 100, 5–20.

Miall, A.D. (1996). *The Geology of Fluvial Deposits*. Berlin: Springer-Verlag.

Michener, C.D. (1979). Biogeography of the bees. *Annals of the Missouri Botanical Garden*, 66, 277–347.

Mietto, P., Avanzini, M. and Rolandi, G. (2003). Human footprints in Pleistocene volcanic ash. *Nature*, 422, 133.

Mikuláš, R. (1990). The ophiuroid *Taeniaster* as a tracemaker of *Asteriacites*, Ordovician of Czechoslovakia. *Ichnos*, 1, 133–137.

Mikuláš, R. (1992). The ichnogenus *Asteriacites*: paleoenvironmental trends. *Vêstnik Ceského geologického ústavu*, 67, 423–433.

Mikuláš, R. (1995). Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic). *Journal of the Czech Geological Society*, 40, 37–45.

Mikuláš, R. (1997). Ethological interpretation of the ichnogenus *Pragichnus* Chlupáč, 1987 (Ordovician, Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie*, *Monatshefte*, 2, 93–108.

Mikuláš, R. (1998). Ordovician of the Barrandian area: Reconstruction of the sedimentary basin, its benthic communities and ichnoassemblages. *Journal of the Czech Geological Society*, 43, 143–159.

Mikuláš, R. (2003): The *Mermia* Ichnofacies across the fossilization barrier: a comparison of the Permian Krkonoše Piedmont Basin (Czech Republic) and modern flood sediments at Prague. VII International Ichnofabric Workshop, Program, Abstracts, pp. 44–45.

Mikuláš, R, (2008). Xylic substrates at the fossilization barrier: oak trunks (*Quercus* sp.) in the Holocene sediments of the Labe River, Czech Republic. In *Current Developments in Bioerosion*, ed. M. Wisshak and L. Tapanila, Berlin: Springer-Verlag, pp. 415–429.

Mikuláš, R. and Cílek, V. (1998). Terrestrial insect bioerosion and the possibilities of its fossilization. *Ichnos*, 5, 325–333.

Mikuláš, R. and Genise, J.F. (2003). Traces within traces: holes, pits and galleries in walls and fillings of insect trace fossils in paleosols. *Geologica Acta*, 1, 339–348.

Miller, G.D. (1986). The sediments and trace fossils of the Rough Rock Group on Cracken Edge, Derbyshire. *Mercian Geologist*, 10, 189–202.

Miller, M.F. (1984). Distribution of biogenic structures in Paleozoic non–marine and marine–margin sequences: an actualistic model. *Journal of Paleontology*, 58, 550–570.

Miller, M.F. (1991). Morphology and paleoenvironmental distribution of Paleozoic *Spirophyton* and *Zoophycos*: implications for the *Zoophycos* ichnofacies. *Palaios*, 6, 410–425.

Miller, M.F. (2000). Benthic aquatic ecosystems across the Permian–Triassic transition: record from biogenic structures in fluvial sandstones, central Transantarctic Mountains. *Journal of African Earth Sciences*, 31, 157–164.

Miller, M.F. and Byers, C.W. (1984). Abundant and diverse early Paleozoic infauna indicated by the stratigraphic record. *Geology*, 12, 40–43.

Miller, M.F. and Collinson, J.W. (1994). Trace fossils from Permian and Triassic sandy braided stream deposits, Central Transantarctic Mountains. *Palaios*, 9, 605–610.

Miller, M.F. and Johnson, K.G. (1981). *Spirophyton* in alluvial-tidal facies of the Catskill deltaic complex: possible biological control of ichnofossil distribution. *Journal of Paleontology*, 55, 1016–1027.

Miller, M.F. and Labandeira, C.C. (2003). Slow crawl across the salinity divide: Delayed colonization of freshwater ecosystems by invertebrates. *GSA Today*, 12, 4–10.

Miller, M.F. and Knox, L.W. (1985). Biogenic structures and depositional environments of a Lower Pennsylvanian coal-bearing sequence, northern Cumberland Plateau, Tennessee, USA. In *Biogenic Structures: their use in interpreting depositional environments*, ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 67–97.

Miller, M.F. and Smail, S.E. (1997). A semiquantitative method for evaluating bioturbation on bedding planes. *Palaios*, 12, 391–396.

Miller, M.F. and White, D.S. (2007). Ecological and evolutionary controls on the composition of marine and lake ichnofacies. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 531–544.

Miller, M.F. and Woodrow, D.L. (1991). Shoreline deposits of the Catskill deltaic complex, Schoharie Valley, New York. *Bulletin of the New York State Museum*, 469, 153–177.

Miller, M.F., Collinson, J.W. and Frisch, R.A. (1991). Depositional setting and history of a Permian post–glacial black shale: Mackellar Formation, Central Transantarctic Mountains. In *Gondwana Seven Proceedings, Sao Paulo*, ed. H. Ulbrich and A.C. Rocha Campos, pp. 201–215.

Miller, M.F., McDowell, T.A., Smail, S.E., Shyr, Y. and Kemp, N.R. (2002). Hardly used habitats: dearth and distribution of burrowing in Paleozoic and Mesozoic stream and lake deposits. *Geology*, 30, 527–530.

Miller, W., III. (1991a). Paleoecology of graphoglyptids. *Ichnos*, 1, 305–312.

Miller, W., III. (1991b). Intrastratal trace fossil zonation, Cretaceous flysch of northern California. *Ichnos*, 1, 161–171.

Miller, W., III (1996). Sabellariid polychaete squatters in *Teredolites*: possible source of composite ichnotaxa in xylic substrates. *Ichnos*, 4, 317–319.

Miller, W., III. (1998). Complex marine trace fossils. *Lethaia*, 31, 29–32.

Miller, W., III. (2002). Complex trace fossils as extended organisms: a proposal. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 3, 147–158.

Miller, W., III. (2003). Paleobiology of complex trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 3–14.

Miller, W., III. and D'Alberto, L. (2001), Paleoethologic implication of *Zoophycos* from Late Cretaceous and Paleocene limestone of the Venetian Prealps, northeastern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 237–247.

Miller, W., III and Vokes, E.H. (1998). Large *Phymatoderma* in Pliocene slope deposits, Northwestern Ecuador: associated ichnofauna, fabrication, and behavioral ecology. *Ichnos*, 6, 23–45.

Milner, G.R. and Smith, V.G. (2005). Carnivore alteration of human bone from a late prehistoric site in illinois. *American. Journal of Physical Anthropology*, 79, 43–49.

Milton, S.J. and Dean, W.R.J. (1990). Mima-like mounds in the southern and western Cape: Are the origins so mysterious? *South African Journal of Science*, 86, 207–208.

Minter, N.J. and Braddy, S.J. (2006a). Walking and jumping with Palaeozoic apterygote insects. *Palaeontology*, 49, 827–835.

Minter, N.J. and Braddy, S.J. (2006). The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA. *Palaeontology*, 49, 1123–1142.

Minter, N.J. and Braddy, S.J. (2009). Ichnology of an Early Permian tidal flat: The Robledo Mountains Formation of the Robledo Mountains, Southern New Mexico, USA. *Special Papers in Palaeontology*, 82, 1–107.

Minter, N.J., Buatois, L.A., Lucas, S.G., Braddy, S.J. and Smith, J.A. (2006). Spiral-shaped Graphoglyptids from an Early Permian Intertidal Flat. *Geology*, 34, 1057–1060.

Minter, N.J., Braddy, S.J., and Davis, R.B. (2007a). Between a rock and a hard place: arthropod trackways and ichnotaxonomy. *Lethaia*, 40, 365–375.

Minter, N.J., Krainer, K., and Lucas, S.G. (2007b). Paleoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA. *Palaeogeography, Paleoclimatology, palaeoecology*, 246, 390–423.

Moloney, C.L., Levin, S.A., Chiariello, N.R. and Buttel, L. (1992). Pattern and scale in a serpentine grassland. *Theoretical Population Biology*, 41, 257–276.

Monaco, P. (1995). Relationships between trace-fossil communities and substrate characteristics in some Jurassic pelagic deposits in the Umbria-Marche Basin, central Italy. *Geobios, Memoire Special*, 18, 299–311.

Monaco, P. and Giannetti, A. (2002). Three-dimensional burrow systems and taphofacies in shallowing-upward parasequences, lower Jurassic carbonate platform (Calcari Grigi, Southern Alps, Italy). *Facies*, 47, 57–82.

Montague, C.L., Bunker, S.M., Haines, E.B., Pace, M.L. and Wetzel, R.L. (1981). Aquatic macroconsumers. In *The Ecology of Salt Marsh*, ed. L.R. Pomeroy and R.G. Wiegert, Springer-Verlag, New York, 69–85.

Montague, K.E., Walton, A.W. and Hasiotis, S.T. (2010). Euendolithic microborings in basalt glass fragments in hyaloclastites: Extending the ichnofabric index to microbioerosion. *Palaios*, 25, 393–399.

Moore, D.G. and Scruton, P.C. (1957). Minor internal structures of some recent unconsolidated sediments. *American Association of Petroleum Geologists, Bulletin*, 41, 2723–2751.

Morales, M. and Haubold, H. (1995). Tetrapod tracks from the Lower Permian DeChelly Sandstone of Arizona: Systematic description. In *Early Permian footprints and facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 251–261.

Moran, D.P. and Reaka, M.L. (1988). Bioerosion and the availability of shelter for benthic reef organisms. *Marine Ecology Progress Series*, 44, 249–263.

Moreno, F., Vegas, R. and Marcos, A. (1976). Sobre la edad de las series Ordovicicas y Cambricas relacionadas con la discordancia "Sárdica" en el anticlinal de Valdelacasa (Monetes de Toledo, España). *Breviora Geologica Astúrica*, 20, 8–16.

Morrissey, L.B. and Braddy, S.J. (2004). Terrestrial trace fossils from the Lower Old Red Sandstone, southeast Wales. *Geological Journal*, 39, 315–336.

Morrissey, L.B., Braddy S.J., Bennett J.P., Marriott S.B. and Tarrant P.R. (2004). Fish trails from the Lower Old Red Sandstone of Tredomen Quarry, Powys, southeast Wales. *Geological Journal*, 39, 337–358.

Morrow, J.R. and Hasiotis, S.T. (2007). Endobenthic response through mass extinction episodes: Predictive models and observed patterns. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Elsevier, Amsterdam, 575–611.

Mountney, N.P. (2004). The sedimentary signature of desert systems and their response to environmental change. *Geology Today*, 20, 101–106.

Mountney, N.P. (2006). Eolian facies models. In *Facies Models Revisited*, ed. H. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 19–83.

Mueller-Dombois, D. and Ellenberg, H. (1980). Methods available for vegetation classification and their suitability for various purposes. In *The IBP Survey of Conservation Sites: An Experimental Study*, ed. A.R. Clapham, IBP Internat'l Series No. 24, Cambridge University Press, 26–54.

Mulder, T. and Syvitski, J.P.M. (1995). Turbidity currents generated at river mouths during exceptional discharges to the world oceans. *Journal of Geology*, 103, 285–299.

Müller, A.H. (1962). Zur Ichnologie, Taxiologie und Okologie fossiler Tiere. *Freiberger Forschungshefte C*, 366, 7–27.

Müller, A.H. (1966). Neue Lebensspuren (Vestigia invertebratorum) aus dem Karbon und der Trias Mitteldeutschlands. *Geologie*, 15, 712–725.

Muñiz, F., Mayoral, E. and Martín, M. (1995). Pistas fósiles intergradacionales en el Mioceno superior del sector suroccidental de la cuenca del Guadalquivir. *Jornadas de Paleontología, Actas*, 11, 119–122.

Muñoz, N.G. (1986). Bioclastic carbonates of Margarita Island, Venezuela, as a key to exploration. *Carbonates and Evaporites*, 1, 13–23.

Muñoz, N.G. (1994). Engineering application of trace fossil analysis for oil reservoir quality and for a dam site in Venezuela. *14th International Sedimentological Congress (Recife)*, *Abstracts of Papers*, S54–S55.

Muñoz, N.G., Casas, J.E., Moreno, J. and Yoris, F. (1997). Flysch Eoceno de La Isla de Margarita y sus Facies Turbidíticas. 8º *Congreso Geológico Venezolano and* 1º *Latinoamericano de Sedimentología*, *Excursión No*. 2, 39.

Musiba, C., Mabula, A., Selvaggio, M. and Magori, C. (2008). Pliocene animal trackways at Laetoli: Research and conservation potential. *Ichnos*, 15, 166–178.

Mustoe, G.E. (2002). Eocene bird, reptile, and mammal tracks from the Chuckanut Formation, Northwest Washington. *Palaios*, 17, 403–413.

Murray, J.M.H., Meadows, A. and Meadows, P.S. (2002). Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. *Geomorphology*, 47, 15–30.

Mutti, E. (1979). Turbidites et cones sous-marins profonds. *Sedimentation detritique (fluviatile, littorale et marine*), *Institut de Geologie de l'University de Fribourg*, *Short Course*, 353–419.

Mutti, E. (1985). Turbidite systems and their relations to depositional sequences. In *Provenance of Arenites*, ed. G.G. Zuffa, Dordrecht: D. Reidel Publishing Company, pp. 65–93.

Mutti, E. (1992). *Turbidite Sandstones*. Parma, Italy: AGIP-Istituto di Geología, Università di Parma.

Mutti E. and Normark, W.R. (1991). An integrated approach to the study of turbidite systems. In *Seismic Facies and Sedimentary Processes of Modern and Ancient Submarine Fans*, ed. P. Weimer and M.H. Link, New York: SpringerVerlag, pp. 75–106.

Mutti, E. and Ricci Lucchi, F. (1972). Turbidite facies and facies associations. In *Examples of Turbidite Facies and Facies Association from Selected Formations of the Northern Apennines*, ed. E. Mutti, G.C. Parea, F. Ricci Lucchi, M. Sagri, G. Zanzucchi, G. Ghibaudo and S. Iaccarino, *Ninth International Congress on Sedimentology, A-11 of Fieldtrip Guidebook*, 21–36.

Mutti, E, Davoli, G., Tinterri, R. and Zavala, C. (1996). The importance of ancient fluvio-deltaic systems dominated by catastrophic flooding in tectonically active basins. *Memorie di Scienze Geologiche, Universita di Padova*, 48, 233–291.

Mynt, M. (2001). *Psilonichnus quietis* isp. nov. from the Eocene Iwaki formation, Shiramizu group, Joban coal field, Japan. *Ichnos*, 8, 1–14.

Mynt, M. (2007). The *Psilonichnus* Ichnofacies: An example from the Iwaki Formation, Shiramizu Group, Joban Coal Field, Japan. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras, and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 335–342.

Myrow, P.M. (1992). Pot and gutter casts from the Chapel Island Formation, southeast Newfoundland. *Journal of Sedimentary Petrology*, 62, 992–1007.

Myrow, P.M. (1995). *Thalassinoides* and the enigma of Early Paleozoic open-framework burrow Systems. *Palaios*, 10, 58–74.

Naiman, R.J., Decamps, H., Pastor, J. and Johnston, C.A. (1988). The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society*, 7, 289–306.

Naiman, R.J., Décamps, H. and McClain, M.E. (2005). *Riparia: Ecology, Conservation and Management of Streamside Communities.* San Diego: Elsevier.

Nair, N.B. and Ansell, A.D. (1968). The mechanism of boring in *Zirphaea crispata* (L) (Bivalvia: Pholadidae). *Proceedings of the Royal Society*, *Series B*, 170, 155–173.

Nara, M. (1995). *Rosselia socialis*: a dwelling structure of a probable terebellid polychaete. *Lethaia*, 28, 171–178.

Nara, M. (1997). High-resolution analytical method for event sedimentation using *Rosselia socialis*. *Palaios*, 12, 489–494.

Nara, M. (2002). Crowded *Rosselia socialis* in Pleistocene inner shelf deposits: benthic Paleoecology during rapid sea-level rise. *Palaios*, 17, 268–276.

Nara, M., Akiyama, H. and Itani, G. (2008). Macrosymbiotic association of the myid bivalve *Cryptomya* with thalassinidean shrimps: Examples from modern and Pleistocene tidal flats of Japan *Palaeogeography, Palaeoclimatology, Palaeoecology*, 261, 100–104.

Narbonne, G.M. (1984). Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada. *Journal of Paleontology*, 58, 398–415.

Narbonne, G.M. (2004). Modular construction of Early Ediacaran complex lifeforms. *Science*, 305, 1141–1144.

Narbonne, G.M. (2005). The Ediacara Biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences*, 33, 421–442.

Narbonne, G. M. and Aitken, J. D. (1990). Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada. *Palaeontology*, 33, 945–980.

Narbonne, G.M. and Gehling, J.G. (2003). Life after snowball: the oldest complex Ediacaran fossils. *Geology*, 31, 27–30.

Narbonne, G.M., Myrow, P.M. and Anderson, M.M. (1987). A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Canadian Journal of Earth Sciences*, 24, 1277–1293.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences, USA*, 105, 19052–19059.

Neal, E.G. and Roper, T.J. (1991). The environmental impact of badgers (*Meles meles*) and their sets. In *The Environmental Impact of Burrowing Animals and Animal Burrows*, ed. P.S. Meadows and A. Meadows, *Symposia of the Zoological Society of London*, 63.

Needham, S.J., Worden, R.H. and Cuadros, J. (2006). Sediment ingestion by worms and the production of bio-clays; a study of macrobiological enhanced weathering and early diagenetic processes. *Sedimentology*, 53, 567–579.

Neef, G. (2004a). Non-marine ?Late Silurian–Early Devonian trace fossils, Darling Basin, western New South Wales. *Alcheringa*, 28, 389–399.

Neef, G. (2004b). Devonian arthropod trackways from the fluvial Revendale Formation, western New South Wales. *Alcheringa*, 28, 401–402.

Neira, C., Sellanes, J., Levin L.A. and Arntz, W.E. (2001). Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. *Deep-Sea Research*, 48, 2453–2472.

Nesbitt, E.A. and Campbell, K.A. (2002). A new *Psilonichnus* ichnospecies attributed to mud-shrimp *Upogebia* in estuarine settings. *Journal of Paleontology*, 76, 892–901.

Nesbitt, E.A. and Campbell. K.A. (2006). The paleoenvironmental significance of *Psilonichnus*. *Palaios*, 21, 187–196.

Neto de Carvalho, C. (2006). Roller coaster behavior in the *Cruziana Rugosa* group from Penha Garcia (Portugal): implications for the feeding program of trilobites. *Ichnos*, 13, 255–265.

Netto, R.G. (1989). Paleoicnologia das sequencias eólicas sotopostas a Formacao Botucatu no Rio Grande do Sul. *Acta Geologica Leopoldensia*, 28, 31–44.

Netto, R.G. and Grangeiro, M.E. (2009). Neoichnology of the seaward side of Peixe Lagoon in Mostardas, southernmost Brazil: the *Psilonichnus* ichnocoenosis revisited. *Revista Brasileira de Paleontologia*, 12, 211–224.

Netto, R.G. and Martini da Rosa, C.L. (2001). A biota vendiana da sub-bacia de Santa Bárbara, Bacia do Camaquã. *17 Congresso Brasileiro de Paleontologia, Sociedade Brasileira de Paleontologia, Boletim de Resumos, Rio Branco*, 94.

Netto, R.G. and Rossetti, D.F. (2003). Ichnology and salinity fluctuations: a case study in the Early Miocene (Lower Barreiras Succession) of São Luís Basin, Maranhão, Brazil. *Revista Brasileira de Paleontologia*, 6, 5–18.

Netto, R.G., Buatois, L.A., Mángano, M.G., and Balistieri, P. (2007). *Gyrolithes* as a multipurpose burrow: an ethologic approach. *Revista Brasileira de Paleontologia*, 10, 157–168.

Neumann, A.C. (1966). Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography*, 11, 92–108.

Neumann, C. and Wisshak, M. (2006). A foraminiferal parasite on the sea urchin *Echinocorys*: ichnological evidence from the Late Cretaceous (Lower Maastrichtian, northern Germany). *Ichnos*, 13, 185–190.

Newell, R.C. (1979). *Biology of Intertidal Animals*. Kent, UK: Marine Ecological Surveys Ltd.

Nichol, R. (1982). Fossilized human footprints in Rangitoto ash on Motutapu Island. *Geological Society of New Zealand Newsletter*, 51, 11–13.

Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. and Ahlberg, P.E. (2010). Tetrapod trackways from the early Middle Devonian period of Poland. *Nature*, 463, 43–48.

Noffke, N. (1999). Erosional remnants and pockets evolving from biotic–physical interactions in a Recent lower supratidal environment. *Sedimentary Geology*, 123, 175–181.

Noffke, N. (2010). *Geobiology: Microbial Mats in Sandy Deposits from the Archaean Era to Today*. Berlin: Springer-Verlag.

Noffke, N., Gerdes, G., Klenke, T. and Krumbein, W.E. (1996). Microbially induced sedimentary structures – examples from modern sediments of siliciclastic tidal flats. *Zentralblatt für Geologie und Paläontologie Teil I*, 1/2, 307–316.

Nogueira, M.S. and Netto, R.G. (2001). Icnofauna da Formação Rio do Sul (Grupo Itararé, Permiano da bacia do Paraná) na Pedreira Itaú Itauna, Santa Catarina, Brasil. *Acta Geologica Leopoldensia*, 52/53, 397–406.

Norris, R.D. (2001). Impact of K-T boundary events on marine life. In *Palaeobiology II*, ed. D.E.G. Briggs and P.G. Crowther, Oxford, UK: Blackwell Science, pp. 229–231.

Nygaard, E. (1983). *Bathichnus* and its significance in the trace fossil association of Upper Cretaceous chalk, Mors, Denmark. *Danmarks Geologiske Undersøgelse Arbog*, 1982, 107–137.

O'Clair, C.E. and Zimmerman, S.T. (1987). Biogeography and ecology of intertidal and shallow subtidal communities. In *The Gulf of Alaska: Physical Environment and Biological Resources*, ed. D.W. Hood and S.T. Zimmerman, Springfield, VA: National Technical Information Service, pp. 305–344.

Olivero, D. and Gaillard, C. (1996). Paleoecology of Jurassic *Zoophycos* from south-eastern France. *Ichnos*, 4, 249–260.

Olivero, E.B., Buatois, L.A. and Scasso, R.A. (2004). *Paradictyodora antarctica*: a new complex vertical spreite trace fossil from the Upper Cretaceous–Paleogene of Antarctica and Tierra del Fuego, Argentina. *Journal of Paleontology*, 78, 783–789.

Olivero, D. and Gaillard, C. (2007). A constructional model for *Zoophycos*. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 466–477.

Olivero, E.B., and López Cabrera, M.I. (2005). *Patagonichnus*: a new trace fossil from the Miocene of Patagonia. A probable fodinichnion of gregarious polychaetes. *Ameghiniana*, 42, 277–294.

Olivero, E.B. and López Cabrera, M.I. (2010). *Tasselia ordamensis*: a biogenic structure of probable deposit-feeding and gardening maldanid polychaetes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 336–348.

Olivero, E.B., Ponce, J.J., Marsicano, C.A. and Martinioni, D.R. (2007). Depositional settings of the basal López de Bertodano Formation, Maastrichtian, Antarctica. *Revista de la Asociación Geológica Argentina*, 62, 521–529.

Olivero, E.B., López, M.I., Malumián, N. and Torres Carbonell P.J. (2010). Eocene graphoglyptids from shallow-marine, highenergy, organic-rich, and bioturbated turbidites, Fuegian Andes, Argentina. *Acta Geologica Polonica*, 60, 77–91.

Olóriz, F. and Rodríguez-Tovar, F.J. (1999). Análisis paleoicnológico del perfil de Puerto Lorente (Kimmeridgense, Sierra de Cazorla, Prebético Externo). *Revista Española de Paleontología nro extraordinario*, 15–28.

Olóriz, F. and Rodríguez-Tovar, F.J. (2002). Trace-fossils and minor discontinuities in a marl limestone rhythmite, Lower–Middle Kimmeridgian, southern Spain. *Geobios*, 35, 581–593.

Olsen, P.E. (1980). Fossil great lakes of the Newark Supergroup in New Jersey. In *Field Studies of New Jersey Geology and Guide to Field Trips*, ed. W.M. Manspeizer, New York State Geological Association, 52nd Annual Meeting, Rutgers University, 352–398.

Olsen, P.E. (1989). Newark Basin, New Jersey. In *Tectonic, Depositional, and Paleoecologic History of Early Mesozoic Rift Basins, Eastern North America*, ed. PE. Olsen, R. Schliche, and P.J. Gore, *International Geological Congress Field Trip Guidebook*, T-351, 2.

Olsen, P.E. and Huber, P. (1998). The oldest Late Triassic footprint assemblage from North America (Pekin Formation, Deep River basin, North Carolina, USA). *Southeastern Geology*, 38, 77–90.

Olsen, P.E., Remington, C.L. and Cornet, B. (1978). Cyclic change in Late Triassic lacustrine communities. *Science*, 201, 729–732.

Olsen, P.E., Shubin, N.H. and Anders, M.H. (1987). New Early Jurassic tetrapod assemblages constrain Triassic–Jurassic tetrapod extinction event. *Science*, 237, 1025–1029.

Olsen, P.E., Smith, J.B. and McDonald, N.G. (1998). Type material of the species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, USA). *Journal of Vertebrate Paleontology*, 18, 586–601.

Olszewski, T. (1996). Segregation of bivalves and brachiopods in the upper Paleozoic: the influence of ecology on macroevolutionary history.In *Abstracts of Papers*, Washington DC: North American Paleontological Convention (NAPC-96), pp. 295.

Onac, B.P., Ettinger, K., Kearns, J. and Balasz, I.I. (2005). A modern, guano-related occurrence of foggite, CaAl(PO4)(OH)2·H2O and churchite-(Y), YPO4·2H2O in Cioclovina Cave, Romania. *Mineralogy and Petrology*, 85, 291–302.

Orłowski, S. (1992). Trilobite trace fossils and their stratigraphical significance in the Cambrian sequence of the Holy Cross Mountains, Poland. *Geological Journal*, 27, 15–34.

Orłowski, S., Radwański, A. and Roniewicz, P. (1970). The trilobite ichnocoenoses in the Upper Cambrian sequence of the Holy Cross Mountains. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 345–360.

Orłowski, S., Radwański, A. and Roniewicz, P. (1971). Ichnospecific variability of the Upper Cambrian Rusophycus from the Holy Cross Mts. *Acta Geologica Polonica*, 21, 341–348.

Orr, P.J. (1994). Trace fossil tiering within event beds and preservation of frozen profiles: An example from the lower Carboniferous of Menorca. *Palaios*, 9, 202–210.

Orr, P.J. (1996). The ichnofauna of the Skiddaw Group (Early Ordovician) of the Lake District, England. *Geological Magazine*, 133, 193–216.

Orr, P.J. (2001). Colonization of the deep-marine environment during the early Phanerozoic: The ichnofaunal record. *Geological Journal*, 36, 265–278.

Orr, P.J. (2003). Ecospace utilization in early Phanerozoic deep-marine environments: deep bioturbation in the Blakely Sandstone (Middle Ordovician), Arkansas, USA. *Lethaia*, 36, 97–106.

Ortí, F., Rosell, L., Anadón, P. (2003). Deep to shallow lacustrine evaporates in the Libros Gypsum (southern Teruel Basin, Miocene, NE Spain): an occurrence of pelletal gypsum rhythmites. *Sedimentology*, 50, 361–386.

Orton, G.J. and Reading, H.G. (1993). Variability of deltaic processes in terms of sediment supply, with particular emphasis on grainsize. *Sedimentology*, 40, 475–512.

Oschmann, W. (1993). Environmental oxygen fluctuations and the adaptive response of marine benthic organisms. *Journal of the Geological Society, London*, 150, 187–191.

Osgood, R.G. Jr. (1970). Trace fossils of the Cincinnati area. *Palaeontographica Americana*, 6, 281–444.

Osgood, R.G. Jr. (1975). The paleontological significance of trace fossils. In *The Study of Trace Fossils: A Synthesis of Principles, Problems and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 87–108.

Ott, J.A., Fuchs, B., Fuchs, R. and Malasek, A. (1976). Observations on the biology of *Callianassa stebbingi* Borrodaille and *Upogebia litoralis* Risso and their effect upon the sediment. *Senckenbergiana Maritima*, 8, 61–79.

Owen, J. (1980). *Feeding Strategy*. Oxford, UK: Oxford University Press.

Ozalas, K., Savrda, C.E. and Fullerton, R.R. Jr. (1994). Bioturbated oxygenation-event beds in siliceous facies; Monterey Formation (Miocene), California. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 112, 63–83.

Pak, R. and Pemberton, S.G. (2003). Ichnology of the Yeoman Formation. *Summary of Investigation 2003, v.1, Saskatchewan Geological Survey, Saskatchewan Industry and Resources, Miscelaneous Report 2003–4.1, CD-ROM Paper*, A-3, 16.

Palmer, J.D. (1967). Daily and tidal components in the persistent rhythmic activity of the crab, *Sesarma*. *Nature*, 215, 64–66.

Palmer, J.D. (1995). *The Biological Rhythms and Clocks of Intertidal Animals*. New York: Oxford University Press.

Palmer, T.J. (1978). Burrows at certain omission surfaces in the Middle Ordovician of the Upper Mississippi Valley. *Journal of Paleontology*, 52, 109–117.

Papentin, F. (1973). A Darwinian evolutionary system III: experiments on the evolution of feeding patterns. *Journal of Theoretical Biology*, 39, 431–445.

Papentin, F. and Röder, H. (1975). Feeding patterns: the evolution of a problem and a problem of evolution. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 184–191.

Pashin, J.C. (2005). Pottsville stratigraphy and the Union Chapel Lagerstaette. *Alabama Paleontological Society, Monographs*, 1, 39–58.

Pattison, S.A.J. (2005). Storm-influenced prodelta turbidite complex in the lower Kenilworth Member at Hatch Mesa, Book Cliffs, Utah, USA: implications for shallow marine facies models. *Journal of Sedimentary Research*, 75, 420–439.

Pattison, S.A.J., Ainsworth, R.B. and Hoffman, T.A. (2007). Evidence of across shelf transport of fine-grained sediments: turbidite-filled shelf channels in the Campanian Aberdeen Member, Book Cliffs, Utah, USA. *Sedimentology*, 54, 1033–1063.

Pearson, D.L. (1988). Biology of tiger beetles. *Annual Reviews*, 33, 123–147.

Pearson, T.H. (1980). Macrobenthos of fjords. In *Fjord Oceanography*, ed. H.J. Freeland, D.M. Farmer and C.E. Kings, New York: Plenum Press, pp. 569–602.

Pearson, T.H. (2001). Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography and Marine Biology Annual Reviews*, 39, 233–267.

Pearson, N.J. and Gingras, M.K. (2006). An ichnological and sedimentological facies model for muddy point-bar deposits. *Journal of Sedimentary Research*, 76, 771–782.

Pearson, N.J., Gingras, M.K., Armitage, I.A. and Pemberton, S.G., (2007). The Significance of Atlantic Sturgeon Feeding Excavations, Mary's Point, Bay of Fundy, New Brunswick, Canada. *Palaios*, 22, 457–464.

Pemberton, S.G. and Frey, R.W. (1982). Trace fossil nomenclature and the *Planolites–Palaeophycus* dilemma. *Journal of Paleontology*, 56, 843–881.

Pemberton, S.G. and Frey, R.W. (1984a). Ichnology of storm–influenced shallow marine sequence: Cardium Formation (Upper Cretaceous) at Seebe, Alberta. In *The Mesozoic of middle North America*, ed. D.F. Stott and D.J. Glass, *Canadian Society of Petroleum Geologists Memoir*, 9, 281–304.

Pemberton, S.G. and Frey, R.W. (1984b). Quantitative methods in ichnology; spatial distribution among populations. *Lethaia*, 17, 33–49.

Pemberton, S.G. and Frey, R.W. (1985). The *Glossifungites* ichnofacies: modern examples from the Georgia coast, USA. In *Biogenic Structures: Their use in interpreting depositional environments*, ed., H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 237–259.

Pemberton, S.G. and Frey, R.W. (1991). William Buckland and his "coprolitic vision". *Ichnos*, 1, 317–325.

Pemberton, S.G. and Gingras M.K. (2005). Classification and characterizations of biogenically enhanced permeability. *American Association of Petroleum Geologists, Bulletin*, 89, 1493–1517.

Pemberton, S.G. and Jones, B. (1988). Ichnology of the Pleistocene Ironshore Formation, Grand Cayman Island, British West Indies. *Journal of Paleontology*, 62, 495–505.

Pemberton, S.G. and MacEachern, J.A. (1995). The sequence stratigraphic significance of trace fossils: Examples from the Cretaceous foreland basin of Alberta, Canada. In *Sequence Stratigraphy of Foreland Basin Deposits: Outcrop and Subsurface Examples from the Cretaceous of North America*, ed. J.C. Van Wagoner and G. Bertram, *American Association of Petroleum Geologists Memoir*, 64, 429–475.

Pemberton, S.G. and MacEachern J.A. (1997). The ichnological signature of storm deposits: The use of trace fossils in event stratigraphy. In *Paleontological Events. Stratigraphic, Ecological and Evolutionary Implications*, ed. C.E. Brett and G.C. Baird, New York: Columbia University Press, pp. 73–109.

Pemberton, S.G. and Magwood, J.P.A. (1990). A unique occurrence of *Bergaueria* in the Lower Cambrian Gog Group near Lake Louise, Alberta. *Journal of Paleontology*, 64, 436–440.

Pemberton, S.G. and Wightman, D.M. (1992). Ichnological characteristics of brackish water deposits. In *Applications of ichnology to petroleum exploration: A core workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 141–167.

Pemberton, S.G., Kobluk, D.R., Yeo, R.K. and Risk, M.J. (1980). The boring *Trypanites* at the Silurian–Devonian disconformity in southern Ontario. *Journal of Paleontology*, 54, 1258–1266.

Pemberton, S.G., Frey, R.W. and Bromley, R.G. (1988). The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences*, 25, 886–892.

Pemberton, S.G., Frey, R.W. and Saunders, T.D.A. (1990). Trace fossils. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 355–362.

Pemberton, S.G., Frey, R.W., Ranger, M.J. and MacEachern, J.A. (1992a). The conceptual framework of ichnology. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 1–32.

Pemberton, S.G., MacEachern, J.A. and Frey, R.W. (1992b). Trace fossils facies models: environmental and allostratigraphic significance. In *Facies Models and Sea Level Changes*, ed. R.G. Walker and N.P. James, Geological Association of Canada, 47–72.

Pemberton, S.G., Van Wagoner, J.C. and Wach, G.D. (1992c). Ichnofacies of a wave-dominated shoreline. In *Applications of ichnology to petroleum exploration: A core workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 339–382.

Pemberton, S.G., MacEachern, J.A. and Ranger, M.J. (1992d). Ichnology and event stratigraphy: the use of trace fossils in recognizing tempestites. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 85–118.

Pemberton, S.G., Spila, M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, D. and Sinclair, I.K. (2001). *Ichnology & Sedimentology of Shallow to Marginal Marine Systems. Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin. Geological Association of Canada Short Course Notes*, 15, St. John's.

Pemberton, S.G., MacEachern, J.A. and Saunders, T. (2004). Stratigraphic applications of substrate-specific ichnofacies: delineating discontinuities in the fossil record. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 29–62.

Pemberton, S.G., MacEachern, J.A., Bann, K.L., Gingras, M.K. and Saunders, T.D.A. (2006). High-latitudinal versus low-latitude: Capturing the elusive signal using trace fossil suites from the ancient record. *Abstracts American Association of Petroleum Geologists 2006 Annual Convention, Houston*, 84.

Pemberton, S.G., Pulham, A., MacEachern, J.A. and Saunders, T.D.A. (2007). The ichnology and sedimentology of the Ferron Sandstone cores of Muddy Creek Canyon, Emery County, SE Utah, USA. In *Ichnological Applications to Sedimentological and Sequence Stratigraphic Problems*, ed. J.A. MacEachern, M.K. Gingras, K.L. Bann and S.G. Pemberton, *Society for Sedimentary Geology Research Conference, Price, Abstract Volume*, 175–209.

Pemberton, S.G., MacEachern, J.A., Gingras, M.K. and Saunders, T.D.A. (2008). Biogenic chaos: cryptobioturbation and the work of sedimentologically friendly organisms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 273–279.

Penland, S. and Suter, J.R. (1989). The geomorphology of the Mississippi River Chenier Plain. *Marine Geology*, 90, 231–258.

Perkins, E.J. (1974). *The Biology of Estuaries and Coastal Waters*. London: Academic Press.

Perry, C.T. (2000). Macroboring of Pleistocene coral communities, Falmouth Formation, Jamaica. *Palaios*, 15, 483–491.

Perry, C.T. and Bertling, M. (2000). Temporal and spatial patterns of coral reef macroboring since the Mesozoic. In *Carbonate Platform Systems: Components and Interactions*, ed. E. Insalaco, P. Skelton and T. Palmer, *Geological Society Special Publication*, 178, 33–50.

Perry, C.T. and Hepburn, L.J. (2008). Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: taphonomic signatures of reef accretion and reef depositional events. *Earth Science Reviews*, 86, 106–144.

Perry, C.T. and Macdonald, I.A. (2002). Impacts of light penetration on the bathymetry of reef microboring communities: Implications for the development of microendolithic trace assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 186, 101–113.

Peterson, K.J. (2005). Macroevolutionary interplay between planktic larvae and benthic predators. *Geology*, 33, 929–932.

Peterson, K.J., Cotton, J.A., Gehling, J.G. and Pisani, D. (2008). The Ediacaran emergence of bilaterians: congruence between the genetic and the geological fossil records. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 1435–1443.

Pflüger, F. (1999). Matground structures and redox facies. *Palaios*, 14, 25–39.

Pharo, C.H. and Carmack, E.C. (1979). Sedimentation processes in a short residence-time intermontane lake, Kamlooops Lake, British Columbia. *Sedimentology*, 26, 523–541.

Pianka, E.R. (1970). On r- and K-selection. *American Naturalist*, 104, 592–597.

Pickerill, R.K. (1981). Trace fossils in a Lower Palaeozoic submarine canyon sequence-the Siegas Formation of northwestern New Brunswick, Canada. *Maritime Sediments and Atlantic Geology*, 17, 36–59.

Pickerill, R.K. (1990). Nonmarine *Paleodictyon* from the Carboniferous Albert Formation of southern New Brunswick. *Atlantic Geology*, 26, 157–163.

Pickerill, R.K. (1992). Carboniferous nonmarine invertebrate ichnocoenoses from southern New Brunswick, eastern Canada. *Ichnos*, 2, 21–36.

Pickerill, R.K. (1994). Nomenclature and taxonomy of invertebrate trace fossils. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 3–42.

Pickerill, R.K. (1995). Deep-water marine *Rusophycus* and *Cruziana* from the Ordovician Lotbiniere Formation of Quebec. *Atlantic Journal*, 31, 103–108.

Pickerill, R.K. and Brenchley, P.J. (1991). Benthic macrofossils as paleoenvironmental indicators in marine siliciclastic facies. *Geoscience Canada*, 18, 119–138.

Pickerill, R.K and Fillion, D. (1983). On the Tremadoc–Arenig and Lower–Upper Tremadoc boundaries in the Bell Island Group, Conception Bay, eastern Newfoundland. *Maritime Sediments and Atlantic Geology*, 19, 21–30.

Pickerill, R.K. and Narbonne, G.M. (1995). Composite and compound ichnotaxa: a case example from the Ordovician of Québec, eastern Canada. *Ichnos*, 4, 53–69.

Pickerill, R.K. and Williams, P.P. (1989). Deep burrowing in the early Palaeozoic deep sea: examples from the Cambrian(?) – Early Ordovician Meguma Group of Nova Scotia. *Canadian Journal of Earth Science*, 26, 1061–1068.

Pickerill, R.K., Fillion, D. and Harland, T.L. (1984). Middle Ordovician trace fossils in carbonates of the Trenton Group between Montreal and Quebec city, St. Lawrence lowland, eastern Canada. *Journal of Paleontology*, 58, 416–439.

Pickerill, R.K., Romano, M. and Meléndez, B. (1984). Arenig trace fossils from the Salamanca area, western Spain. *Geological Journal*, 19, 249–269.

Pickering, K.T., Hiscott, R. and Hein, F.J. (1989). *Deep-marine Environments: Clastic Sedimentation and Tectonics*. London: Unwin Hyman.

Pieńkowski, M.H. (1983). Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. *Marine Ecology Progress Series*, 11, 141–150.

Pieńkowski, G. and Niedźwiedzki, G. (2009) Invertebrate trace fossil assemblages from the Lower Hettangian of Sołtyków, Holy Cross Mountains, Poland. *Volumina Jurassica*, 6, 109–13.

Pierce, C. (1992). Effects of pocket gopher burrowing on archaeological deposits: a simulation approach. *Geoarchaeology*, 7, 185–208.

Pirazzoli, P.A., Thommeret, J., Thommeret, Y., Laborel, J. and Montaggioni, L. (1982). Crustal block movements from Holocene shorelines: Crete and Antikythira (Greece). *Tectonophysics*, 86, 27–43.

Pirmez, C., Beaubouef, R.T., Friedmann, S.J. and Mohrig, D.C. (2000). Equilibrium profile and base level in submarine channels: examples from Late Pleistocene systems and implications for the architecture of deepwater reservoirs. In *Deepwater Reservoirs of the World*, ed. P. Weimer, R.M. Slatt, J. Coleman, N.C. Rosen, H. Nelson, A.H. Bouma, M.J. Styzen and D.T. Lawrence, *Society for Sedimentary Geology, Gulf Coast Section, 20th Annual Research Conference*, 782–805.

Pirrone, C.A., Buatois, L.A. and Bromley, R.G. (2010). Naming trace fossils in bones. *Latin American Symposium on Ichnology, Abstract Volume*, p. 52.

Plink-Björklund, P. and Steel, R. (2004). Initiation of turbidity currents: evidence for hyperpycnal flow turbidites in Eocene Central Basin of Spitsbergen. *Sedimentary Geology*, 165, 29–52.

Plint, A.G. (1988). Sharp-based shoreface sequences and "offshore bars" in the Cardium Formation of Alberta: their relationship to relative changes in sea-level. In *Sea-Level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross and J.C. Van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 357–370.

Plint, A.G. (2000). Sequence stratigraphy and paleogeography of a Cenomanian deltaic complex; the Dunvegan and lower Kaskapau formations in subsurface and outcrop, Alberta and British Columbia, Canada. *Bulletin of Canadian Petroleum Geology*, 48, 43–79.

Plint, A.G. and Nummedal, D. (2000). The falling stage systems tract: recognition and importance in sequence stratigraphic analysis; sedimentary responses to forced regressions. In *Sedimentary Responses to Forced Regressions*, eds. D. Hunt and R.L. Gawthorpe. *Geological Society Special Publications*, 172, 1–17.

Plint, A.G., and Pickerill, R.K. (1985). Non-marine *Teredolites* from the middle Eocene of southern England. *Lethaia*, 18, 341–347.

Plotnick, R.E. (2007). Chemoreception, odor landscapes, and foraging in ancient marine landscapes. *Palaeontologia Electronica*, 10.

Plotnick, R.E. (2009). Movement Paleoecology and the taphonomy of behavior. *9th North American Paleontological Convention Abstracts, University of Cincinati, Cincinati*, 309.

Plotnick, R.E. and Koy, K. (2005). Let us prey: simulations of grazing traces in the fossil record. 8*th International Conference on GeoComputation, Ann Arbor*.

Plotnick, R.E., Dornbos, S.Q. and Chen, J. (2010). Information landscapes and sensory ecology of the Cambrian Radiation. *Paleobiology*, 36, 303–317.

Pollard, J.E. (1988). Trace fossils in coal-bearing sequences. *Journal of the Geological Society, London*, 145, 339–350.

Pollard, J.E. (1985). *Isopodichnus*, related arthropod traces and notostracans from Triassic fluvial sediments. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 76, 273–285.

Pollard, J.E. and Hardy, P.G. (1991). Trace fossils from the Westphalian D of Writhlington Geological Nature Reserve, nr. Radstock, Avon. *Proceedings of the Geologists Association*, 102, 169–178.

Pollard, J.E. and Walker, E. (1984). Reassessment of sediments and trace fossils from Old Red Sandstone (Lower Devonian) of Dunure, Scotland, described by John Smith (1909). *Geobios*, 17, 567–576.

Pollard, J.E., Goldring, R. and Buck, S.G. (1993). Ichnofabrics containing *Ophiomorpha*: significance in shallow-water facies interpretation. *Journal of the Geological Society of London*, 150, 149–164.

Pollard, J.E., Steel, R.J. and Undersrud, E. (1982). Facies sequences and trace fossils in lacustrine/fan delta deposits, Hornelen Basin (M. Devonian), western Norway. *Sedimentary Geology*, 32, 63–87.

Pomeroy, L.R., Darley, W.M., Dunn, E.L., Gallagher, J.L., Haines, E.B. and Whitney, D.M. (1981). Primary production. In *Ecology of a Salt Marsh*, ed. L.R. Pomeroy and W. Wiegert, New York: Springer-Verlag, pp. 39–67.

Ponce, J.J. and Carmona, N.B. (2010). Miocene deep-marine hyperpycnal channel-levee complexes Tierra del Fuego, Argentina: facies associations and architectural elements. In *Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology*, 61, in press.

Ponce, J.J., Olivero, E.B., Martinioni, D.R. and López Cabrera, M.I. (2007). Sustained and episodic gravity flow deposits and related bioturbation patterns in Paleogene turbidites (Tierra del Fuego, Argentina). In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 253–266.

Porębski, S.J. and Steel, R.J. (2006). Deltas and sea-level change. *Journal of Sedimentary Research*, 76, 390–403.

Posamentier, H.W. (2001). Lowstand alluvial bypass systems: Incised vs. unincised. *American Society of Petroleum Geologists, Bulletin*, 85, 1771–1793.

Posamentier, H.W. and Allen, G.P. (1993). Siliciclastic sequence stratigraphic patterns in foreland ramp-type basins. *Geology*, 21, 455–458.

Posamentier, H.W. and Allen, G.P. (1999). Siliciclastic sequence stratigraphy: concepts and applications. *Society for Sedimentary Geology Concepts in Sedimentology and Paleontology*, 7.

Posamentier, H.W. and Kolla, V. (2003). Seismic geomorphology and stratigraphy of depositional elements in deep-water settings. *Journal of Sedimentary Research*, 73, 367–388.

Posamentier, H.W. and Vail, P.R. (1988). Eustatic controls on clastic deposition II: sequence and system tract models. In *Sea-level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross and J.C. van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 125–154.

Posamentier, H.W. and Walker, R.G. (2006). Deep-water turbidites and submarine fans. In *Facies Models Revisited*, ed. H.W. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 397–520.

Posamentier, H.W., Jervey, M.T. and Vail, P.R. (1988). Eustatic controls on clastic deposition I: conceptual framework. In *Sea-level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross and J.C. van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 109–124.

Posamentier, H.W., Allen, G.P., James, D.P. and Tesson, M. (1992). Forced regressions in a sequence stratigraphic framework: concepts, examples, and exploration significance. *American Association of Petroleum Geologists, Bulletin*, 76, 1687–1709.

Potter, P.E., Maynard, J.B. and Depetris, P.J. (2005). *Mud and Mudstone: Introduction and overview.* Berlin: Springer.

Powichrowski, L.K. (1989). Trace fossils from the Helminthoid Flysch (Upper Cretaceous-Palaeocene) of the Ligurian Alps (Italy): development of deep marine ichnoassociations in fan and basin plain environments. *Eclogae Geologicae Helvetiae*, 82, 385–411.

Prantl, F. (1945). Two new problematic trails from the Ordovician of Bohemia. *Académie Tchéque des Sciences, Bulletin International, Classe des Sciences Mathematiques et Naturelles et de la Médecine*, 46, 49–59.

Prather, B.E., Booth, J.R., Steffens, G.S. and Craig, P.A. (1998). Classification, lithologic calibration and stratigraphic succession of seismic facies of intraslope basins, deep-water Gulf of Mexico. *American Association of Petroleum Geologists, Bulletin*, 82, 701–728.

Pratt, B. (1998). Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. *Lethaia*, 31, 73–88.

Prave, A.R. (2002). Life on land in the Proterozoic: evidence from the Torridonian rocks of northwest Scotland. *Geology*, 30, 811–814.

Price, S. and McCann, T.M. (1990). Environmental significance of *Arenicolites* ichnosp. in Pliocene lake deposits of southwest Turkey. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, H11, 687–694.

Prince, N.K. and Lockley, M.G. (1989). The sedimentology of the Purgatoire tracksite region, Morrison Formation of southeastern Colorado. In *Dinosurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 155–163.

Pryor, W.A. (1975). Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. *Geological Society of America Bulletin*, 86, 1244–1254.

Pruss, S. and Bottjer, D.J. (2004). Early Triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-Permian mass extinction. *Palaios*, 19, 551–564.

Pruss, S., Fraiser, M. and Bottjer, D.J. (2004). Proliferation of Early Triassic wrinkle structures: implications for environmental stress following the end-Permian mass extinction. *Geology*, 32, 461–464.

Pruss, S.B., Corsetti, F.A. and Bottjer, D.J. (2005). Environmental trends of Early Triassic biofabrics: implications for understanding the aftermath of the end-Permian mass extinction. In *Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Toward an Integrated Approach*, ed. J.D. Morrow, D.J. Over and P.B. Wignall, Amsterdam: Elsevier, pp. 313–332.

Quiroz, L.I., Buatois, L.A., Mángano, M.G., Jaramillo, C.A. and Santiago, N. (2010). Is the trace fossil *Macaronichnus* an indicator of temperate to cold waters? Exploring the paradox of its occurrence in tropical coasts. *Geology*, 38, 651–654.

Radwański, A. (1969). Lower Tortonian transgression onto the southern slopes of the Holy Cross Mountains. *Acta Geologica Polonica*, 19, 1–164.

Radwański, A. (1977). Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 227–264.

Radwański, A. and Roniewicz, P. (1963). Upper Cambrian trilobite ichnocoenosis from Wielka Wisniowka (Holy Cross Mountains, Poland). *Acta Palaeontologica Polonica*, 8, 259–280.

Radwański, A. and Roniewicz, P. (1972). A long trilobite trackway, *Cruziana semiplicata* Salter, from the Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area (Franconia, south-eastern Germany). *Paläontologische Zeitschrift*, 75, 71–96.

Rahmani, R.A. (1988). Estuarine tidal channel and nearshore sedimentation of a Late Cretaceous epicontinental sea, Drumheller, Alberta, Canada. In *Tide-influenced Sedimentary Environments*, ed. P.L. Boer, A. van Gelder and S.D. Nio, Dordrecht: D. Reidel, pp. 433–471.

Raichlen, D.A., Pontzer, H. and Sockol, M. (2008). The Laetoli footprints and early hominin locomotor kinematics. *Journal of Human Evolution*, 54, 112–117.

Ranger, M.J. and Pemberton, S.G. (1988). Marine influence in the McMurray Formation in the Primrose area, Alberta. In *Sequences, Stratigraphy, Sedimentology: Surface and Subsurface*, ed. P.D. James and D.A. Leckie, *Canadian Society of Petroleum Geologists Memoir*, 15, 439–450.

Ranger, M.J. and Pemberton, S.G. (1992). The sedimentology and ichnology of estuarine point bars in the McMurray Formation of the Athabasca Oil Sands Deposit, northeastern Alberta, Canada. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 401–421.

Rasmussen, B., Bose, P.K., Sarkar, S., Banerjee, S., Fletcher, I.R. and McNaughton, N.J. (2002a). 1.6 Ga U-Pb zircon age for the Chorhat Sandstone, lower Vindhyan, India: possible implications for early evolution of animals. *Geology*, 30, 103–106.

Rasmussen, B., Bengtson, S., Fletcher, I.R. and McNaughton, N. (2002b). Discoidal impressions and trace-like fossils more than 1200 million years old. *Science*, 296, 1112–1115.

Ratcliffe, B.C. and Fagerstrom, J.A. (1980). Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance. *Journal of Paleontology*, 54, 614–630.

Raup D.M. (1979). Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science*, 206, 217–218.

Raup D.M. (1992). Large-body impact and extinction in the Phanerozoic. *Paleobiology*, 18, 80–88.

Raup, D.M. and Seilacher, A. (1969). Fossil foraging behaviour: computer simulation. *Science*, 166, 994–995.

Ray, J.S., Martin, M.W., Veizer, J. and Bowring, S.A. (2002). U-Pb zircon dating and Sr isotope systematics of the Vindhyan Supergroup, India. *Geology*, 30, 131–134.

Reading, H.G. and Richards, M. (1994). Turbidite systems in deep-water basin margins classified by grain size and feeder system. *American Association of Petroleum Geologists, Bulletin*, 78, 792–822.

Reese, E.S. (1966). The complex behavior of echinoderms. In *Physiology of Echinodermata*, ed. R.A. Boolootian, New York: Interscience Publishers, pp. 157–218.

Reineck, H.-E. (1958). Longitudinale schrägschicht in Watt. *Geologische Rundschau*, 47, 73–82.

Reineck, H.-E. (1963). Sedimentgefüge im Bereich der südliche Nordsee. *Abhandlungen Senckenbergischen Naturforsche de Gesellschaft*, 505, 1–138.

Reineck, H.-E. (1967). Layered sediments of tidal flat beaches, and shelf bottoms of the North Sea. In *Estuaries*, ed. G.H. Lauff, *American Association for the Advancement of Science Special Publication*, 83, 191–206.

Reinson, G.E. (1984). Barrier island and associated stand-plain systems. In *Facies Models, Second edition*, ed. R.G. Walker, *Geological Association of Canada, Geoscience Canada Reprint Series*, 1, 119–140.

Reise, K. (1985). *Tidal Flat Ecology: An Experimental Approach to Species Interactions. Ecological Studies* 54. Berlin: Springer-Verlag.

Reise, K. and Volkenborn, N. (2004). Large worms as ecosystem engineers in intertidal Sediments. In *Proceedings of the Sysmposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments from Individual Behaviour to their Roles as Ecosystem Engineers*, Japan: Nagasaki University Press, 95.

Remane, A. and Schlieper, C. (1971). *Biology of Brackish Water*. New York: John Wiley and Sons.

Retallack, G.J. (1990). *Soils of the Past*. London: Unwin-Hyman.

Retallack, G.J. (1996). Early Triassic therapsid footprints from the Sydney basin, Australia. *Alcheringa* 20, 301–314

Retallack, G.J. (2001). *Scoyenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. *Palaeontology*, 44, 209–235.

Retallack, G.J. and Feakes, C.R. (1987). Trace fossil evidence for Late Ordovician animals on land. *Science*, 235, 61–63.

Rhoads, D.C. (1974). Organism-sediment relations in the muddy sea floor. *Oceanography and Marine Biology Annual Review*, 12, 263–300.

Rhoads, D.C. (1975). The paleoecological and environmental significance of trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 147–160.

Rhoads, D.C. and Germano, J.D. (1982). Characterization of organism–sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (Remote System). *Marine Ecology Progress Series*, 8, 115–128.

Rhoads, D.C. and Morse, J.W. (1971). Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia*, 4, 413–428.

Rhoads, D.C. and Young, D.K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structures. *Journal of Marine Research*, 28, 150–178.

Richter, R. (1928). Psychische reaktionen fossiler tiere. *Palaeobiologica*, 1, 225–245.

Richter, G. and Baszio, S. (2001). Traces of a limnic food web in the Eocene Lake Messel: a preliminary report based on fish coprolite analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 345–368.

Richter, G. and Wedmann, S. (2005). Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 223, 147–161.

Riggs, S.R., Ambrose, W.G. Jr., Cook, J.W., Snyder, S.W. and Snyder, S.W. (1998). Sediment production on sediment-starved continental margins: The interrelations between hard bottoms, sedimentological and benthic community processes, and storm dynamics. *Journal of Sedimentary Research*, 68, 155–168.

Rindsberg, A.K. (1990a). Ichnological consequences of the 1985 International Code of Zoological Nomenclature. *Ichnos*, 1, 59–63.

Rindsberg, A.K. (1990b). Freshwater to marine trace fossils of the Mary Lee Coal zone and overlying strata (Westphalian A), Pottsville Formation of northern Alabama. In *Carboniferous Coastal Environments and Paleocommunities of the Mary Lee Coal Zone, Marion and Walker Counties, Alabama*, ed. R.A. Gastaldo, T.M. Demko and Y. Liu, A *Guidebook for Field Trip VI: Southeastern Section, Geological Society of America, Tuscaloosa, Alabama, Geological Survey of Alabama*, pp. 82–95.

Rindsberg, A.K. (1992). Holocene ichnology of eastern Mississippi Sound, Alabama. *Circular-Geological Society of Alabama, Report*, 167, 1–75.

Rindsberg, A.K. (1994). Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous Formations. *Geological Survey of Alabama Bulletin*, 158, 1–107.

Rindsberg, A.K. (2005). Gas-escape structures and their paleoenvironmental significance at the Steven C. Minkin Paleozoic Footprint Site (Early Pennsylvanian, Alabama). In *Pennsylvanian Footprints in the Black Warrior Basin of Alabama*, ed. R.D. Buta, A.K. Rindsberg, and D.C. Kopaska-Merkel, *Alabama Paleontological Society Monograph*, 1, 177–183.

Rindsberg, A.K. and Martin, A.J. (2003). *Arthrophycus* in the Silurian of Alabama (USA) and the problem of compound trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 187–219.

Rine, J.M. and Ginsburg, R.N. (1985). Depositional facies of a mud shoreface in Suriname, South America: a mud analogue to sandy nearshore marine deposits. *Journal of Sedimentary Petrology*, 55, 633–652.

Risk, M.J. and Tunnicliffe, V.J. (1978). Intertidal spiral burrows: *Paraonis fulgens* and *Spiophanes wigleyi* in the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology*, 48, 1287–1292.

Röder, H. (1971). Gangsysteme von *Paraonis fulgens* Levinsen 1883 (Polychaeta) in ökologischer, ethologischer und aktuopaläontologischer Sicht. *Senckenbergiana Maritima*, 3, 3–51.

Röder, H. (1977). Zur Beziehung zwischen Konstruktion und Substrat bei mechanisch bohrenden Bohrmuscheln (Pholadidae, Teredinidae). *Senckenbergiana Maritima*, 9, 105–213.

Roberts, D.L. (2008). Last interglacial hominid and associated vertebrate fossil trackways in coastal eolianites, South Africa. *Ichnos*, 15, 190–207.

Roberts, G. (2009). Ephemeral, subfossil mammalian, avian and hominid footprints within Flandrian sediment exposures at Formby Point, Sefton Coast, North West England. *Ichnos*, 16, 33–48.

Rodriguez-Aranda, J.P. and Calvo, J.P. (1998). Trace fossils and rhizoliths as a tool for sedimentological and palaeoenvironmental analysis of ancient continental evaporite successions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 140, 383–399.

Rodriguez-de la Rosa, R.A., Aguillon-Martinez, M.C., Lopez-Espinoza, J. and Eberth, D.A. (2004). The fossil record of vertebrate tracks in Mexico. *Ichnos*, 11, 27–37.

Rodríguez-Tovar, F.J. (2005). Fe-oxide spherules infilling *Thalassinoides* burrows at the Cretaceous-Paleogene (K–P) boundary: Evidence of a near-contemporaneous macrobenthic colonization during the K–P event. *Geology*, 33, 585–588.

Rodriguez-Tovar, F.J. and Delgado, J. (2006). Cuantificación del grado de consolidación del substrato: aplicacion en analisis icnológicos. *Ameghiniana*, 43, 503–508.

Rodríguez-Tovar, F.J. and Uchman, A. (2004a). Ichnotaxonomic analysis of the Cretaceous/Palaeogene boundary interval in the Agost section, south-east Spain. *Cretaceous Research*, 25, 635–647.

Rodríguez-Tovar, F.J. and Uchman, A. (2004b). Trace fossils after the K–T boundary event from the Agost section, SE Spain. *Geological Magazine*, 141, 429–440.

Rodríguez-Tovar, F.J. and Uchman, A. (2006). Ichnological analysis of the Cretaceous-Palaeogene boundary interval at the Caravaca section, SE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242, 313–325.

Rodriguez-Tovar, F.J. and Uchman, A. (2008). Bioturbational disturbance of the Cretaceous-Palaeogene (K-Pg) boundary layer: Implications for the interpretation of the K–P boundary impact event. *Geobios*, 41, 661–667.

Rodriguez-Tovar, F.J., Martinez-Ruiz, F. and Bernasconi, S.M. (2006). Use of high resolution ichnological and stable isotope data for assessing completeness of a K–P boundary section, Agost, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237, 137–146.

Rodríguez-Tovar, F.J., Pérez-Valera, F. and Pérez-López, A. (2007). Ichnological analysis in high-resolution sequence stratigraphy: The *Glossifungites* ichnofacies in Triassic successions from the Betic Cordillera (southern Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 198, 293–307.

Rodríguez-Tovar, F.J., Uchman, A., Payros, A., Orue-Etxebarria, X., Apellaniz, E. and Molina, E. (2010a). Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285, 50–65.

Rodríguez-Tovar, F. J, Morgado, A. and Lozano, J.A. (2010b). Using ichnofossils to characterize chert tools: a preliminary study from Southern Iberia. *Geoarchaeology: An International Journal*, 25, 514–526.

Rodríguez-Tovar, F. J, Morgado, A. and Lozano, J.A. (2010c). Ichnological analysis: a non-destructive tool in archaeology. *Lethaia*, 43, 587–590.

Rogers, D.A. (1990). Probable tetrapod tracks rediscovered in the Devonian of Scotland. *Journal of the Geological Society, London*, 147, 746–748.

Rokas, A., Krüger, D. and Carroll, S.B. (2005). Animal evolution and the molecular signature of radiations compressed in time. *Science*, 310, 1933–1938.

Rona, P.A., Seilacher, A., de Vargas, C., Gooday, A.J., Bernhard, J. M., Bowser, S., Vetriani, C., Wirsen, C.O., Mullineaux, L., Sherrell, R., Grassle, J.F., Low, S. and Lutz, R.A. (2009). A living fossil on the deep-sea floor. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 56, 1700–1712.

Root, R.B. (1967). The niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs*, 37, 317–350.

Roubik, D.W. (1989). *Ecology and Natural History of Tropical Bees*. New York: Cambridge University Press.

Roubik, D.W. and Michener, C.D. (1980). The seasonal cycle and nests of *Epicharis zonata*, a bee whose cells are below the wet-season water table (Hymenoptera, Anthophoridae). *Biotropica*, 12, 56–60.

Runnegar, B. (1992a). Proterozoic metazoan trace fossils. In *The Proterozoic Biosphere*, ed. J.W. Schopf and C. Klein, Cambridge, UK: Cambridge University Press, pp. 1009–1015.

Runnegar, B. (1992b). Oxygen and the early evolution of the Metazoa. In *Metazoan life Without Oxygen*, ed. C. Bryant, London: Chapman & Hall, pp. 65–87.

Ruppert, E.E., Fox, R.S. and Barnes, R.D. (2004). *Invertebrate Zoology: A Functional Evolutionary Approach.* Belmont, CA: Thomson-Brooks/Cole.

Rydell, J., Hammarlund, J. and Seilacher, A. (2001). Trace fossil associations in the Swedish Mickwitzia sandstone (Lower Cambrian): did trilobites really hunt for worms? *Geologiska Föreningens i Stockholm Förhandlingar [GFF]*, 123, 247–250.

Rytel, M.M. (1962). Trephinations in ancient Peru. *Polish Medical Sciences Historical Bulletin*, 5, 42–45.

Sadler, C.J. (1993). Arthropod trace fossils from the Permian De Chelly Sandstone, northeastern Arizona. *Journal of Paleontology*, 67, 240–249.

Salimullah, A.R.M. and Stow, D.A.V. (1995). Ichnofacies recognition in turbidites/hemiturbidites using enhaced FMS images: examples from ODP Leg 129. *The Log Analyst*, 36, 38–48.

Sanders, H.L. (1968). Marine benthic diversity: a comparative study. *American Naturalist*, 102, 243–282.

Sanders, H.L. (1969). Marine benthic diversity and the stability-time hypothesis. *Brookhaven Symposia on Biology*, 22, 71–81.

Sanders, H.L., Mangelsdorf, P.C. and Hampson, G.R. (1965). Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limnology and Oceanography*, 10, R216-R229.

Sands, W.A. (1969). The association of termites and fungi. In *Biology of Termites*, *Volume 1*, ed. K. Krishna, and F.M. Weesner, New York: Academic Press, pp. 495–524.

Sands, W.A. (1987). Ichnocoenoses of probable termite origin from Laetoli. In *Laetoli: A Pliocene Site in Northern Tanzania*, ed. M.D. Leakey, and J.M. Harris, Oxford, UK: Clarendon Press, pp. 409–433.

Sarjeant, W.A.S. (1967). Fossil footprints from the Middle Triassic of Nottinghamshire and Derbyshire. *Mercian Geologist*, 2, 327–341.

Sarjeant, W.A.S. (1975). Plant trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 51–69.

Sarjeant, W.A.S. (1996). Pisadas en las arenas del tiempo: Pisadas de vertebrados y la interpretación de paleoambientes sedimentarios. Perspectiva histórica y principales aplicaciones. *Asociación Paleontológica Argentina, Publicación Especial*, 4, 31–46.

Sarjeant, W.A.S. and Langston, W. Jr. (1994). Vertebrate footprints and invertebrate traces from the Chadronian (late Eocene) of Trans-Pecos Texas. *Texas Memorial Museum Bulletin*, 36, 1–86.

Sarjeant, W.A.S. and Mossman, D.J. (1978). Vertebrate footprints from the Carboniferous sediments of Nova Scotia: a historical review and description of newly discovered forms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 279–306.

Sarjeant, W.A.S. and Reynolds, R.E. (1999). Camel and horse footprints from the Miocene of California. *San Bernadino County Museum Association Quarterly*, 46, 3–19.

Sarjeant, W.A.S., Reynolds, R.E. and Kissell-Jones, M.M. (2002). Fossil creodont and carnivore footprints from California, Nevada, and Wyoming. In *Between the Basins: Exploring the Western Mojave and Southern Basin and Range Province*, ed. R.E Reynolds, Fullerton, CA: California State University, pp. 37–50.

Sarkar, S. and Chaudhuri, A.K. (1992). Trace fossils in Middle to Late Triassic fluvial redbeds, Pranhita-Godavari Valley, south India. *Ichnos*, 2, 7–19.

Savazzi, E. (1982). Shell sculpture and burrowing in the bivalves *Scapharca inaequivalvis* and *Acanthocardia tuberculata*. *Stuttgarter Beiträge zur Naturkunde Serie A*, 353, 1–12.

Savazzi, E. (1991). Burrowing in the inarticulate brachiopod *Lingula anatina*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 85, 101–106.

Savrda, C.E. (1991a). *Teredolites*, wood substrates, and sea-level dynamics. *Geology*, 19, 905–908.

Savrda, C.E. (1991b). Ichnology in sequence stratigraphic studies: an example from the Lower Paleocene of Alabama. *Palaios*, 6, 39–53.

Savrda, C.E. (1992). Trace fossils and benthic oxygenation. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 172–196.

Savrda, C. (1993). Ichnosedimentologic evidence for a noncatastrophic origin of Cretaceous–Tertiary boundary sand in Alabama. *Geology*, 21, 1075–1078.

Savrda, C.E. (1998). Ichnology of the Bridge Creek Limestone Member: Evidence for temporal and spatial variations in paleo-oxygenation in The Western Interior Seaway. In *Stratigraphy and Paleoenvironments of the Western Interior Seaway along the Kansas-Colorado-Utah Drilling Transect*, ed. W.E. Dean and M.A. Arthur, *Society for Sedimentary Geology Concepts in Sedimentology and Paleontology*, 6, 127–136.

Savrda, C.E. (2002). Equilibrium responses reflected in a large *Conichnus* (Upper Cretaceous Eutaw Formation, Alabama, USA). *Ichnos*, 9, 33–40

Savrda, C.E. (2007a). Trace fossils and marine benthic oxygenation. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 149–158.

Savrda, C.E. (2007b). Taphonomy of trace fossils. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 92–109.

Savrda, C.E. and Bottjer, D.J. (1986). Trace fossil model for reconstruction of paleo-oxygenation in bottom waters. *Geology*, 14, 3–6.

Savrda, C.E. and Bottjer, D.J. (1987). Trace fossils as indicators of bottom-water redox conditions in ancient marine environments. In *New Concepts in the Use of Biogenic Sedimentary Structures for Paleoenvironmental Interpretation*, ed. D.J. Bottjer, *Society for Sedimentary Geology Pacific Section, Volume and Guidebook*, 52, 3–26.

Savrda, C.E. and Bottjer, D.J. (1989). Trace fossil model for reconstructing oxygenation histories of ancient marine bottom waters: application to Upper Cretaceous Niobrara Formation, Colorado. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 74, 49–74.

Savrda, C.E. and Bottjer, D.J. (1991). Oxygen-related biofacies in marine strata: an overview and update. In *Modern and Ancient Continental Shelf Anoxia*, ed. R.V. Tyson and T.H. Pearson, *Geological Society Special Publication*, 58, 201–219.

Savrda, C.E. and Bottjer, D.J. (1994). Ichnofossils and ichnofabrics in rhythmically bedded pelagic/hemipelagic carbonates: recognitions and evaluation of benthic redox and scour cycles. In *Orbital Forcing and Cyclic Sequences*, ed. P. de Boer and D.G. Smith, *International Association of Sedimentologists Special Publication*, 19, 195–210.

Savrda, C.E. and King, D.T. Jr. (1993). Log-ground and *Teredolites* lagerstätte in a transgressive sequence, Upper Cretaceous (Lower Campanian) Mooreville Chalk, central Alabama. *Ichnos*, 3, 69–77.

Savrda, C.E. and Nanson, L.L. (2003). Ichnology of fair-weather and storm deposits in an Upper Cretaceous estuary (Eutaw Formation, western Georgia, USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 202, 67–83.

Savrda, C.E. and Ozalas, K. (1993). Preservation of mixed-layer ichnofabrics in oxygenation-event beds. *Palaios*, 8, 609–613.

Savrda, C.E., and Smith, M.W. (1996). Behavioural implications of branching and tube-lining in *Teredolites*. *Ichnos*, 4, 191–198.

Savrda, C.E. and Uddin, A. (2005). Large *Macaronichnus* and their behavioural implications (Cretaceous Eutaw Formation, Alabama, USA). *Ichnos*, 12, 1–9.

Savrda, C.E., Bottjer, D.J. and Seilacher, A. (1991). Redox-related benthic events. In *Cycles and Events in Stratigraphy*, ed. G. Einsele, W. Ricken and A. Seilacher, Berlin: Springer-Verlag, pp. 524–541.

Savrda, C.E., Ozalas, K., Demko, T.H., Hichison, R.A. and Scheiwe, T.D. (1993). Log-grounds and the ichnofossil *Teredolites* in transgressive deposits of the Clayton Formation (Lower Paleocene), Western Alabama. *Palaios*, 8, 311–324.

Savrda, C.E., Locklair, R.E., Hall, J.K., Sadler, M.T., Smith, M.W. and Warren, J.D. (1998). Ichnofabrics, ichnocoenoses, and ichnofacies implications of an Upper Cretaceous tidal-inlet sequence (Eutaw Formation, Central Alabama). *Ichnos*, 6, 53–74.

Savrda, C.E., Blanton-Hooks, A.D. Collier, J.W., Drake, R.A., Graves, R.L., Hall, A.G., Nelson, A.I., Slone, J.C., Williams, D.D. and Wood, H.A. (2000). *Taenidium* and associated ichnofossils in fluvial deposits, Cretaceous Tuscaloosa Formation, eastern Alabama, southeastern U.S.A. *Ichnos* 7, 227–242.

Savrda, C.E., Browning, J.V., Krawinkel, H., and Hesselbo, S.P. (2001). Firmground ichnofabrics in deep-water sequence stratigraphy, Tertiary Clinoform-toe Deposits, New Jersey Slope. *Palaios*, 16, 294–305.

Savrda, C.E., Counts, J., McCormick, O., Urash, R. and Williams, J. (2005). Log-grounds and *Teredolites* in transgressive deposits, Eocene Tallahatta Formation (southern Alabama, USA). *Ichnos*, 12, 47–57.

Scarboro, D.D. and Tucker, M.E. (1995). Amphibian footprints from the mid-Carboniferous of Northumberland, England: sedimentological context, preservation and significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 113, 335–349.

Scasso, R.A. and Bellosi, E.S. (2004). Cenozoic continental and marine trace fossils at the Bryn Gwyn Paleontological Park, Chubut. In *First International Congress on Ichnology, Trelew, Argentina*, ed. R.A. Scasso and E.S. Bellosi, *Museo Paleontológico Egidio Feruglio, Bryn Gwyn Guidebook*, 1–19.

Scasso, R., Olivero, E.B. and Buatois, L.A. (1991). Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine fan/shelf depositional system (Upper Cretaceous, James Ross Island, Antarctica). *Journal of South American Earth Science*, 4, 239–260.

Schaeffer-Novelli, Y., Cintron-Molero, G. and Soares, M.L.G. (2002). Mangroves as indicators of sea level change in the muddy coasts of the world. In *Muddy Coasts of the World: Processes, Deposits and Function*, ed. T. Healy, Y. Wang and J.-A. Healy, Amsterdam: Elsevier, 245–262.

Schäfer, W. (1962). *Aktuo-Paläontologie nach Studien in der Nordsee*. Frankfurt am Main: Waldemar Kramer.

Schäfer, W. (1972). *Ecology and Palaeoecology of Marine Environments*. Chicago, IL: University of Chicago Press.

Schatz, E.R., M.G. Mángano, L.A. Buatois and Limarino, C.O. (2011). Life in the Late Paleozoic Ice Age: trace fossils from glacially influenced deposits in a late Carboniferous Fjord-valley of Western Argentina. *Journal of Paleontology*, 85, 502–518.

Schieber, J. (1999). Microbial mats in terrigenous clastics: The challenge of identification in the rock record. *Palaios*, 14, 3–12.

Schieber, J. (2002). The role of an organic slime matrix in the formation of pyritized burrow trails and pyrite concretions. *Palaios*, 17, 104–109.

Schieber, J. (2003). Simple gifts and buried treasures; implications of finding bioturbation and erosion surfaces in black shales. *The Sedimentary Record*, 1, 4–8.

Schieber, J., Bose, P.K., Eriksson, P.G., Banerjee, S., Sarkar, S., Altermann, W. and Catuneanu, O. (2007). *Atlas of Microbial Mat Features Preserved Within the Siliciclastic Rock Record. Atlases in Geology 2*. Amsterdam: Elsevier.

Schimper, W.P. and Schenk, A. (1890). Palaeophytologie. In *Handbuch de Palaeontologie, Teil II*, ed. K.A. Zittel, Leipzig: Oldenbourg, pp. 958.

Schlager, W. (2005). Carbonate Sedimentology and Sequence Stratigraphy. *Society for Sedimentary Geology Concepts in Sedimentology and Paleontology*, 8.

Schlirf, M. (2000). Upper Jurassic trace fossils from the Boulonnais (northern France). *Geologica et Palaeontologica*, 34, 145–213.

Schlirf, M. and Uchman, A. (2005). Revision of the ichnogenus *Sabellarifex* Richter, 1921 and its relationship to *Skolithos* Haldeman, 1840 and *Polykladichnus* Fürsich, 1981. *Journal of Systematic Palaeontology*, 3, 115–131.

Schlirf, M., Uchman, A. and Kümmel, M. (2001). Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area

(Franconia, south-eastern Germany). *Paläontologische Zeitschrift*, 75, 71–96.

Schoener, T.W. (1987). A brief history of optimal foraging ecology. In *Foraging Behavior*, ed. A.C. Kamil, J.R. Krebs and H.R. Pulliam, New York: Plenum Press, pp. 5–68.

Scholle, P.A., Arthur, M.A. and Ekdale, A.A. (1983). Pelagic environment. In *Sandstone Depositional Environments*, ed. P.A. Scholle and D. Spearing, *American Association of Petroleum Geologists Memoir*, 31, 220–291.

Schram, F.R., Feldmann, R.M. and Copeland, M.J. (1978). The Late Devonian Paleaopalaemonidae and the earliest decapod crustaceans. *Journal of Paleontology*, 52, 1375–1387.

Schuppers, J.D. (1993). Quantification of turbidite facies in a reservoir-analogous submarine fan channel sandbody, south-central Pyrinees, Spain. In *The Geological Modelling of Hydrocarbon Reservoirs and Outcrop Analogues*, ed. S.S. Flint and I.D. Bryant, *International Association of Sedimentologists Special Publication*, 15, 99–112.

Scott, A.C. (1992). Trace-fossils of plant–arthropod interactions. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 197–223.

Scott, J.J., Renaut, R.W, Buatois, L.A. and Mángano, M.G. (2007a). Saline lake ichnology: Examples of shoreline fluctuations from the Green River Formation, Wyoming, USA and the Kenya Rift. *5th Annual Meeting of the Mercosur, Ushuaia*, 30.

Scott, J.J., Renaut, R.W., Owen, R.B., Sarjeant, W.A.S., (2007b). Biogenic activity, trace formation, and trace taphonomy in the marginal sediments of saline, alkaline Lake Bogoria, Kenya Rift Valley. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J. Genise, and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 309–330.

Scott, J.J., Renaut, R.W. and Owen, B.R. (2008). Preservation and Paleoenvironmental Significance of a Footprinted Surface on the Sandai Plain, Lake Bogoria, Kenya Rift Valley. *Ichnos*, 15, 208–231.

Scott, J.J., Renaut, R.W., Owen, R.B. and Buatois, L.A. (2009). Trace fossils in exhumed surfaces around saline lakes: an example from Lake Bogoria, Kenya Rift Valley. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 176–198.

Scott, J.J., Renaut, R.W. and Owen, R.B. (2010). Taphonomic controls on animal tracks at saline, alkaline Lake Bogoria, Kenya Rift Valley: impact of salt efflorescence and clay mineralogy *Journal of Sedimentary Research*, 80, 639–665.

Scrivner, P.J. and Bottjer, D.J. (1986). Neogene avian and mammalian tracks from Death Valley National Monurnent, Califomia: their context, classification and preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 57, 285–331.

Seike, K. (2008). Burrowing behaviour inferred from feeding traces of the opheliid polychaete *Euzonus* sp. as response to beach morphodynamics. *Marine Biology*, 153, 1199–1206.

Seike, K. (2009). Influence of beach morphodynamics on the distribution of the opheliid polychaete *Euzonus* sp. and its feeding burrows on a sandy beach: paleoecological and paleoenvironmental implications for the trace fossil *Macaronichnus segregatis*. *Palaios*, 24, 799–808.

Seike, K. and Curran, A.H. (2010). Burrow morphology of the Bahamian land crab *Gecarcinus lateralis. Workshop on Crustacean Bioturbation, Fossil and Recent*, ed. J.M. Gibert de, F. Muñiz, E. Mayoral, Z. Belaústegui, *Abstract Volume*, 91–94.

Seilacher, A. (1953a). Studien zur Palichnologie. I. Über die Methoden der Palichnologie. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 96, 421–452.

Seilacher, A. (1953b). Studien zur Palichnologie. II. Die fossilen Ruhespuren (Cubichnia). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 98, 87–124.

Seilacher, A. (1954). Die Geologische Bedeutung Fossiler Lebensspuren. *Zeitschrift Deutschen Geologische Gesellschaft*, 105, 214–227.

Seilacher, A. (1955a). Spuren und Lebensspuren der Trilobiten. In *Beitrage zur Kenntnis des Kambriums in der Salt Range (Pakistan)*, ed. O.H. Schindewolf and A. Seilacher, *Akademie der Wissenschaften und der Literatur zu Mainz, Mathematisch–Naturwissenschaftliche Klasse, Abhandlungen*, 10, 342–372.

Seilacher, A. (1955b). Spuren und Fazies im Unterkambrium. In *Beitrage zur Kenntnis des Kambriums in der Salt Range (Pakistan)*, ed. O.H. Schindewolf and A. Seilacher, *Akademie der Wissenschaften und der Literatur zu Mainz, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen*, 10, 373–399.

Seilacher, A. (1956). Der Beginn des Kambriums als biologische Wende. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 103, 155–180.

Seilacher, A. (1958). Zur ökologische n Charakteristik von Flysch und Molasse. *Eclogae Geologicae Helvetiae*, 51, 1062–1078.

Seilacher, A. (1960). Lebensspuren als Leitfossilien. *Geologische Rundschau*, 49, 41–50.

Seilacher, A. (1962). Paleontological studies on turbidite sedimentation and erosion. *Journal of Geology*, 70, 227–234.

Seilacher, A. (1963a). Umlagerung und Rolltransport von Cephalopodengehäuse. *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 11, 593–615.

Seilacher, A. (1963b). Lebensspuren und sakinitatsfazies. *Fortschritte in der Geologie Rheinland und Westfalen*, 10, 81–94.

Seilacher, A. (1964a). Biogenic sedimentary structures. In *Approaches to Paleoecology*, ed. J. Imbrie, and N. Newell, Chichester, UK: John Wiley & Sons, pp. 296–316.

Seilacher, A. (1964b). Sedimentological classification and nomenclature of trace fossils. *Sedimentology*, 3, 256–253.

Seilacher, A. (1967a). Fossil behaviour. *Scientific American*, 217, 72–80.

Seilacher, A. (1967b). Bathymetry of trace fossils. *Marine Geology*, 5, 413–428.

Seilacher, A. (1968). Sedimentationprozesse in Ammonitengehäusen. *Akademie der Wissenschaften und der Literatur in Mainz, Abhandlungen der mathematisch-naturwissenschaftlichen Klasse*, Jahrgang 1967, 191–204.

Seilacher, A. (1970). *Cruziana* stratigraphy of "non–fossiliferous" Palaeozoic sandstones. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 447–476.

Seilacher, A. (1974). Flysch trace fossils: evolution of behavioural diversity in the deep-sea. *Neues Jahrbuch für Geologie und Palaontologie, Monatshefte*, 233–245.

Seilacher, A. (1977a). Pattern analysis of *Paleodictyon* and related trace fossils. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 289–334.

Seilacher, A. (1977b). Evolution of trace fossil communities. In *Patterns of Evolution*, ed. A. Hallam, Amsterdam: Elsevier, pp. 359–376.

Seilacher, A. (1978). Use of trace fossils for recognizing depositional environments. In *Trace Fossil Concepts*, ed. P.B. Basan, *Society for Sedimentary Geology Short Course Notes*, 5, 167–181.

Seilacher, A. (1984). Late Precambrian and Early Cambrian Metazoa: Preservational or real extinctions? In *Patterns of Change in Earth Evolution*, ed. H.D. Holland and A.F. Trendall, Berlin: Springer-Verlag, pp. 159–168.

Seilacher, A. (1985). Trilobite paleobiology and substrate relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 76, 231–237.

Seilacher, A. (1986). Evolution of behavior as expressed in marine trace fossils. In *Evolution of Animal Behavior: Paleontological and Field Approaches*, ed. J.A. Kitchell and M.H. Nitecki, New York: Oxford University Press, pp. 62–87.

Seilacher, A. (1989). Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia*, 22, 229–239.

Seilacher, A. (1990a). Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology*, 3, 289–311.

Seilacher, A. (1990b). Paleozoic trace fossils. In *The Geology of Egypt*, ed. R. Said, Rotterdam: A.A. Balkema, pp. 649–670.

Seilacher, A. (1992a). An updated *Cruziana* stratigraphy of Gondwanan Palaeozoic sandstones. In *The Geology of Lybia 5*, ed. M.J. Salem, Amsterdam: Elsevier, pp. 1565–1580.

Seilacher, A. (1992b). Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society, London*, 149, 607–613.

Seilacher, A. (1994). How valid is *Cruziana* stratigraphy? *Geologische Rundschau*, 83, 752–758.

Seilacher, A. (1996). Evolution of burrowing behaviour in Silurian trilobites: ichnosubspecies of *Cruziana acacensis*. In *The Geology of the Sirt Basin. Volumes I-III*, ed. M.J. Salem, Amsterdam: Elsevier, pp. 523–530.

Seilacher, A. (1997). *Fossil Art*. Drumheller: The Royal Tyrrell Museum of Paleontology.

Seilacher, A. (1999). Biomat-related lifestyles in the Precambrian. *Palaios*, 14, 86–93.

Seilacher, A. (2000). Ordovician and Silurian arthrophycid ichnostratigraphy. In *Geological Exploration in Murzuk Basin*, ed. M.A. Sola and D. Worsley, Amsterdam: Elsevier, pp. 237–258.

Seilacher, A. (2005). Silurian trace fossils from Africa and Argentina mapping a trans-Gondwanan seaway? *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 129–141.

Seilacher, A. (2007a). *Trace Fossil Analysis*. Heidelberg: Springer-Verlag.

Seilacher, A. (2007b). Principles of ichnostratigraphy. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J. Genise and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 53–56.

Seilacher, A. (2008). Biomats, biofilms, and bioglue as preservational agents for arthropod trackways: *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 252–257.

Seilacher, A. and Alidou, S. (1988). Ordovician and Silurian trace fossils from northern Benin (W-Africa). *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 431–439.

Seilacher, A. and Crimes, P.T. (1969). "European" species of trilobite burrows in eastern Newfoundland. In *North Atlantic Geology and Continental drift*, ed. M. Kay, *American Association of Petroleum Geologists Memoir*, 12, 145–148.

Seilacher, A. and Pflüger, F. (1994). From biomats to benthic agriculture: A biohistoric revolution. In *Biostabilization of sediments*, ed. W.E. Krumbein, D.M. Peterson and L.J. Stal, Odenburg: Bibliotheks und Informationssystem der Carl von Ossietzky Universität, pp. 97–105.

Seilacher, A. and Seilacher, E. (1994). Bivalvian trace fossils: A lesson from actuopaleontology. *Courier Forschungsinstitut Institut Senckenberg*, 169, 5–15.

Seilacher, A., Reif, W.-E. and Westphal, F. (1985). Sedimentological, ecological and temporal paterns of fossil Lagerstätten. *Royal Society of London Philosophical Transactions, B*, 311, 5–23.

Seilacher, A., Bose, P.K. and Pflüger, F. (1998). Triploblastic animals more than 1 billion years ago: Trace fossil evidence from India. *Science*, 282, 80–83.

Seilacher, A., Lüning, S., Martin, M., Klitzsch, E., Khoja, A. and Craig, J. (2002). Ichnostratigraphic correlation of Lower Paleozoic clastics in the Kufra Basin (SE Libia). *Lethaia*, 35, 257–262.

Seilacher, A., Grazhdankin, D. and Legouta, A. (2003). Ediacaran biota: The dawn of animal life in the shadow of giant protists. *Paleontological Research*, 7, 43–54.

Seilacher, A., Cingolani, C. and Varela, R. (2004). Ichnostratigraphic correlation of Early Palaeozoic sandstones in North Africa and Central Argentina. In *Geology of NW Libya*, ed. M.J. Salem and T.M. Oun, Libya: Earth Science Society of Libya, 1, 275–292.

Seilacher, A., Buatois, L.A., Mángano, M.G. (2005). Trace fossils in the Ediacaran-Cambrian transition: Behavioural diversification, ecological turnover and environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227, 323–356.

Seilacher-Drexler, E. and Seilacher, A. (1999). Undertraces of sea pens and moon sails and possible counterparts. *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 9, 521–540.

Seiple, W. (1981). The ecological significance of the locomotor activity rhythms of *Sesarma cinereum* and *Sesarma reticulatum*. *Crustaceana*, 40, 5–15.

Sellers, W.I. and Manning, P.L. (2007). Estimating maximum running speeds using evolutionary robotics. *Proceedings of the Royal Society, Series B: Biological Sciences*, 274, 2711–2716.

Selley, R.C. (1970). Ichnology of Paleozoic sandstones in the Southern Desert of Jordan: A study of trace fossils in their sedimentologic context. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 477–488.

Sellwood, B.W. (1971). A *Thalassinoides* burrow containing the crustacean *Glyphaea udressieri* (Meyer) from the Bathonian of Oxfordshire. *Palaeontology*, 14, 589–581.

Sepkoski, J.J. Jr. (1981). A factor analytic description of the marine fossil record. *Paleobiology*, 7, 36–53.

Sepkoski, J.J. Jr. (1988). Alpha, beta, or gamma: where does all the diversity go? *Paleobiology*, 14, 221–234.

Sepkoski, J.J. Jr. (1991). A model of onshore–offshore change in faunal diversity. *Paleobiology*, 17, 58–77.

Sepkoski, J.J. Jr. (1992). A compendium of fossil marine animal families. second edition. *Milwaukee Public Museum Contributions in Biology and Geology*, 83, 1–156.

Sepkoski, J.J. Jr. (1995). The Ordovician radiations: diversification and extinction shown by global genus-level taxonomic data. *7th International Symposium on the Ordovician System, Society for Sedimentary Geology, Pacific Section*, 393–396.

Sepkoski, J.J. Jr. (1997). Biodiversity: past, present, and future. *Journal of Paleontology*, 71, 533–539.

Sepkoski, J.J. Jr. and Miller, A.I. (1985). Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In *Phanerozoic Diversity Patterns: Profiles in Macroevolution*, ed. J.W. Valentine, Princeton, NJ: Princeton University Press, pp. 153–190.

Sepkoski, J.J. Jr. and Sheehan, P.M. (1983). Diversification, faunal change, and community replacement during the Ordovician radiations. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenum Press, pp. 673–718.

Sereno, P.C. and Novas, F.E. (1992). The complete skull and skeleton of an early dinosaur. *Science*, 258, 1137–1140.

Shanley, K.W., McCabe, P.J. and Hettinger, R.D. (1992). Tidal influence in Cretaceous fluvial strata from Utah, USA: a key to sequence stratigraphic interpretation, *Sedimentology*, 39, 905–930.

Shapiro, R.S. (2007). Stromatolites: a 3.5-billion-year ichnologic record. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 382–390.

Shaw, J. and Lesemann, J.E. (2003). Subglacial outburst floods and extreme sedimentary events in the Labrador Sea. In *Extreme Depositional Environments: Mega End Members in Geologic Time*, ed. M.A. Chan and A.W. Archer, *Geological Society of America, Special Paper*, 370, 25–41.

Sheehan, P.M. (2001). History of marine biodiversity. *Geological Journal*, 36, 231–249.

Sheehan, P.M. and Schiefelbein, D.R.J. (1984). The trace fossil *Thalassinoides* from the Upper Ordovician of the eastern Great Basin: deep burrowing in the Early Paleozoic. *Journal of Paleontology*, 58, 440–447.

Shen, B., Xiao, S., Dong, L., Zhou, C. and Liu, J. (2007). Problematic macrofossils from Ediacaran successions in the North China and Chaidam blocks: implications for their evolutionary roots and biostratigraphic significance. *Journal of Paleontology*, 81, 1396–1411.

Shi, G.R. and Weldon, E.A. (2002). Permian stratigraphy, sedimentology and paleontology of the southern Sydney Basin, eastern Australia. *First International Palaeontological Congress, IPC2002 Australasia, Pre–4 Field Excursion Guidebook, Daekin University, School of Ecology and Environment, Technical Paper*, 1, 1–65.

Shinn, E.A. (1968). Burrowing in recent lime sediments of Florida and the Bahamas. *Journal of Paleontology*, 42, 879–894.

Short, A.D. (1991). Macro-meso tidal beach morphodynamics, an overview. *Journal of Coastal Research*, 7, 417–436.

Shu, D.G., Conway Morris, S., Han, J., Li, Y., Zhang, X.L., Hua, H., Zhang, Z.F., Liu, J. N., Guo, J.F., Yao, Y. and Yasui, K. (2006). Lower Cambrian vendobionts from China and early diploblast evolution. *Science*, 312, 731–734.

Shultz, M.R. and Hubbard, S.M. (2005). Sedimentology, stratigraphic architecture and ichnology of gravity-flow deposits partially ponded in a growth-fault-controlled slope minibasin, Tres Pasos Formation (Cretaceous), Southern Chile. *Journal of Sedimentary Research*, 75, 440–453.

Sidi, F.H., Nummedal, D., Imbert, P., Darman, H. and Posamentier, H.W. (2003) (eds.). *Tropical deltas of Southeast Asia: Sedimentology, stratigraphy and petroleum geology*. *Society for Sedimentary Geology Special Publication*, 76.

Sidor, C.A., Miller M.F. and Isbell, J.L. (2008). Tetrapod burrows from the Triassic of Antarctica. *Journal of Vertebrate Paleontology*, 28, 277–284.

Siggerud, E.I.H., and Steel, R.J. (1999). Architecture and trace-fossil characteristics of a 10,000–20,000 year, fluvial-to-marine sequence, SE Ebro Basin, Spain. *Journal of Sedimentary Research*, 69, 365–383.

Signor, P.W. III and Brett, C.E. (1984). The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology*, 10, 229–245.

Simpson, E.L. (1991), An exhumed, Lower Cambrian tidal flat: the Antietam Formation, central Virginia, U.S.A. In *Clastic Tidal Sedimentology*, ed. D.G. Smith, G.E. Reinson, B.A. Zaitlin and R.A. Rahmani, *Canadian Society of Petroleum Geology, Memoir*, 16, 123–134.

Simpson, S. (1957). On the trace fossil *Chondrites*. *Quarterly Journal Geological Society of London*, 112, 475–479.

Simpson, S. (1970). Notes on *Zoophycos* and *Spirophyton*. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 505–514.

Skilleter, G.A. and Peterson, C.H. (1994). Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. *Oecologia*, 100, 268–278.

Slobodkin, L.B. and Sanders, H.L. (1969). On the contribution of environmental predictability to species diversity. *Brookhaven Symposia on Biology*, 22, 82–95.

Smith, A.B. and Crimes, T.P. (1983). Trace fossils formed by heart urchins: a study of *Scolicia* and related traces. *Lethaia*, 16, 79–92.

Smith, C.R., Levin, L.A., Hoover, D.J., McMurtry, G. and Gage, J.D. (2000). Variations in bioturbation across the oxygen minimum zone in the northwest Arabian Sea. In *Benthic Processes in the Deep Arabian Sea: Biogeochemistry, Biodiversity and Ecology, Deep Sea Research Part II*, ed. J.D. Gage, L.A. Levin and G.A. Wolff, *Tropical Studies in Oceanography*, 47, 227–257.

Smith, D.C. and Douglas, A.E. (1987). *The Biology of Symbiosis*. London: Edward Arnold Publishers Ltd.

Smith, J.J. and Hasiotis, S.T. (2008). Traces and burrowing behaviors of the cicada nymph *Cicadetta calliope*: neoichnology and paleoecological significance of extant soil-dwelling insects. *Palaios*, 23, 503–513.

Smith, J.J., Hasiotis, S.T., Kraus, M.J. and Woody, D. (2008a). *Naktodemasis bowni*: new ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Bighorn Basin, Wyoming. *Journal of Paleontology*, 82, 267–278.

Smith, J.J., Hasiotis, S.T., Kraus, M.J. and Woody, D.T. (2008b). Relationship of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Wyoming, during the Paleocene-Eocene Thermal Maximum. *Palaios*, 23, 683–699.

Smith, P.R., Harper, A.S. and Wood, M.F. (1982). Nonmarine trace fossils in the Mio–Pliocene Ridge Basin Group, southern California. In *Geologic History of Ridge Basin, Southern California*, ed. J.C. Cromwell and M.H. Link, *Society for Sedimentary Geology Pacific Section*, 253–258.

Smith, R. (2004). Silled sub-basins to connected tortuous corridors: Sediment distribution systems on topographically complex subaqueous slopes. In *Confined Turbidite Systems*, ed. S.A. Lomas and P. Joseph, *Geological Society Special Publication*, 222, 23–43.

Smith, R.M.H. (1987). Helical burrow casts of Therapsid origin from the Beaufort Group (Permian) of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 60, 155–170.

Smith, R.M.H. (1993). Sedimentology and ichnology of floodplain paleosurfaces in the Beaufort Group (Late Permian), Karoo Sequence, South Africa. *Palaios*, 8, 339–357.

Smith, R.M.H., Mason, T.R. and Ward, J.D. (1993). Flash–flood sediments and ichnofacies of the Late Pleistocene Homeb Silts, Kuiseb River, Namibia. *Sedimentary Geology*, 85, 579–599.

Smith, R.M.H., Marsicano, C.A., Wilson, J.A. (2009). Sedimentology and paleoecology of a diverse early Jurassic tetrapod tracksite in Lesotho, Southern Africa. *Palaios*, 24, 672–684.

Snelgrove, P.V.R. and Butman, C.A. (1994). Animal–sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology Annual Review*, 32, 111–177.

Soja, C.M. (1991). Silurian trace fossils in carbonate turbidites from the Alexander arc of southeastern Alaska. *Ichnos*, 1, 173–182.

Solan, M. and Wigham, B.D. (2005). Biogenic particle reworking and bacterial–invertebrate interactions in marine sediments. In *Interactions Between Macro- and Microorganisms in Marine Sediments*, ed. E. Kristensen, J.E. Kostka and R.R. Haese, Washington DC: American Geophysical Union, pp. 105–124.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. and Srivastava, D.S. (2004a). Extinction and ecosystem function in the marine benthos. *Science*, 306, 1177–1180.

Solan, M., Wigham, B.D., Hudson, I.R., Kennedy, R., Coulon, C.H., Norling, K., Nilsson, H.C. and Rosenberg, R. (2004b). *In situ* quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. *Marine Ecology Progress Series*, 271, 1–12.

Solan, M., Batty, P., Bulling, M.T. and Godbold, J.A. (2008). How biodiversity affects ecosystem processes: Implications for ecological revolutions and benthic ecosystem function. *Aquatic Biology*, 2, 289–301.

Solan, M., Godbold, J.A., Symstad, A., Flynn D.F.B. and Bunker, D. (2009). Biodiversity–ecosystem function research and biodiversity futures: Early bird catches the worm or a day late and a dollar short? In *Biodiversity, Ecosystem Functioning and Human Wellbeing: An Ecological and Economic Perpective*, ed. S. Naeem, D.E. Bunker, A. Hector, M. Loreau and C. Perrings, Oxford, UK: Oxford University Press, pp. 30–45.

Soler-Gijón, R. and Moratalla, J.J. (2001). Fish and tetrapod trace fossils from the Upper Carboniferous of Puertollano, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 171, 1–28.

Spaargaren, D.H. (1979). Hydrodynamic properties of benthic marine crustacean. *Marine Ecology*, 1, 351–359.

Spaargaren, D.H. (1995). A functional model for describing the responses to salinity stress in aquatic animals. *Comparative Biochemistry and Physiology A*, 111, 501–506.

Sperling, E.A. and Vinther, J. (2010). A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolutiom and Development*, 12, 201–209.

Spila, M.V., Pemberton, S.G. and Sinclair, I.K. (2005). Comparison of marine and brackish/stressed ichnological signatures in the Ben Nevis amd Avalon Formations, Jeanne d'Arc Basin. In *Petroleum Resources and Reservoirs of the Grand Banks, Eastern Canadian Margin*, ed. R.N. Hiscott and A.J. Pulham, *Geological Association of Canada Special Paper*, 43, 73–94.

Squires, R.L. and Advocate, D.M. (1984). Meniscate burrows from Miocene lacustrine–fluvial deposits, Diligencia Formation, Oro copia Mountains, southern California. *Journal of Paleontology*, 58, 593–597.

Stanley, K.O. and Fagerstrom, J.A. (1974). Miocene invertebrate trace fossils from a braided river environment, Nebraska, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 15, 63–82.

Stanley, D.C.A. and Pickerill, R.K. (1993). *Fustiglyphus annulatus* from the Ordovician of Ontario, Canada, with a systematic review of the ichnogenera *Fustiglyphus* Vialov 1971 and *Rhabdoglyphus* Vassoievich 1951. *Ichnos*, 3, 57–67.

Stanley, D.C.A. and Pickerill, R.K. (1998). Systematic ichnology of the Late Ordovician Georgian Bay Formation of Southern Ontario, Eastern Canada. *Royal Ontario Museum, Life Sciences Contributions*, 162, 1–56.

Stanley, S.M. (1970). Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America, Memoir*, 25, 1–269.

Stearley, R.F. and Ekdale, A.A. (1989). Modern marine bioerosion by macroinvertebrates, Northern Gulf of California. *Palaios*, 4, 453–467.

Steele-Petrovic, H.M. (1979). The physiological differences between articulate brachiopods and filter-feeding bivalves as a factor in the evolution of marine level-bottom communities. *Palaeontology*, 22, 101–134.

Stössel, I. (1995). The discovery of a new Devonian tetrapod trackway in SW Ireland. *Journal of the Geological Society of London*, 152, 407–413.

Stow, D.A.V. (1985). Deep-sea clastics: Where are we and where are we going? In *Sedimentology Recent Developments and Applied Aspects*, eds. P. J. Brenchley and B. P. J. Williams. *Geological Society of London, Special Publication*, 18, 67–93.

Stow, D.A.V. and Wetzel, A. (1990). Hemiturbidite: a new type of deep-water sediment. *Proceedings Ocean Drilling Program, Scientific Results*, 116, 25–34.

Stow, D.A.V., Reading, H.G. and Collinson, J.D. (1996). Deep seas. In *Sedimentary Environments*, ed. H.G. Reading, Oxford, UK: Blackwell Science, pp. 395–454.

Strother, P.K. (2000). Cryptospores: the origin and early evolution of the terrestrial flora. In *Phanerozoic Terrestrial ecosyStems*, ed. R.A. Gastaldo and W.A. DiMichele, *The Paleontological Society Papers*, 6, 3–20.

Strother, P.K., Al-Hajri, S. and Traverse, A. (1996). New evidence of land plants from the lower Middle Ordovician of Saudi Arabia. *Geology*, 24, 55–58.

Strother, P.K. and Beck, J.H. (2000). Spore-like microfossils from Middle Cambrian strata: expanding the meaning of the term cryptospore. In *Pollen and Spores: Morphology and Biology*, ed. M.M. Harley, C.M. Morton and S. Blackmore, Kew, London: Royal Botanic Gardens, pp. 413–424.

Sturm, H. (1955). Beiträge zur Ethologie einiger mitteldeutscher Machiliden. *Zeitschrift für Tierpsychologie*, 12, 337–363.

Sutcliffe, O.E. (1997). An ophiuroid trackway from the Lower Devonian Hunsrück Slate, Germany. *Lethaia*, 30, 33–39.

Suwa, G. (1984). Could *Australopithecus afarensis* have made the hominid tracks at Laetoli? *Journal of Physical Anthropology*, 963, 224–225.

Swinbanks, D.D. and Murray, J.W. (1981). Biosedimentological zonation of Boundary Bay tidal flats, Fraser River Delta, British Columbia. *Sedimentology*, 28, 201–237.

Systra, Y.J. and Jensen, S. (2006). Trace Fossils from the Dividalen Group of northern Finland with remarks on early Cambrian trace fossil provincialism. *Geologiska Föreningens I Stockholm Förhandlingar*, 128, 321–325.

Syvitski, J.P., Burrell, D.C. and Skei, J.M. (1987). *Fjords: Processes and Products*. New York: Springer-Verlag.

Szajna, M.J. and Hartline, B.W. (2003). A new vertebrate footprint locality from the Late Triassic Passaic Formation near Birdsboro, Pennsylvania. In *The Great Rift Valleys of Pangea in Eastern North America*, ed. P.M. LeTourneau and P.E. Olsen, New York: Columbia University Press, 264–272.

Tanner, L.H., Lucas, S.G. and Chapman, M.G. (2004). Assessing the record and causes of Late Triassic extinction. *Earth Sciences Reviews*, 65, 103–139.

Tapanila, L. (2005). Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: trace fossil evidence. *Lethaia*, 38, 89–99.

Tapanila, L. (2008). The endolithic guild: an ecological framework for residential cavities in hard substrates. In *Current Developments in Bioerosion*, ed. M. Wisshak and L. Tapanila, Erlangen Earth Conference Series, Berlin: Springer-Verlag, pp. 3–20.

Tapanila, L. and Ekdale, A.A. (2007). Early history of symbiosis in living substrates: Trace-fossil Evidence from the marine record. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 345–355.

Tapanila, L. and Holmer, L.E. (2006). Endosymbiosis in Ordovician–Silurian corals and stromatoporoids: a new lingulid and its trace from eastern Canada. *Journal of Paleontology*, 80, 750–759.

Taylor, A.M. and Gawthorpe, R.L. (1993). Application of sequence stratigraphy and trace fossil analysis to reservoir description: Examples from the Jurassic of the North Sea. In *Petroleum Geology of Northwest Europe*, *Proceedings of the 4th Conference*, ed. J.R. Parker, London: Geological Society, pp. 317–335.

Taylor, A.M. and Goldring, R. (1993). Description and analysis of bioturbation and ichnofabric. *Journal of the Geological Society, London*, 150, 141–148.

Taylor, A.M., Goldring, R. and Gowland, S. (2003). Analysis and application of ichnofabrics. *Earth Science Reviews*, 60, 227–259.

Taylor. A.M. and Pollard, J. (1999). Ichnofabrics in Jurassic strata, North Yorkshire Coast, England. Field Trip Guide Fifth International Ichnofabric Workshop.

Taylor, A.M. and Skinner, J.D. (2000). Associative feeding between aardwolves (*Proteles cristatus*) and aardvarks (*Orycteropus afer*). *Mammal Review*, 30, 141–143.

Taylor, J.H. (1964). Some aspects of diagenesis. *Advancement in Science*, 18, 417–436.

Taylor, P.D. and Wilson, M.A. (2003). Palaeoecology and evolution of marine hard substrate communities. *Earth Science Reviews*, 62, 1–103.

Tchoumatchenco, P. and Uchman, A. (2001). The oldest deep-sea *Ophiomorpha* and *Scolicia* and associated trace fossils from the Upper Jurassic–Lower Cretaceous deep-water turbidite deposits of SW Bulgaria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 169, 85–99.

Tedesco, L.P. and Wanless, H.R. (1991). Generation of sedimentary fabrics and facies by repetitive excavation and storm infilling of burrow networks, Holocene of South Florida and Caicos Platform, B.W.I. *Palaios*, 6, 326–343.

Terwindt, J.H.J. (1988). Palaeo-tidal reconstructions of inshore tidal depositional environments. *In Tide-influenced Sedimentary Environments*, ed. P.L. de Boer, A van Gelder and S.D. Nio, Dordrecht: D. Reidel Publishing Company, pp. 233–263.

Tevis, L. and Newell, I.M. (1962). Studies on the biology and seasonal cycle of the giant red velvet mite, *Dinothrombium pandorae*. (Acari, Trombidiidae). *Ecology*, 43, 497–505.

Thayer, C.W. (1979). Biological bulldozers and the evolution of marine benthic communities. *Science*, 203, 458–461.

Thayer, C.W. (1983). Sediment–mediated biological disturbance and the evolution of marine benthos. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenum Press, pp. 479–625.

Thomas, M.A. and Anderson, J.A. (1994). Sea-level controls on the architecture of the Trinity/Sabine incised-Valley System, Texas continental shelf. In *Incised-Valley Systems: Origin and sedimentary sequence*, ed. R.W. Dalrymple, R. Boyd and B.A. Zaitlin, *Society for Sedimentary Geology Special Publication*, 51, 63–82.

Thomas, R.G., Smith, D.G., Wood, J.M., Visser, J., Caverley-Range, E.A. and Koster, E.H. (1987). Inclined heterolithic stratification: Terminology, description, interpretation and significance. *Sedimentary Geology*, 53, 123–179.

Thomas, R.D.K. (1986). Taphonomy: ecology's loss is sedimentology's gain. *Palaios*, 1, 206.

Thomason, J.R. and Voorhies, M.R. (1990). Grasslands and grazers. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Scientific Publications, pp. 84–87.

Thorne, B.L., Grimaldi, D.A. and Krishna, K. (2000). Early fossil history of the termites. In *Termites: Evolution, Sociality, Symbioses, Ecology*, ed. T. Abe, D.E. Bignell and M. Higashi, Dordrecht: Kluwer Academic, pp. 77–93.

Thulborn, R.A. (1990). *Dinosaur Traces*. London: Chapman & Hall.

Thum, A.B. and Griffiths, C.L. (1977). Ecology of the meiofauna from a subtidal biogenous ripple system. *Proceedings of the 3rd International Meiofauna Conference Hamburg*, abstract.

Ting, H.H., Huang, C.Y. and Wu, L.C. (1991). Paleoenvironments of the Late Neogene sequences along the Nantzuhsien River, southern Taiwan. *Petroleum Geology of Taiwan*, 26, 121–149.

Titschak, J., Bromley, R.G. and Freiwald, A. (2005). Plio-Pleistocene cliff-bound, wedge-shaped, warm-temperate carbonate deposits from Rhodes (Greece): sedimentology and facies. *Sedimentary Geology*, 180, 29–56.

Tognoli, F.M.W. and Netto, R. (2003). Ichnofabric patterns of the Paleozoic estuarine deposits from the Rio Bonito-Palermo succession, eastern of the Paraná Basin, Brazil. In *Icnología: Hacia una convergencia entre Geología y Biología*, ed. L.A. Buatois and M.G. Mángano, *Asociación Argentina de Paleontología Publicación Especial*, 9, 141–155.

Törnqvist, T.E., Kidder, T.R., Autin, W.J., van der Borg, K., de Jong, A.F.M., Klerks, C.J.W., Snijders, E.M.A., Storms, J.E.A., van Dam, R.L. and Wiemann, M.C. (1996). A revised chronology for Mississippi River subdeltas. *Science*, 273, 1693–1696.

Tomkin, N.S., McIlroy, D., Meyer, R. and Moore-Turpin, A. (2010). Bioturbation influence of reservoir quality: A case study from the Cretaceous Ben Nevis Formation, Jeanne'dArc Basin, offshore Newfoundland, Canada. *Bulletin of the American Association of Petroleum Geologists*, 94, 1059–1078.

Trewin, N.H. (2000). The ichnogenus *Undichna*, with examples from the Permian of the Falkland Islands. *Palaeontology*, 43, 979–997.

Trewin, N.H. and McNamara, K.J. (1995). Arthropods invade the land: Trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 85, 177–210.

Trueman, E.R. (1966). Bivalve molluscs: fluid dynamics of burrowing. *Science*, 152, 523–525.

Trueman, E.R., (1967). The dynamics of burrowing in *Ensis* (Bivalvia). *Proceedings of the Royal Society of London B*, 166, 459–476.

Trueman, E.R. (1968a). Burrowing habit and the early evolution of body cavities. *Nature*, 218, 96–98.

Trueman, E.R. (1968b). The burrowing activities of bivalves. *Symposia of the Zoological Society of London*, 22, 176–186.

Trueman, E.R. (1971). The control of burrowing and the migratory behaviour of *Donax denticulatus* (Bivalvia: Tellinacea). *Journal of Zoology, London*, 165, 453–469.

Trueman, E.R. (1975). *The Locomotion of Soft-Bodied Animals*. New York: Elsevier.

Trueman, E.R. and Ansell, A.D. (1969). The mechanism of burrowing into soft substrates by marine animals. *Oceanography and Marine Biology Annual Review*, 7, 315–366.

Trueman, E.R., Brand, A.R. and Davis, P. (1966). The dynamics of burrowing of some common littoral bivalves. *Journal of Experimental Biology*, 44, 469–492.

Tufail, A., Meadows, P.S. and McLaughlin, P. (1989). Meso- and microscale heterogeneity in benthic community structure and the sedimentary environment on an intertidal muddy-sand beach. *Scientia Marina*, 53, 2–3.

Tunis, G. and Uchman, A. (1996a). Trace fossils and facies changes in Cretaceous-Eocene flysch deposits of the Julian Prealps (Italy and Slovenia): Consequences of regional and world-wide changes. *Ichnos*, 4, 169–190.

Tunis, G. and Uchman, A. (1996b). Ichnology of Eocene flysch deposits of the Istria Peninsula, Croatia and Slovenia. *Ichnos*, 5, 1–22.

Turek, V. (1989). Fish and amphibian trace fossils from Westphalian Sediments of Bohemia. *Palaeontology*, 32, 623–634.

Turner, B.R. (1978). Trace fossils from the Upper Triassic fluviatile Molteno Formation of the Karoo (Gondwana) Supergroup, Lesotho. *Journal of Paleontology*, 52, 959–963.

Turner, B.R., Stanistreet, I.G. and Whateley, M.K.G. (1981). Trace fossil and palaeoenvironments in the Ecca Group of the Nongoma Graben, northern Zululand, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 36, 113–123.

Turner, J.S. (2000). *The Extended Organism. The Physiology of Animal-Built Structures*, Cambridge, MA: Harvard University Press.

Turner, J.S. (2003). Trace Fossils and extended organisms: a physiological perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 15–31.

Turner, J.S. (2004). Extended phenotypes and extended organisms. *Biology and Philosophy*, 19, 327–352.

Tuttle R.H. (1987). Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1,G-2/3 and A. In *Laetoli: A Pliocene Site in Northern Tanzania*, ed. M.D. Leakey and J.M. Harris, Oxford, UK: Clarendon Press, pp. 503–523.

Tuttle, R.H. (1996). The Laetoli hominid G footprints. Where do they stand today? *Kaupia*, 6, 97–102.

Tuttle, R.H. (2008). Footprint clues in hominid evolution and forensics: lessons and limitations. *Ichnos*, 15, 158–165.

Tuttle, R.H., Webb, D., Weidi, E. and Baksh, M. (1990). Further progress on the Laetoli trails. *Journal of Archeological Science*, 17, 347–362.

Twitchett, R.J. (1999). Palaeoenvironments and the faunal recovery after the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 154, 27–37.

Twitchett, R.J. and Barras, C.G. (2004). Trace fossils in the aftermath of mass extinction events. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 397–418.

Twitchett, R.J. and Wignall, P.B. (1996). Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 124, 137–151.

Tyson, R.V. and Pearson, T.H. (1991). Modern and ancient continental shelf anoxia: An overview. In *Modern and Ancient Continental Shelf Anoxia*, ed. R.V. Tyson and T.H. Pearson, *Geological Society Special Publication*, 58, 1–24.

Uchman, A. (1991a). "Shallow water" trace fossils in Paleogene flysch in the southern part of the Magura nappe, Polish Outer Carpathians. *Annales Societatis Geologorum Poloniae*, 61, 61–75.

Uchman, A. (1991b). Trace fossils from stress environments in Cretaceous–Palaeogene of Polish Outer Carpathians. *Annales Societatis Geologorum Poloniae*, 61, 207–220.

Uchman, A. (1991c). Diverse tiering patterns in Paleogene flysch trace fossils of the magura nappe, Carpathian Mountains, Poland. *Ichnos*, 1, 287–292.

Uchman, A. (1992). An opportunistic trace-fossil assemblage from the flysch of the Inoceramian beds (Campanian-Paleocene), Bystrica zone of the Magura Nappe, Carpathians, Poland. *Cretaceous Research*, 13, 539–547.

Uchman, A. (1995). Taxonomy and paleoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria*, 15, 1–115.

Uchman, A. (1998). Taxonomy and ethology of flysch trace fossils; revision of the Marian Książkiewicz Collection and studies of complementary material. *Annales Societatis Geologorum Ploniae*, 68, 105–218.

Uchman, A. (1999). Ichnology of the Rhenodanubian Flysch (Lower Cretaceous-Eocene) in Austria and Germany. *Beringeria*, 25, 67–173.

Uchman, A. (2001). Eocene flysch trace fossils from the Hecho Group of the Pyrenees, northern Spain. *Beringeria*, 28, 3–41.

Uchman, A. (2003). Trends in diversity, frequency and complexity of graphoglyptid trace fossils: Evolutionary and palaeoenvironmental aspects. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 192, 123–142.

Uchman, A., (2004a). Phanerozoic history of deep-sea trace fossils. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 125–139.

Uchman, A. (2004b). Deep-sea trace fossils controlled by palaeo-oxygenation and deposition: an example from the Lower Cretaceous dark flysch deposits of the Silesian Unit, Carpathians, Poland. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils & Strata*, 51, 39–57.

Uchman, A. (2007). Deep-Sea Ichnology: Development of Major Concepts. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 248–267.

Uchman A. (2008a). Stop 11, Słopnice, Ropianka Formation (Senonian-Palaeocene) and variegated shale (Eocene). In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch, The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 136–138.

Uchman, A. (2008b). Stop 8, Zbludza, Beloveza Formation (Eocene) and Bystriaca Formation (Eocene): Outer fan ichnology and sequential colonization of turbidites. In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 124–130.

Uchman, A. (2009). The *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies: Characteristics and constraints. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 276, 107–119.

Uchman, A. and Álvaro J.J. (2000). Non-marine invertebrate trace fossils from the Tertiary Calatayud-Teruel Basin, NE Spain. *Revista Española de Paleontología*, 15, 203–218.

Uchman, A. and Cieszkowski, M. (2008a). Stop 2, Rzyki – Siliceous marl and the lowermost part of the Godula Beds: ichnology of the calcareous turbidites. In *The Second International Congress on Ichnology, Cracow, Ichnological Sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, ed. G. Pieńkowski and A. Uchman, The Pre-congress and post-congress field trip Guidebook, Polish Geological Institute, 104–109.

Uchman, A. and Cieszkowski, M. (2008b). Stop 5, Szczawa, Glebieniec, upper part of the Ropianka Formation (Palaeocene): *Nereites* ichnosubfacies of the *Nereites* ichnofacies and ichnological evidences of turbiditic sedimentation in shales. In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 115–118.

Uchman, A. and Cieszkowski, M. (2008c). Stop 4, Szczawa-Centrum, Grybów beds (Early Oligocene) and sub-Cergowa beds (early Oligocene): *Diplocraterion* in deep-sea sediments. In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 110–114.

Uchman, A. and Demircan, H. (1999). Trace fossils of Miocene deep-sea fan fringe deposits from the Cingöz Formation, southern Turkey. *Annales Societatis Geologorum Poloniae*, 69, 125–153.

Uchman, A. and Pervesler, P. (2006). Surface Lebensspuren produced by amphipods and isopods (Crustaceans) from the Isonzo delta tidal flat, Italy. *Palaios*, 21, 384–390.

Uchman, A., Bubniak, I. and Bubniak, A. (2000). The *Glossifungites* ichnofacies in the area of its nomenclatural archetype, Lviv, Ukraine. *Ichnos*, 7, 183–195.

Uchman, A., Demircan, H., Toker, V., Derman, S., Sevim, S. and Szulc, J. (2002). Relative sea level changes recorded in borings from a Miocene rocky of the Mut Basin, southern Turkey. *Annales Societatis Geologorum Poloniae*, 72, 263–270.

Uchman, A., Janbu, N.E. and Nemec, W. (2004a). Trace fossils in the Cretaceous-Eocene flysch of the Sinop-Boyabat Basin, central Pontides, Turkey. *Annales Societatis Geologorum Poloniae*, 74, 197–235.

Uchman, A., Pika-Biolzi, M. and Hochuli, P.A. (2004b). Oligocene trace fossils from temporary fluvial plain ponds: An example from the Freshwater Molasse of Switzerland. *Eclogae Geologicae Helvetia*, 97, 133–148.

Uchman, A., Nemec, W., Ilgar, A. and Messina, C. (2007). Lacustrine trace fossils and environmental conditions in the Early Miocene Ermenek Basin, southern Turkey. *Annales Societatis Geologorum Poloniae*, 77, 123–139.

Uchman, A., Kazakauskas, V. and Gaigalas, A. (2009). Trace fossils from Late Pleistocene varved lacustrine sediments in eastern Lithuania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 199–211.

Unwin, D.M. and Corbet, S.A. (1991). *Insects, Plants and Microclimate*. Slough, UK: Richmond Publishing Company Ltd.

Vader, W.J.M. (1964). A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. *Netherlands Journal of Sea Research*, 2, 189–222.

Vail, P.R., Mitchum, R.M. Jr. and Thompson, S. III. (1977). Seismic stratigraphy and global changes of sea level, part 3: relative changes of sea level from coastal onlap. In *Seismic Stratigraphy: Applications to Hydrocarbon Exploration*, ed. C.E. Payton, *American Association of Petroleum Geologists Memoir*, 26, 63–81.

Valentine, J.W. (2004). *On the Origin of Phyla*. Chicago, IL: Chicago University Press.

Vannier, J. and Chen, J.-Y. (2005). Early Cambrian food chain: New evidence from fossil aggregates in the Maotianshan Shale Biota, SW China. *Palaios*, 20, 3–26.

Vannier, J., Calandra, I., Gaillard, C. and Żylińska, A. (2010). Priapulid worms: pioneer horizontal burrowers at Precambrian-Cambrian boundary. *Geology*, 38(8), 711–714.

Van Loon, A.J. (2008). The nature of *Mawsonites* (Ediacara fauna). *Gondwana Research*, 14, 175–182.

Van Wagoner, J.C., Mitchum, R.M., Campion, K.M. and Rahmanian, V.D. (1990). Siliciclastic sequences, stratigraphy in well logs, cores, and outcrops. *American Association of Petroleum Geologists, Methods in Exploration Series*, 7, 1–55.

Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebre, B., el Hariri, K. and Briggs, D.E.G. (2010). Ordovician faunas of Burgess Shale type. *Nature*, 465, 215–218.

Varricchio, D.J., Martin, A.J. and Katsura, Y. (2007). First trace and body fossil evidence of a burrowing, denning dinosaur. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1361–1368.

Verde, M. and Martínez, S. (2004). A new ichnogenus for crustacean trace fossils from the Upper Miocene Camacho Formation of Uruguay. *Palaeontology*, 47, 39–49.

Verde, M., Ubilla, M., Jimenez, J.J. and Genise, J.F. (2007). A new earthworm trace fossil from paleosols; aestivation chambers from the late Pleistocene Sopas Formation of Uruguay. *Palaeogeography, Paleoclimatology, Palaeoecology*, 243, 339–347.

Vermeij, G.J. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, 3, 245–258.

Vermeij, G.J. (1987). *Evolution and Escalation. An Ecological History of Life*. Princeton, NJ: Princeton University Press.

Vernberg, W.B. (1983). Responses to estuarine stress. In *Estuaries and Enclosed Seas. Ecosystems of the World 26*, ed. B.H. Ketchum, New York: Elsevier Scientific, pp. 43–60.

Vidal, G., Jensen, S. and Palacios, T. (1994). Neoproterozoic (Vendian) ichnofossils from Lower Alcudian strata in central Spain. *Geological Magazine*, 131, 169–179.

Viohl, G. (1990). *Taphonomy; Taphonomy of Fossil-lagerstatten; Solnhofen Lithographic Limestones*. Oxford, UK: Blackwell Scientific Publications.

Virtasalo, J.J., Kotilainen, A.T. and Gingras, M.K. (2006). Trace fossils as indicators of environmental change in Holocene sediments of the Archipelago Sea, northern Baltic Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240, 453–467.

Vizcaíno, S.F. and De Iuliis, G. (2003). Evidence for advanced carnivory in fossil armadillos (Mammalia: Xenarthra: Dasypodidae). *Paleobiology*, 29, 123–138.

Vizcaíno, S.F. and Fariña, R.A. (1999). On the flight capabilities and distribution of the giant Miocene bird *Argentavis magnificens* (Teratornithidae). *Lethaia*, 32, 271–278.

Vizcaíno, S.F., Fariña, R.A. and Janis, C. (2001). *Biomechanics and Paleobiology of Vertebrates*. *Acta Paleontologica Polonica, Special Issue*, 46.

Vogel, K. and Marincovich, L. Jr. (2004). Paleobathymetric implications of microborings in Tertiary strata of Alaska, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 206, 1–20.

Vogel, K., Bundschuh, M., Glaub, I., Hofmann, K., Radtke, G. and Schmidt, H. (1995). Hard substrate ichnocoenoses and their relationships to light intensity and marine bathymetry. *Neues Jahrbuch fuer Geologie und Palaeontologie, Abhandlungen*, 195, 49–61.

Vogel, K., Balog, S., Bundusch, M., Gektidis, M., Glaub, I., Krutschinna, J. and Radtke, G. (1999). Bathymetrical studies in fossil reefs, with microendoliths as paleoecological indicators. *Profil*, 16, 181–191.

Vogel, K., Gektids, M., Golubic, S., Kiene, W. and Radtke, G. (2000). Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: Implications for paleoecological reconstructions. *Lethaia*, 33, 190–204.

Voigt, E. (1959). Die ökologische Bedeuyung der Hartgründe ("Hardgrounds") in der oberen Kreide. *Paläontologische Zeitschrift*, 33, 129–147.

Voigt, E. (1974). Über die Bedeutung der Hartgründe ("Hardgrounds") für die Evertebratenfauna der Maastrichter Tuffkreide. *Natuurhistorisch Maandblad*, 63, 32–39.

Voigt, S. and Hoppe, D. (2010). Mass occurrence of penetrative trace fossils in Triassic lake deposits (Kyrgyzstan, Central Asia). *Ichnos*, 17, 1–11.

Voigt, S., Berman, D.S. and Henrici, A.C. (2007). First well-established track–trackmaker association of Paleozoic tetrapods based on *Ichniotherium* trackways and diadectid skeletons from the Lower Permian of Germany. *Journal of Vertebrate Paleontology*, 27, 553–570.

Voorhies, M.R. (1975). Vertebrate burrows. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 325–350.

Vossler, S.M. and Pemberton, S.G. (1988a). Superabundant *Chondrites*: a response to storm buried organic material? *Lethaia*, 21, 94

Vossler, S.M. and Pemberton, S.G. (1988b). *Skolithos* in the Upper Cretaceous Cardium Formation: an ichnofossil example of opportunistic ecology. *Lethaia*, 21, 351–362.

Vossler, S.M. and Pemberton, S.G. (1989). Ichnology and plaeoecology of offshore deposits in the Cardium Formation (Turonian, Alberta, Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 74, 217–239.

Wada, M., Kinoshita, K. and Kogure, K. (2004). Mud shrimp burrows as traps of tidal-flat organic matters. In *Proceedings of the Symposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublitoral Sediments: From Individual Behavior to their Role as Ecosystem Engineers*, ed. A. Tamaki, Nagasaki, Japan: Nagasaki University, pp. 101–106.

Waisfeld, B.G., Sánchez, T.M. and Carrera, M.G. (1999). Biodiversification patterns in the Early Ordovician of Argentina. *Palaios*, 14, 198–214.

Waisfeld, B.G., Sánchez, T.M., Benedetto, J.L. and Carrera, M.G. (2003). Early Ordovician (Arenig) faunal assemblages from western Argentina: biodiversification trends in different geodynamic and palaeogeographic settings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 196, 343–373.

Waldron, J.W.F. (1992). The Goldenville-Halifax transition, Mahone Bay, Nova Scotia: Relative sea-level rise in the Maguma source terrane. *Canadian Journal of Earth Sciences*, 29, 1091–1105.

Walker, E.F. (1985). Arthropod ichnofauna of the Old Red Sandstone at Dunure and Montrose, Scotland. *Transactions Royal Society of Edinburgh: Earth Sciences*, 76, 287–297.

Walker, K.R. and Bambach, R.K. (1974). Feeding by benthic invertebrates: classification and terminology for paleoecological analysis. *Lethaia*, 7, 67–78.

Walker, R.G. (1978). Deep-water sandstone facies and ancient submarine fans: models for exploration for stratigraphic traps. *American Association of Petroleum Geologists, Bulletin*, 62, 932–966.

Walker, R.G. (1984). General Introduction: Facies, Facies Sequences and Facies Models. In *Facies Models*, ed. R.G. Walker, *Geoscience Canada Reprint Series*, 1–9.

Walker, R.G. and Plint, A.G. (1992). Wave- and storm-dominated shallow marine systems. In *Facies Models, response to sea level change*, ed. R.G. Walker and N.P. James, St John's, NL: Geological Association of Canada, pp. 219–238.

Walker, S.E. and Behrens-Yamada, S.B. (1993). Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. *Palaeontology*, 36, 735–741.

Walker, S.E. and Miller, W. (1992). Organism–substrate relations: toward a logical terminology. *Palaios*, 7, 236–238.

Walker, S.E., Holland, S.M. and Gardiner, L. (2003). *Coenobichnus currani* (new ichnogenus and ichnospecies): fossil trackway of a land hermit crab, early Holocene, San Salvador, Bahamas. *Journal of Paleontology*, 77, 576–582.

Walter, H. (1983). Zur taxonomie, okologie und biostratigraphie der ichnia limnisch–terrestrischer arthropoden des mitteleuropaischen Jungpalaozoikums. *Freiberger Forschungssheft C*, 382, 146–193.

Walter, H. (1985). Zur ichnologie des Pleistozans von Liebegast. *Freiberger Forschungssheft* C, 400, 101–116.

Walter, H. and Suhr, P. (1998). Lebesspuren aus kaltzeitlichen Bändersedimenten des Quartärs. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden*, 43/44, 311–328.

Walter, M.R., Elphinstone, R. and Heys, G.R. (1989). Proterozoic and Early Cambrian trace fossils from the Amadeus and Georgina Basins, central Australia. *Alcheringa*, 13, 209–256.

Wang, M., Qi, Y.A., Yang, W.T. and Zhou, F. (2009). Stop 4: *Skolithos* and *Beaconites* ichnofabrics in fluvial deposits from the Middle Triassic Youfangzhuang Formation, Nanshan Foreest Park, Jiyuan city, Henan. *The Tenth International Ichnofabric Workshop, Program and Abstracts with Field Trip Guidebook*, p. 107–118.

Wang, Y., Zhu, D.K. and Wu, X.G. (2002). Tidal flats and associated muddy coast of China. In *Muddy Coasts of the World: Process, Deposits and Function*, ed. T. Healy, Y. Wang and J.A. Healy, Amsterdam: Elsevier, pp. 319–345.

Wang, Y., Lin, J.-P., Zhao Y.-L. and Orr, P.J. (2009). Palaeoecology of the trace fossil *Gordia* and its interaction with nonmineralizing taxa from the early Middle Cambrian Kaili Biota, Guizhou province, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 277, 141–148.

Ward, J.V., Tockner, K. and Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: cotones and connectivity. *Regulated Rivers: Research and Management*, 15, 125–139.

Ward, J.V., Tockner, K., Arscott, D.B. and Claret, C. (2002). Riverine landscape diversity. *Freshwater Biology*, 47, 517–539.

Warren, J.W. and Wakefield, N.A. (1972). Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature*, 238, 469–470.

Warman, C.G., O' Hare, T.J. and Naylor, E. (1991). Vertical swimming in wave-induced currents as a control mechanism of intertidal migration by a sand-beach isopod. *Marine Biology*, 111, 49–50.

Warme, J.E. (1977). Carbonate borers: their role in reef ecology and preservation. In *Reefs and Related Carbonates: Ecology and Sedimentology*, ed. S.H. Frost, M.P. Weiss and J.B. Saunders, *American Association of Petroleum Geologists Studies in Geology*, 4, 261–279.

Watanabe, Y., Martini, J.E.J. and Ohmoto, H. (2000). Geochemical evidence for terrestrial ecosystems 2.6 billion years ago. *Nature*, 408, 574–578.

Webb, S., Cupper, M.L. and Robins, R. (2005). Pleistocene human footprints from the Willandra lakes, southeastern Australia. *Journal of Human Evolution*, 50, 405–413.

Webby, B.D. (1983). Lower Ordovician arthropod trace fossils from western New South Wales. *Proceedings of the Linnean Society of New South Wales*, 107, 59–74.

Weber, B. and Braddy, S.J. (2004). A marginal marine ichnofauna from the Blaiklock Glacier Group (?Lower Ordovician) of the Shackleton Range, Antarctica. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 94, 1–20.

Weimer, R.J., Howard, J.D. and Lindsay, D.R. (1981). Tidal flats and associated tidal channels. In *Sandstone Depositional Environments*, ed. P.A. Scholle and D. Spearing, *American Association of Petroleum Geologists Memoir*, 31, 191–246.

Wellman, C.H., Osterloff, P.L. and Mohluddin, U. (2003). Fragments of the earliest land plants. *Nature*, 425, 282–285.

Werner, F. and Wetzel, A. (1982). Interpretation of biogenic structures in oceanic sediments. *Bulletin de l'Institute de Géologie du Bassin d'Aquitaine*, 31, 275–288.

West, D.J. and Hasiotis, S.T. (2007). Trace fossils in an archaeological context: Examples from bison skeletons, Texas, USA. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 428–441.

West, R.R. and Ward, E.L. (1990). *Asteriacites lumbricalis* and a protasterid ophiuroid. In *Evolutionary Paleobiology of Behavior and Coevolution*, ed. A.J. Boucot, Amsterdam: Elsevier, pp. 321–327.

Westaway, R., Guillou, H., Yurtmen, S., Beck, A., Bridgeland, D., Demir, T., Scaillet, S. and Rowbotham, G. (2006). Late Cenozoic uplift of Western Turkey: Improved dating of the Kula Quaternary volcanic filed and numerical modeling of the Gediz River terrace staircase. *Global and Planetary Change*, 51, 131–171.

Wetzel, A. (1981). Ökologische und stratigraphische Bedeutung biogener Gefüge in quartären Sedimenten am NW-afrikanischen Kontinentalrand. *"Meteor" Forschungs-Ergebnisse C*, 34, 1–47.

Wetzel, A. (1983). Biogenic structures in modern slope to deep-sea sediments in the Sulu Sea Basin (Philippines). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 42, 285–304.

Wetzel, A. (1984). Bioturbation in deep-sea fine-grained sediments, influence of sediment texture, turbidite frequency and rates of environmental change. In *Fine-grained Sediments: Deep Water Processes and Facies*, ed. D.A.V. Stow and D.J.W. Piper, *Geological Society Special Publication*, 15, 595–608.

Wetzel, A. (1991). Ecological interpretation of deep-sea trace fossil communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 85, 47–69.

Wetzel, A. (1992). The New Zealand *Zoophycos* revisited: morphology, ethology, and paleoecology; some notes for clarification. *Ichnos*, 2, 91–92.

Wetzel, A. (1999). Tilting marks: a wave-produced tool mark resembling a trace fossil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 145, 251–254.

Wetzel, A. (2002). Modern *Nereites* in the South China Sea: ecological association with redox conditions in the sediment. *Palaios*, 17, 507–515.

Wetzel, A. (2003). *International Ichnofabric Workshop Field Guide*, Basel, Switzerland.

Wetzel, A. (2008). Recent bioturbation in the Deep South China Sea: a uniformitarian ichnologic approach. *Palaios*, 23, 601–615

Wetzel, A. (2009). The preservation potential of ash layers in the deep-sea: the example of the 1991-Pinatubo ash in the South China Sea. *Sedimentology*, 56, 1992–2009.

Wetzel, A. (2010). Deep-sea ichnology: observations in modern sediments to interpret fossil counterparts. *Acta Geologica Polonica*, 60, 125–138.

Wetzel, A. and Aigner, T. (1986). Stratigraphic completeness: Tiered trace fossils provide a measuring stick. *Geology*, 14, 234–237.

Wetzel, A. and Balson, P. (1992). Sedimentology of fine-grained turbidites inferred from continuously recorded physical properties data. *Marine Geology*, 104, 165–178.

Wetzel, A. and Uchman, A. (1997). Ichnology of deep-sea fan overbank deposits of the Ganei Slates (Eocene, Switzerland): A classical flysch trace fossil locality studied first by Oswald Heer. *Ichnos*, 5, 139–162.

Wetzel, A. and Uchman, A. (1998a). Deep-sea benthic food content recorded by ichnofabrics: A conceptual model based on observations from Paleogene Flysch, Carpathians, Poland. *Palaios*, 13, 533–546.

Wetzel, A. and Uchman, A. (1998b). Biogenic sedimentary structures in mudstones: an overview. In *Shales and Mudstones* I, eds. J. Schieber, W. Zimmerle and P. Sethi, E. Schweizeirbart'sche, Stuttgart: Verlagbuchhandlung, p. 351–369.

Wetzel A. and Uchman, A. (2001). Sequential colonization of muddy turbidites in the Eocene Beloveza Formation, Carpathians, Poland. *Paleogeography, Paleoclimatology, Paleoecology*, 168, 171–186.

Wetzel, A. and Werner, F. (1981). Morphology and ecological significance of *Zoophycos* in deep-sea sediments off NW Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 32, 185–212.

Wetzel, A., Blechschmidt, I., Uchman, A. and Matter, A. (2007). A highly diverse ichnofauna in Late Triassic deep-sea fan deposits of Oman. *Palaios*, 22, 567–576.

Wetzel, A., Werner, F., and Stow, D.A.V. (2008). Bioturbation and biogenic sedimentary structures in contourites. In *Contourites*, ed. M. Rebesco and A. Camerlenghi, Developments in Sedimentology, Elsevier, 60, 183–202.

Wetzel, A., Tjallingii, R. and Stattegger, K. (2010). *Gyrolithes* in Holocene estuarine incised-valley fill deposits, offshore southern Vietnam. *Palaios*, 25, 239–246.

Wheatcroft, R.A. (1989). Comment on "Characteristic trace-fossil associations in oxygen-poor sedimentary environments". *Geology*, 17, 674.

Wheatcroft, R.A. (1990). Preservation potential of sedimentary event layers. *Geology*, 18, 843–845.

Whicker, A.D. and Detling, J.K. (1988). Ecological consequences of prairie dog disturbances. *Bioscience*, 38, 778–785.

Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213–251.

White, D.S. and Miller, M.F. (2008). Benthic invertebrate activity in lakes: Linking present and historical bioturbation patterns. *Aquatic Biology*, 2, 269–277.

Whitford, W.G. (2002). *Ecology of Desert Systems*. London: Academic Press.

Whitford, W.G. and Kay, F.R. (1999). Biopedoturbation by mammals in deserts: a review. *Journal of Arid Environments*, 41, 203–230.

Whittington, H.B. (1992). *Fossils Illustrated, Volume 2, Trilobites*. Woodbridge, UK: The Boydell Press.

Wiggins, G.B. and Wichard, W. (1989). Phylogeny and pupation in Trichoptera, with proposals on the origin and higher classification of the order. *Journal of the North American Benthological Society*, 8, 260–276.

Wightman, D.M., Pemberton, S.G. and Singh, C. (1987). Depositional modelling of the Upper Mannville (Lower Cretaceous), east-central Alberta: Implications for the recognition of brackish water deposits. In *Reservoir Sedimentology*, ed. R.W. Tillman and K.J. Weber, *Society for Sedimentary Geology Special Publication*, 40, 189–220.

Wignall, P.B. (1991). Dysaerobic trace fossils and ichnofabrics in the Upper Jurassic Kimmeridge Clay of southern England. *Palaios*, 6, 264–270.

Wignall, P.B. (1993). Distinguishing between oxygen and substrate control in fossil benthic assemblages. *Journal of the Geological Society of London*, 150, 193–196.

Wignall, P.B. (2001). End Permian mass extinction. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 226–229.

Wilf, P., Labandeira, C.C., Kress, W.J., Staines, C.L., Windsor, D.M., Allen, A.L. and Johnson, K.R. (2000). Timing the radiations of leaf beetles: Hispines on gingers from latest Cretaceous to Recent. *Science*, 289, 291–294.

Wilf, P., Labandeira, C.C., Johnson, K.R., Coley, P.D. and Cutter, A.D. (2001). Insect herbivory, plant defense and Early Cenozoic climate change. *Proceedings of the National Academy of Sciences, USA*, 98, 6221–6226.

Willey, P., Watson, P.J., Crothers, G. and Stolen, J. (2009). Holocene human footprints in North America. *Ichnos*, 16, 70–75.

Wills, L.J. and Sarjeant, W.A.S. (1970). Fossil vertebrate and invertebrate tracks from boreholes through the Bunter series (Triassic) of Worcestershire. *Mercian Geology*, 3, 399–414.

Williams, M., Siveter, D.J. and Peel, J.S. (1996). *Isoxys* (Arthropoda) from the Early Cambrian Sirius Passet Lagerstätte, North Greenland. *Journal of Paleontology*, 70, 947–954.

Willis, B.J. (2005). Tide-influenced river delta deposits. In *River Deltas: Concepts, Models, and Examples*, ed. L. Giosan and J.P. Bhattacharya, *Society for Sedimentary Geology Special Publication*, 83, 87–129.

Wilson, D.P. (1954). The attractive factor in the settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biological Association of the United Kingdom*, 33, 361–380.

Wilson, D.P. (1955). The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biology Association of the United Kingdom*, 34, 513–543.

Wilson, J.B. (1982). Shelly faunas associated with temperate offshore tidal deposits. In *Offshore tidal sands*, ed. A.H Stride, London: Chapman & Hall, pp. 126–171.

Wilson, J.B. (1986). Faunas of tidal current and wave-dominated continental shelves and their use in the recognition of storm deposits. In *Shelf Sands and Sandstones*, ed. R.J. Knight and J.R. McLean, *Memoir of the Canadian Society of Petroleum Geology*, 11, 313–326.

Wilson, J.L. (1975). *Carbonate Facies in Geologic History*. Heidelberg: Springer-Verlag.

Wilson, M.A. (2007). Macroborings and the evolution of bioerosion. In *Trace Fossils: Concepts, Problems, Prospects*, *ed.* W. Miller III, Amsterdam: Elsevier, pp. 356–367.

Wilson, M. A. and Palmer, T. J. (1998). The earliest *Gastrochaenolites* (Early Pennsylvanian, Arkansas, U.S.A.): an Upper Paleozoic bivalve boring? *Journal of Paleontology*, 72, 769–772.

Wilson, M.A. and Palmer, T.J. (2001). The Ordovician bioerosion revolution. *Geological Society of America Abstracts with Programs* A, 33, 248.

Wilson, M.A. and Palmer, T.J. (2006). Patterns and processes in the Ordovician bioerosion revolution. *Ichnos*, 13, 109–112.

Wilson, M.A., Allen, C. and White, B. (1998). Paleontological evidence of a brief global sea-level event during the last interglacial. *Lethaia*, 31, 241–250.

Wing, S.L., Hasiotis, S.T. and Bown, T.M. (1995). First ichnofossils of flank-buttressed trees (late Eocene), Fayum Depression, Egypt. *Ichnos*, 3, 281–286.

Wisshak, M. (2006). High-Latitude Bioerosion. *The Kosterfjord Experiment. Lecture Notes in Earth Sciences*, 109, 1–202.

Wisshak, M. and Neumann, C. (2006). A symbiotic association of a boring polychaete and an echinoid from the Late Cretaceous of Germany. *Acta Palaeontologica Polonica*, 51, 589–597.

Wisshak, M. and Porter, D. (2006). The new ichnogenus *Flagrichnus*: a paleoenvironmental indicator for cold-water settings? *Ichnos*, 13, 135–145.

Wisshak, M. and Rüggeberg, A. (2006). Colonisation and bioerosion of experimental substrates by benthic foraminifera from euphotic to aphotic depths (Kosterfjord, SW-Sweden). *Facies*, 52, 1–17.

Wisshak, M., Volohonsky, E. and Blomeier, D. (2004). Acanthodian fish trace fossils from the early Devonian of Spitsbergen. *Acta Palaentologica Polonica*, 49, 629–634.

Wisshak, M., Gektids, M., Freiwald, A. and Lundalv, T. (2005). Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study. *Facies*, 51, 93–117.

Wolcott, T.G. (1973). Physiological ecology and intertidal zonation in limpets (Acmaea): A critical look at "limiting factors". *Biological Bulletin, Marine National Laboratory, Woods Hole*, 145, 389–422.

Wolf, T. (1960). The hadal community: an introduction. *Deep-Sea Research*, 6, 95–124.

Wolfe, J.A. and Russell, D.A. (2001). Impact of K-T boundary events on terrestrial life. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 232–234.

Wolff, W.J. (1973). The estuary as a habitat. An analysis of data on the soft-bottom macro-fauna of the estuarine area of the rivers Rhine, Meuses, and Scheldt. *Zoologische Verhandlungen Leiden*, 126, 1–242.

Wolff, W.J. (1983). Estuarine benthos. In *Estuaries and Enclosed Seas, Ecosystems of the World 26*, ed. B.H. Ketchum, Amsterdam: Elsevier, pp. 151–182.

Woolfe, K.J. (1990). Trace fossils as paleoenvironmental indicators in the Taylor Group (Devonian) of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 80, 301–310.

Wooton, R.J. (1988). The historical ecology of aquatic insects: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62, 477–492.

Wright, L.D. (1977). Sediment transport and deposition at river mouths: a synthesis. *Geological Society of America, Bulletin*, 88, 857–868.

Wright, J.P. and Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience*, 56, 203–209.

Wu, X. (1982). Storm-generated depositional types and associated trace fossils in Lower Carboniferous shallow-marine carbonates of Three Cliffs Bay and Ogmore-by-sea, South Wales.

Palaeogeography, Palaeoclimatology, Palaeoecology, 39, 187–202.

Yang, B.C., Dalrymple, R.W. and Chun, S.S. (2005). Sedimentation on a wave-dominated, open-coast tidal flat, south-western Korea: a summer tidal flat–winter shoreface. *Sedimentology*, 52, 235–252.

Yang, B., Dalrymple, R.W. and Chun, S. (2006). The significance of hummocky cross-stratification (HCS) wavelengths: evidence from an open-coast tidal flat, South Korea. *Journal of Sedimentary Research*, 76, 2–8.

Yang, B.C., Dalrymple, R.W., Chun, S.S., Johnson, M.F. and Lee, H.J. (2008a). Tidally modulated storm sedimentation on open-coast tidal flats, southwestern coast of Korea: distinguishing tidal-flat from shoreface storm deposits. In *Recent Advances in Modelsof Siliciclastic Shallow-Marine Stratigraphy*, ed. G.J. Hampson, R.J. Steel, P.B. Burgess and R.W. Dalrymple, *SEPM Special Publication*, 90, 161–176.

Yang, B.C., Gingras, M.K., Pemberton, S.G. and Dalrymple, R.W. (2008b). Wave-generated tidal bundles as an indicator of wave-dominated tidal flats. *Geology*, 36, 39–42.

Yang, S.L., Li, H., Ysebaert, T., Bouma, T.J., Zhang, W.X., Wang, Y.Y., Li, P., Li, M. and Ding, P.X. (2008b). Spatial and temporal variations in sediment grain size in tidal wetlands, Yangtze Delta: on the role of physical and biotic controls. *Estuarine, Coastal and Shelf Science*, 77, 657–671.

Yang, B., Dalrymple, R.W., Gingras, M.K. and Pemberton, S.G. (2009). Autogenic occurrence of *Glossifungites* ichnofacies: examples from wave-dominated macrotidal flats, southwestern coast of Korea. *Marine Geology*, 260, 1–5.

Yeo, R.K. and Risk, M.J. (1981). The sedimentology, stratigraphy, and preservation of intertidal deposits in the Minas Basin system, Bay of Fundy. *Journal of Sedimentary Petrology*, 51, 245–260.

Yochelson, E.L. and Fedonkin, M.A. (1993). Paleobiology of *Climactichnites*, an enigmatic late Cambrian fossil. *Smithsonian Contributions to Paleobiology*, 74, 1–34.

Yochelson, E.L. and Fedonkin, M.A. (1997). The type specimens (Middle Cambrian) of the trace fossil *Archaeonassa* Fenton and Fenton. *Canadian Journal of Earth Sciences*, 34, 1210–1219.

Yonge, C.M. (1936). Mode of life, feeding, digestion and symbiosis with zooxanthellae in the Tridacnidae. *Scientific Report on the Great Barrier Reef Expedition British Museum*, 1, 283–321.

Yoshida, S., Steel, R.J. and Dalrymple, R.W. (2007). Changes in depostional processes: an ingredient in a new generation of sequence stratigraphic models. *Journal of Sedimentary Research*, 77, 447–460.

Zaitlin, B.A. and Shultz, B.C. (1990). Wave-influenced estuarine sand body, Senlac heavy oil pool, Saskatchewan, Canada. In *Sandstone Petroleum Reservoirs*, ed. J H. Barwis, J.G. McPherson and J.R. Strudlick, New York: Springer-Verlag, pp. 363–387.

Zaitlin, B.A., Dalrymple, R.W. and Boyd, R. (1994). The stratigraphic organization of incised-valley systems associated with relative sea-level changes. In *Incised Valley Systems: Origin and Sedimentary Sequence*, ed. R. Boyd, B.A. Zaitlin and R. Dalrymple, *Society for Sedimentary Geology Special Publication*, 51, 45–60.

Zavala, C., Arcuri, M., Di Meglio, M., Gamero, H. and Contreras, C. (2011). a genetic facies tract for the analysis of sustained hyperpycnal flow deposits. *In Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology* 61, in press.

Zavala, C.A., Grill, S.C., Martinez, D., Ortiz, H.O. and Gonzalez, R. (1992). Análisis paleoambiental de depósitos cuaternarios. Sitio paleoicnológico Monte Hermoso I, Provincia de Buenos Aires. *3º Jornadas Geológicas Bonaerenses (La Plata), Actas*, 31–37.

Zawiskie, J.M., Collinson, J.W. and Hammer, W.R. (1983). Trace fossils of the Permian-Triassic Takrouna Formation, Northern Victoria Land, Antartica. In *Antartic Earth Science*, ed. J.R. Oliver, P.R. James and J.B. Jago, Canberra, Australia: Australian Academy of Science, pp. 215–220.

Zhang, D.D. and Li, S.H. (2002). Optical dating of Tibetan human hand- and footprints: an implication for the palaeoenvironment of the last glaciation of the Tibetan Plateau. *Geophysical Research Letters*, 29, 1072–1074.

Zhang, G., Buatois, L.A., Mángano, M.G. and Aceñolaza, F.G. (1998). Sedimentary facies and environmental ichnology of a Permian playa-lake complex in western Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 138, 221–243.

Zhang, J., Li, D., Li, M., Lockley, M.G. and Bai, Z. (2006). Diverse dinosaur-, pterosaur-, bird track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research*, 27, 44–55.

Zhang, X.G., Bergström, J., Bromley, R.G. and Hou, X.G. (2007). Diminutive trace fossils in the Chengjiang Lagerstätte. *Terra Nova*, 19, 407–412.

Zhang Y. and Golubic, S. (1987). Endolithic microfossils (cyanophyta) from early Proterozoic stromatolites, Hebei, China. *Acta Micropaleontologica Sinica*, 4, 1–12.

Zhu, M.-Y., Vannier, J., Van Iten, H., and Zhao, Y.-L. (2004). Direct evidence of predation on trilobites in the middle Cambrian. *Proceedings of the Royal Society B: Biological Sciences*, 271, 277–280.

Zhuravlev, A.Y., Gámez Vintaned, J.A. and Ivantsov, A.Y. (2009). First finds of problematic Ediacaran fossil Gaojiashania in Siberia and its origin. *Geological Magazine*, 146, 775–780.

Zonneveld, J.P. and Pemberton S.G. (2003). Ichnotaxonomy and behavioral implications of Lingulide-derived trace fossils from the Lower and Middle Triassic of western Canada. *Ichnos*, 10, 23–35.

Zonneveld, J.-P., Pemberton, S.G. and Saunders, T.D.A. (2002). Large, robust *Cruziana* from the Middle Triassic of northeastern British Columbia: ethologic, biostratigraphic, and paleobiologic significance. *Palaios*, 17, 435–448.

Zonneveld, J.P., Lavigne, J.M., Bartels, W.S. and Gunnell, G.F. (2006). *Lunulichnus tuberosus* ichnogen. and ichnosp. nov. from the Early Eocene Wasatch Formation, Fossil Butte National Monument, Wyoming: An Arthropod-Constructed Trace Fossil Associated with Alluvial Firmgrounds. *Ichnos*, 13, 87–94.

Zonneveld, J.-P., Beatty, T.W. and Pemberton, S.G. (2007). Lingulide brachiopods and the trace fossil *Lingulichnus* from the Triassic of western Canada: Implications for faunal recovery after the end-Permian mass extinction. *Palaios*, 22, 74–97.

Zonneveld, J.P., Gingras, M.K. and Beatty, T.W. (2010). Diverse ichnofossils assemblages following the P-T mass extinction, Lower Triassic, Alberta and British Columbia, Canada: Evidence for shallow marine refugia on the Northwestern coast of Pangea. *Palaios*, 25, 368–392.

Żylińska, A. (1999). Trace maker of *Cruziana semiplicata* in the Upper Cambrian of the Holy Cross Mts. (Poland). *5th Field Conference of the Cambrian Stage Subdivision Working Group*, *Abstracts of Papers*, 62–63.

Index

Luis Buatois and M. Gabriela Mángano

Ichnology

Organism-Substrate Interactions in Space and Time

CAMBRIDGE

Ichnology

Organism–substrate interactions in space and time

Ichnology is the study of traces, such as burrows, trackways, and borings, created in the substrate by living organisms. It is an increasingly important field, having recently been transformed into a multifaceted science at the crossroads of many disciplines.

This is the first book to systematically cover the conceptual framework of the discipline and the wide breadth of applications in both paleobiology and sedimentology, bridging the gap between the two main facets of the field. It emphasizes the importance of understanding ecological controls on benthic fauna distribution and the role of burrowing organisms in changing their environments.

A detailed analysis of the ichnology of a full range of depositional environments is presented using examples from the Precambrian to the Recent, and the use of trace fossils in facies analysis and sequence stratigraphy is discussed. By presenting ichnological information within a macroevolutionary perspective, the authors provide an up-to-date overview of the subject and highlight the potential of biogenic structures to provide valuable information and solve problems in a wide range of fields.

An invaluable resource for researchers and graduate students in paleontology as well as in sedimentology and sequence stratigraphy, this book will also be of interest to oil industry professionals working in reservoir and exploration geology.

LUIS A. BUATOIS is a Full Professor at the University of Saskatchewan, specializing in paleoenvironmental and stratigraphic aspects of ichnology. He has received awards from the Argentinean Paleontological Association, the Egidio Feruglio Foundation, and the Argentinean Academy of Sciences, and the Argentinean Secretary of Science and Technology. Currently President of the International Ichnological Association, and formerly Vice-President of the International Palaeontological Association, he has carried out field and subsurface work in many different countries. Professor Buatois has published four other books, edited three journal special issues, and is the author of over 150 scientific papers. He is also a member of the editorial board of a number of journals, including *Lethaia* and *Ichnos*.

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Ichnology

Organism–substrate interactions in space and time

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We dedicate this book to Melanie, Gabriel, Michelle, and also Sebastian and Milly

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Introduction

Worms have played a more important part in the history of the world that most persons would at first suppose.

Charles Darwin
The Formation of Vegetable Mould Through the Action
of Worms with Observations on their Habits (1881)

When looking at depositional sequences, no one gets upset when they see a ripple mark, but the presence of a few burrows frequently will divide the field party into two factions. One group falls asleep while the other group begins a lengthy discussion on phylogeny, ontogeny, nutrient upwelling, biochemistry, and the "Voyage of the Beagle".

Jim Howard
"Sedimentology and trace fossils" (1978)

Jim Howard's ironic comment elegantly illustrates both the joys and risks of practicing and communicating the science of organism–substrate interactions to a broad audience. Ichnology is a science located right at the crossroads of paleontology (and biology) and sedimentology (and stratigraphy). Trace fossils link paleontology and sedimentology in ways that most body fossils cannot achieve. In this context, ichnological investigations provide dynamic links among numerous fields. Analysis of specific ichnofaunas results in meaningful contributions to paleoecology, sedimentology, sequence stratigraphy, reservoir characterization, diagenesis, paleoclimatology, paleooceanography, biostratigraphy, evolutionary paleoecology, paleoanthropology, and archaeology. Such studies illustrate how an integrated approach that articulates ichnological information with other sources of data results in a better understanding of depositional setting, stratigraphic architecture, reservoir permeability, organism behavior, and ecosystem reconstruction and evolution. Thus, a multifaceted approach to ichnology will help bridge the gap between biologists and geologists, as well as between theoretical frameworks and applications. Because of this close link between ichnology and several other fields, we will often visit some of these neighboring disciplines in search for connections.

We have subdivided the book into three parts. The first one deals with conceptual tools and methods, and addresses the conceptual background of the field, ichnotaxonomy, burrowing and locomotion mechanisms, the ichnofacies model, and the ichnofabric approach. The second part focuses on spatial trends, and attempts to summarize paleoecological aspects, environmental controls, and the ichnology of different depositional environments. The third part deals with temporal trends, including developments in sequence stratigraphy, biostratigraphy, evolutionary paleoecology, paleoanthropology, and archaeology. In almost every instance, we have tried to avoid including previous illustrations by elaborating new ones or redesigning other author drawings based on our own perspective. Each of the chapters is focused on providing an update of the most pertinent aspects covered in ichnological research. To do so, it is necessary to generalize based on a limited number of case studies. However, some readers may still prefer to learn from specific examples. To avoid that potential problem, we have included boxes that either supply a more in-depth treatment of selected topics or summarize case studies that illustrate significant advances in our understanding of the field.

This book attempts to provide a balance between our own personal experience, and a comprehensive synthesis of previous and current research in the field of animal–substrate interactions. In the first place, our personal experience and interests are reflected throughout the book by the choice of topics and philosophical perspective. The book emphasizes invertebrate ichnology rather than vertebrate ichnology, and bioturbation rather than bioerosion, although a conscious (perhaps not entirely successful) effort has been made to counterbalance our biases. Second, we use many examples drawn from our own work. These include research undertaken in deposits ranging from the Ediacaran to the Recent that have accumulated in a wide variety of environments and geographic locations. We consider ourselves really lucky to have been able to explore such a vast timescale and variety of settings. However, we also offer extensive coverage of the work done by the different working groups in the last few decades.

In *Time's Arrow, Time's Cycle*, Steven Jay Gould (1987) emphasized the tension between time's arrow and time's cycle in our understanding of Earth's history. Time's arrow sees history as an irreversible sequence of unrepeatable events. Time's cycle emphasizes a non-directional time, in which events are repeated according to a recurrent pattern. This dichotomy is expressed in ichnology as a tension between studies that apply ichnofacies models in facies analysis and sequence stratigraphy, and those that underscore the utility of trace fossils in evolutionary paleobiology. The very same notion of ichnofacies recurrence, irrespective of age, is strongly rooted in a cyclic idea of geological time. However, this view of ichnology stands in apparent opposition to the study of secular changes in bioturbation and trace fossils as evidence of the changing ecology of the past and a dynamic landscape, which is never the same. The structure of the book attempts to honor both facets of ichnology.

In that sense, our approach is rather eclectic, trying to incorporate information from the two main schools: that using the ichnofacies model and its wide potential (mostly western Canadian-based), and that employing the ichnofabric approach (rooted in continental Europe and the United Kingdom). One of the advantages of having grown as scientists in such a geographically remote country as Argentina is that one gets a good balance of tradition and freedom. Tradition is revealed by a long and rich history of paleontological research in the country. However, at the same time, being far from the authoritative centers of scientific production gives a sense of freedom that prevents tradition from suffocating critical thinking. Hopefully, by the end of the book eclecticism will have paid, and the gap between the Voyage of the Beagle and the Reservoir Model may have narrowed a little bit.

Part I Conceptual tools and methods

1 The basics of ichnology

> These "-ichnial" ethologic categories are useful tools for organizing important paleoecologic information about a particular organism community. Of course, semantic distinctions between the different categories may be carried to the extreme, and confusion rather than clarification results. For example, imagine the trackway created by a man running across a mudflat at low tide. Do his footprints represent repichnia (perhaps he was jogging for his health) or fugichnia (perhaps he was being chased by someone with harmful intentions) or praedichnia (perhaps he was chasing sea gulls for a special gourmet dinner)? Imagine that the man fell flat on his face in the mud. If he got up and continued his journey, the impression he left behind would be a cubichnial trace. If, on the other hand, he died where he fell and his body decayed away totally, the remaining impression would be a body fossil (i.e., external mould) and not a trace fossil at all!
>
> Tony Ekdale
> "Paleoecology of the marine endobenthos" (1985)

Ichnology involves the study of traces produced by organisms (both animals and plants) on or within a substrate, and includes all issues related to bioturbation, bioerosion, and biodeposition (Pemberton *et al*., 1992a; Bromley, 1990, 1996). As such, ichnology encompasses both the study of processes, and their resulting products. The processes are all those involved in the interaction between organisms and substrates. The products are the traces themselves, which comprise individual and distinctive structures of biogenic origin, particularly those related more or less directly to the morphologies of the producers (Frey, 1973), and any sedimentary fabric resulting from biogenic reworking of the substrate, including non-discrete mottlings (i.e. biodeformational structures). Ichnology comprises two main fields: neoichnology (the study of modern traces or *lebensspuren* of classic German papers) and paleoichnology (the study of their fossil counterparts: trace fossils or ichnofossils). In this chapter, we review the conceptual framework of ichnology. We start by introducing basic concepts and outlining the 10 most important characteristics of trace fossils. Then we discuss aspects of trace-fossil preservation, including different schemes to classify biogenic structures in this respect. Finally, we turn our attention to the potential of trace fossils as sources of behavioral information, providing an in-depth discussion of the ethological classification.

1.1 BASIC CONCEPTS

During the seventies, attempts were made to provide a general classification framework for ichnology and related fields. Biogenic structures, defined as any evidence of organism activity other than the production of body parts (Frey and Wheatcroft, 1989), were regarded as the most inclusive category. The alternative term "ethologic structures" was suggested subsequently to emphasize the behavioral significance of these structures (Pickerill, 1994). In addition, a number of concepts were introduced in order to group trace fossils (Box 1.1). The most popular scheme was proposed by Frey (1971, 1973) and experienced minor modifications in subsequent years (Frey and Pemberton, 1984, 1985; Frey and Wheatcroft, 1989; Pemberton *et al*., 1990, 1992a). This scheme subdivided biogenic structures into three major categories: (1) biogenic sedimentary structures; (2) bioerosion structures; and (3) other evidence of activity. Biogenic sedimentary structures are biogenic structures produced by the activity of an organism upon or within an unconsolidated substrate (Frey and Wheatcroft, 1989). In turn, biogenic sedimentary structures were subdivided into bioturbation structures, biodeposition structures, and biostratification structures. Bioturbation structures are biogenic sedimentary structures reflecting the disruption of stratification features or sedimentary fabrics by the activity of an organism (Frey and Wheatcroft, 1989). Tracks (impressions left by an individual locomotory appendage) and the related term trackway for a series of tracks (Fig. 1.1a), trails (continuous grooves produced during locomotion; Fig. 1.1b), and burrows (more or less permanent structures excavated within the sediment; Fig. 1.1c) fall into this group.

Biodeposition structures (Fig. 1.1e) were not recognized as a separate entity in the original scheme by Frey (1971, 1973), but were later incorporated as a discrete category (Frey and Pemberton, 1984). They were defined as biogenic sedimentary structures reflecting production or concentration of sediment by the activities of an organism (Frey and Wheatcroft, 1989). This category embraces coprolites, fecal pellets, pseudofeces, and fecal castings (Frey and Pemberton, 1984; Frey and Wheatcroft, 1989).

Biostratification structures (Fig. 1.1f) referred to as biogenic sedimentary structures consist of stratification features imparted by the activity of an organism (Frey and Wheatcroft, 1989). Stromatolites, byssal mats, biogenic graded bedding, and thrombolites are included in this category (Frey, 1973; Frey and Pemberton, 1984, 1985; Frey and Wheatcroft, 1989; Pemberton *et al*., 1990, 1992a). Interestingly, experimental studies showed that some organisms (e.g. the pistol shrimp *Alpheus bellulus*) are even able to produce a structure similar to cross lamination (McIlroy, 2010).

Bioerosion structures (Fig. 1.1d) comprise biogenic structures produced mechanically or biochemically in rigid substrates by an organism, such as hardgrounds, clasts, bones, or rocks (Frey and

Box 1.1 Grouping trace fossils

There are many terms currently in use to group trace fossils. Some of these terms are more descriptive, while others involve various degrees of interpretation. Some groupings imply recurrence in time, while others are more restricted in temporal scale. Because there is a need for consistency in terminology, the most important concepts are reviewed here.

Ichnoassemblage or trace-fossil assemblage: Groups of trace fossils preserved in a rock unit or sedimentary facies, with no assumptions in regards to time of emplacement or recurrence in the stratigraphic record.

Trace-fossil suite: A more restricted group of trace fossils that reflects contemporaneous time of emplacement. Traditionally, it has been applied to successive groups of trace fossils emplaced under different degrees of consolidation of the substrate (e.g. a hardground suite cross-cutting firmground and softground suites). It has also been referred to as pre- and post-event suites in the case of environments affected by storms or turbidity currents. In this sense, suite is almost a synonym of ichnocoenose.

Ichnocoenose or ichnocommunity: This term has been used in many different ways. The present consensus is that it refers to a group of trace fossils produced by a biological community.

Ichnofacies: Conceptual construct based on the identification of key features shared by different ichnocoenoses of a wide range of ages formed under a similar set of environmental conditions. To avoid confusion with other terms used to group trace fossils at different scales, ichnofacies are commonly referred to as Seilacherian or archetypal ichnofacies. The archetypal nature of ichnofacies relies on a "distillation" process that extracts the key features shared by actual ichnocommunities (see Chapter 4).

Ichnofabric: Any aspect of the texture and internal structure of a substrate resulting from bioturbation and bioerosion at any scale (see Chapter 5).

Trace-fossil association or ichnoassociation: As with ichnocoenose, this term has been used in a loose way. However, and in contrast to ichnocoenose, there is no present consensus on a more precise meaning. On occasions, it has been used in a temporal sense (i.e. as recording the work of a community), essentially approaching the meaning of ichnocoenose or trace-fossil suite. In other cases, a mere spatial connotation is implied, becoming in practice a synonym of trace-fossil assemblage. In a trace-fossil association, biogenic structures are "associated", but the cause may be merely coincidental (i.e. trace-fossil assemblage) or ecological (i.e. ichnocoenose).

Ichnosubfacies: A group of trace fossils representing a subdivision within an ichnofacies.

Ichnoguild: A group of trace fossils defined on the basis of: (1) bauplan, (2) food source, and (3) use of space. The use of this term is intimately linked to ichnofabric and tiering analysis (see Section 5.4).

Ichnofauna: Very general term to group trace fossils having no scale or genetic connotation.

References: Bromley (1990, 1996); Hunt and Lucas (2007); MacEachern *et al.* (2007a).

Wheatcroft, 1989). Bioerosion structures include macroborings (down to the millimeter scale) and microborings (smaller than a millimeter) (Bromley, 1994). Borings, embedment structures, rasps and scrapes, surface etching scars, durophagous damage, and drill holes define the wide range of bioerosion structures (Bromley, 1992, 1994). Different types of structures are placed under "other evidence of activity", including spider webs and egg cases (Frey and Pemberton, 1984, 1985; Pemberton *et al.*, 1990, 1992a).

As with most classifications, some fields are vague and gray zones haunt the researcher who ventures towards the margins of a discipline. Although occasionally ichnology is regarded as the study of all biogenic structures, this is not strictly true. Not all biogenic structures fulfill the requirements to be considered organism traces. Every ichnologist agrees that all biogenic sedimentary structures (both discrete trace fossils and undifferentiated biodeformational structures) qualify, and there is general consensus that biostratification structures (e.g. stromatolites and biogenic graded bedding) do not because they do not reveal the functional anatomy of the producer (Frey and Pemberton, 1985). Accordingly, very few regard stromatolites as trace fossils, and those are only rarely treated in the ichnological literature (e.g. Shapiro, 2007). However, issues become more contentious when we move into the gray zones of the classification. Egg cases are currently regarded outside of the field, but a review on fossil eggs (Hirsch, 1994) was included in a trace fossil book (Donovan, 1994). In any case, eggs may be preserved within fossil nesting sites (e.g. Chiappe *et al.*, 2004, 2005), which in turn fall within the realm of ichnology because they provide direct evidence of reproductive behavior.

In addition, some of the research produced during the last decade has expanded ichnology by providing systematic treatment of biogenic structures that were not considered in previous classifications. One of these lines of research is the study of plant–arthropod interactions, as revealed by biogenic structures preserved in wood, leaves, and seeds (e.g. Scott, 1992; Genise, 1995; Labandeira *et al.*, 1997; Labandeira, 1998, 2002; Wilf *et al.*, 2000). The placement of this group of structures in the traditional scheme of classification of biogenic structures is unclear. Damage of plant tissues preserved in leaves has sometimes been linked to bioerosion (e.g. Labandeira *et al.*, 1997). However, plant tissue is not strictly a rigid substrate comparable to rockgrounds or hardgrounds. Traditionally, traces in wood have been regarded as borings produced by bioerosion (e.g. Bromley *et al.*, 1984; Mikuláš, 2008; Bertling and Hermanns, 1996; Savrda and Smith, 1996), although it may be argued that traces in

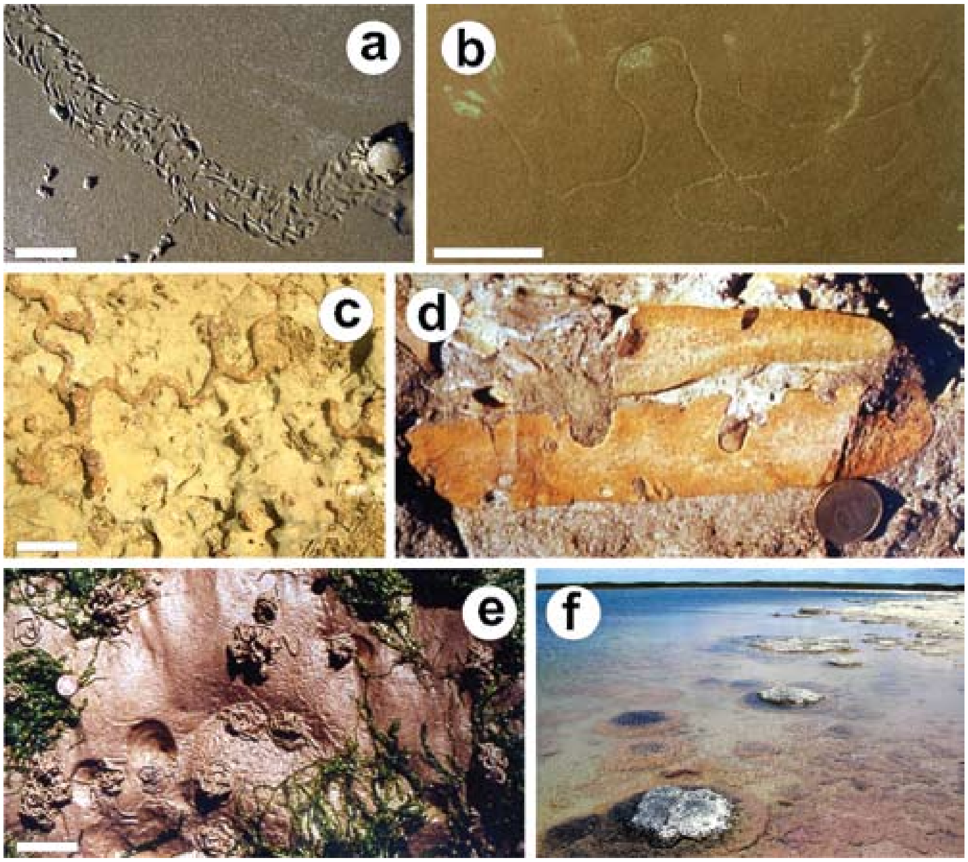


Figure 1.1 Examples of biogenic structures. (a) A trackway produced by a crab (on the right). Tidal flats nearby Estancia Maria Luisa, Tierra del Fuego, Argentina. Scale bar is 5 cm. (b) A trail assigned to the ichnospecies *Gordia marina*. Upper Carboniferous, Guandacol Formation, Río Frío, western Argentina. Scale bar is 1 cm. (c) Burrow system assigned to the ichnospecies *Sinusichnus sinuosus*. Middle Miocene, Socorro Formation, Quebrada El Pauji, northwestern Venezuela. Scale bar is 1 cm. See Buatois *et al.* (2009a). (d) The boring bivalve *Gastrochaenolites* in a clast. Lower Miocene, Chenque Formation, Comodoro Rivadavia, southern Argentina. Coin is 1.8 cm. (e) Fecal casts of *Arenicola marina*. Tidal flats in Gower Peninsula, Wales. Scale bar is 5 cm. (f) Stromatolites, Tethys Lake, western Australia.

wood do not reflect bioerosion in a strict sense. Similiar problems are involved in the study of bioerosion structures in bones (Pirrone *et al.*, 2010). Another line of research focused on the whole array of insect traces produced in terrestrial settings, mostly those of termites, bees, and beetles, but also wasps and ants (e.g. Genise and Bown, 1994a, b; Genise and Hazeldine, 1998; Genise, 2000, 2004). Many of them contribute to destruction of the primary fabric and, therefore, should be considered bioturbation structures. However, placement of some other insect traces within the available classification framework is hardly straightforward. One of these problematic structures is *Chubutolithes gaimanensis*, a nest produced by pompellid wasps (Genise and Bown, 1990). *Chubutolithes* represents an edifice built upon the substrate and constructed with material extraneous to the preserving sediment (see Section 1.4). This structure cannot be regarded as a bioturbation structure, but as a nest constructed by its producer in isolation from the preserving substrate. As such, it may be included within the broad category of "other evidence of activity". Regardless of the precise placement of arthropod traces in plant material and of some of these nests, it is clear that they fulfill the criteria to be considered trace fossils.

Another field of increased activity is the study of microbially induced sedimentary structures (Gerdes *et al.*, 1994, 2000; Noffke *et al.*, 1996; Schieber *et al.*, 2007; Noffke, 2010). These structures record the complex interaction of two sets of processes, those related with the depositional dynamics of the environment and those reflecting the activity of phototrophic microorganisms inhabiting the substrate (Noffke *et al.*, 1996). Stromatolites produced by overgrowth of cyanobacteria are widely recognized examples of microbially induced sedimentary structures in carbonate sediments and, as previously mentioned, have been regarded as biostratification structures (Frey, 1973). This category may also embrace other structures resulting from microbial activity that are commonly preserved in siliciclastic tidal flats. Bacterial activity may contribute to sediment stabilization generating a wide variety of structures, including wrinkled bed surfaces, domal buildups, pinnacles, bulges, and several types of biolaminations in microbial mats (e.g. Schieber, 1999; Gerdes *et al.*, 2000; Noffke, 2010). Although microbially induced sedimentary structures are biogenic structures, they should not be regarded as trace fossils because they fail to reveal any evidence on the morphology of the producers.

There is another group of structures that may be confused with trace fossils, and that, in fact, are not even biogenic structures. These are impressions that result from the passive contact between part of the organism's body and the substrate. Some of these structures are referred to as "death marks", and are illustrated by dead animals dragged by a current along a substrate (Frey and Pemberton, 1985) or carcasses landing on the substrate (Seilacher, 2007a). No behavior is involved; the organism is acting as an inert sedimentary particle. Some of these structures may vaguely resemble animal traces, such as the tilting marks documented by Wetzel (1999), which are produced by wave dragging of shells. Roll and tumbling marks may be produced by ammonites impacting on the sea floor (Seilacher, 1963a). The sweeping motion of a tethered

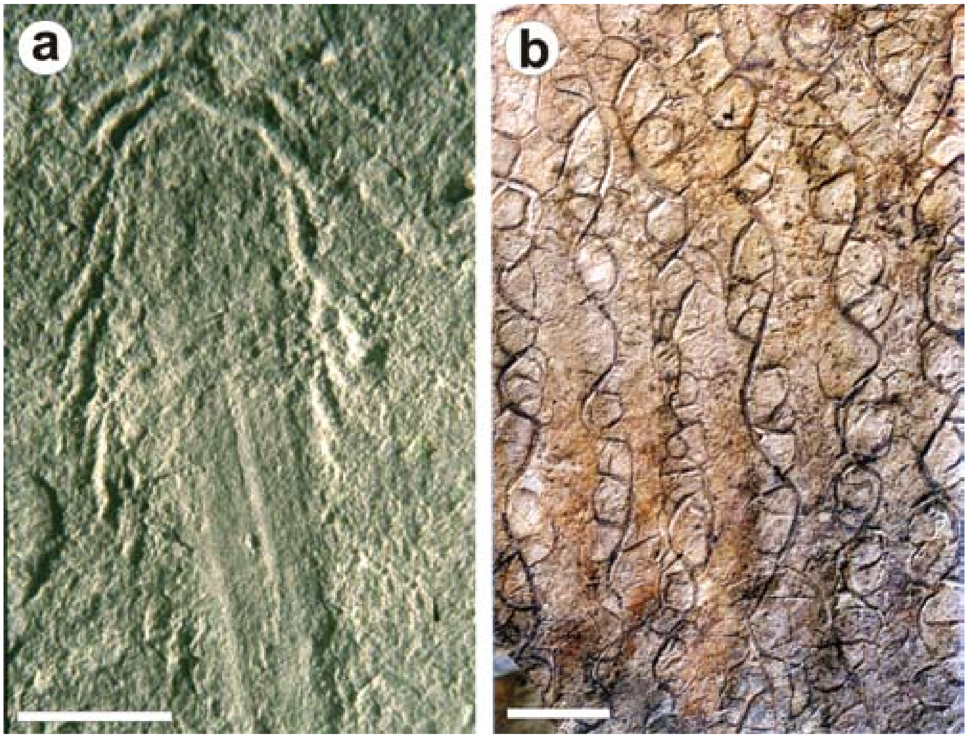


Figure 1.2 Pseudotraces. (a) Inorganic sole mark transitional between groove and chevron mark that superficially may resemble a resting trace. Upper Carboniferous, Agua Colorada Formation, Cantera La Laja, Sierra de Narváez, northwest Argentina. Scale bar is 1 cm. (b) Synaeresis cracks resembling grazing or feeding trace fossils ("Manchuriophycus"). Upper Carboniferous–Lower Permian, Santa Elena Formation, Sierra de Uspallata, western Argentina. Scale bar is 10 cm.

object may be the origin of the supposed trace fossil *Laevicyclus* (D'Alessandro, 1980; Jensen *et al.*, 2002). Scratch circles may be formed by plant stems (Metz, 1991). There is also a gray zone here. Living animals may be dragged by currents leaving marks on the substrate. In most cases, this is just a passive relationship and no behavior is involved, representing a similar situation to that of the death marks. However, it is not unreasonable to suppose that in some instances the animal caught in the current may have raked the sediment. Apparently, this is illustrated by straight to sigmoidal scratch marks, commonly grouped in sets, and repeated laterally that are attributed to trilobites and included in the ichnogenus *Monomorphichnus* (Crimes, 1970a). In order to support this interpretation, the axis of erosional current structures is expected to be parallel to the scratch marks.

Some structures are morphologically similar to organism traces, but careful analysis demonstrates that physical and chemical processes were involved in their production and are, therefore, pseudotraces or pseudo-*lebensspuren*. Turbidite sole marks, particularly chevron and impact marks, are typical examples (Fig. 1.2a). The paleontological and geological literature is plagued with names and descriptions of supposed trace fossils that are actually pseudotraces (e.g. "Manchuriophycus") (Fig. 1.2b). In a few cases, the true nature of some structures remains controversial and even distinction between trace fossils and body fossils may be problematic. Is Ediacaran *Mawsonites* a backfilled burrow system, a medusoid body fossil, or a sand-volcano interacting with a biomat? (Seilacher, 1984, 1989; Seilacher *et al.*, 2005; van Loon, 2008). Finally, there is a nice twist to this story. Some pseudotraces are, in fact, not the result of inorganic processes, but of microbial activity, so they at least qualify as biogenic structures. Corrugations, concentric circles, and spiral and meandering structures are common in microbial matgrounds due to shrinkage of cohesive material on rippled surfaces (Noffke *et al.*, 1996; Pflüger, 1999; Seilacher, 1999; Gerdes *et al.*, 2000). Reinterpretations are made on a regular basis, particularly in the case of Precambrian structures. Beware! Today's trace fossil may become tomorrow's shrinkage crack!

1.2 CHARACTERISTICS OF TRACE FOSSILS

Trace fossils have their own peculiarities that distinguish them from body fossils. These peculiarities, reflecting both their mode of formation and their taphonomic histories, allow the establishment of a rich conceptual framework for ichnology (Seilacher, 1964a; Frey, 1975; Ekdale *et al.*, 1984; Frey and Pemberton, 1985; Pemberton *et al.*, 1990, 2001; Bromley, 1990, 1996; Buatois *et al.*, 2002a). The importance of ichnology in various fields, such as paleoecology, sedimentology, stratigraphy, and macroevolution derives from these basic characteristics. Regrettably, its own limitations also result from this set of main features. In previous studies, this conceptual framework has been expressed as a list of characteristics (Seilacher, 1964a; Frey, 1975) or ichnological principles (Ekdale *et al.*, 1984; Bromley, 1990, 1996). Here, we integrate both schemes to define a series of basic characteristics of trace fossils (Buatois and Mángano, 2008a).

1.2.1 TRACE FOSSILS REPRESENT EVIDENCE OF BEHAVIOR

This is arguably the essence of trace fossils. As expressed by Seilacher (1967a), trace fossils are evidence of fossil behavior.

Analysis of the morphology and architecture of trace fossils reveals valuable information on the anatomy and ethology of their producers (e.g. mode of life, trophic type, and locomotion mechanisms). As outlined below (see Section 1.4), this feature lies at the core of the ethological classification of trace fossils. The behavior involved is, of course, highly variable, from the simple trace of a worm-like animal moving through the substrate (Fig. 1.3a) to the amazing complexities of the work of social insects as illustrated by the termite nest *Termitichnus* (Genise and Bown, 1994b) (Fig. 1.3b). In any case, releasing the behavioral signal unlocked in a biogenic structure is a real challenge in any ichnological analysis.

1.2.2 THE SAME ORGANISM MAY PRODUCE MORE THAN ONE ICHNOTAXON

In a way, this characteristic derives from the former because different behaviors may be attributed to a single animal. Therefore, a single organism may be responsible for producing several ichnospecies and ichnogenera. The classic example is that of the multiple possible behaviors of a trilobite moving through a substrate (Seilacher, 1955a, 1985; Crimes, 1970a) (Fig. 1.4a). The bilobate trail ornamented with scratch marks resulting from the burrowing activity along the sand–mud interface either reflecting simple locomotion or feeding activities is called *Cruziana*. The trackway consisting of series of impressions of individual walking appendages on the substrate due to simple locomotion is referred to as *Diplichnites*. The asymmetrical trackway with two different types of impressions, long straight or sigmoidal (rakers) and short and blunt ones (pushers), attributed to grazing activities, is called *Dimorphichnus*. Short bilobate coffee-bean or heart-shaped traces reflecting resting, nesting, or predation, are known as *Rusophycus*. Deep trilobite burrows are referred to the ichnogenus *Cheiichnus* (Jensen and Bergström, 2000). Cleft-foot deposit-feeding bivalves represent another example of this principle. Chevronate locomotion trace fossils represent the ichnogenus *Protovirgularia*, while the almond-shaped resting or dwelling traces are known as *Lockeia* (Seilacher and Seilacher, 1994; Mángano *et al.*, 1998; Ekdale

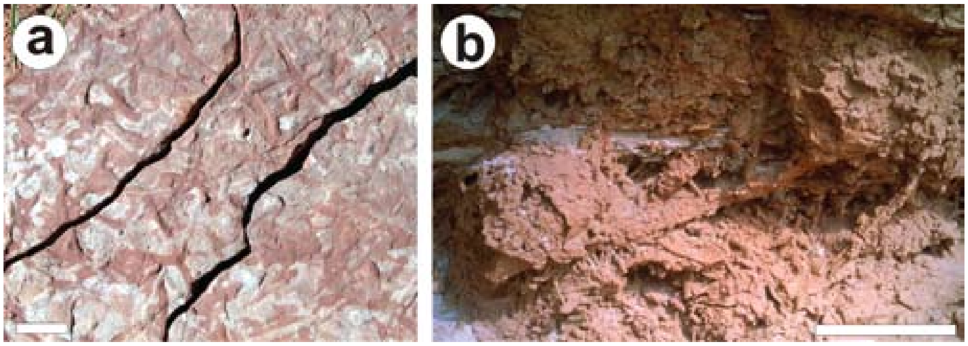


Figure 1.3 Characteristics of trace fossils. Trace fossils represent evidence of behavior. (a) *Palaeophycus tubularis*, a simple trace fossil produced by worm-like animals or insects Lower Permian, Abo Formation, Jemez Mountains, New Mexico. Scale bar is 1 cm. (b) *Termitichnus qatranii*, a termite nest. Upper Eocene–Lower Oligocene, Jebel Qatrani Formation, Fayum Depression, Egypt. Scale bar is 10 cm. See Genise and Bown (1994b).

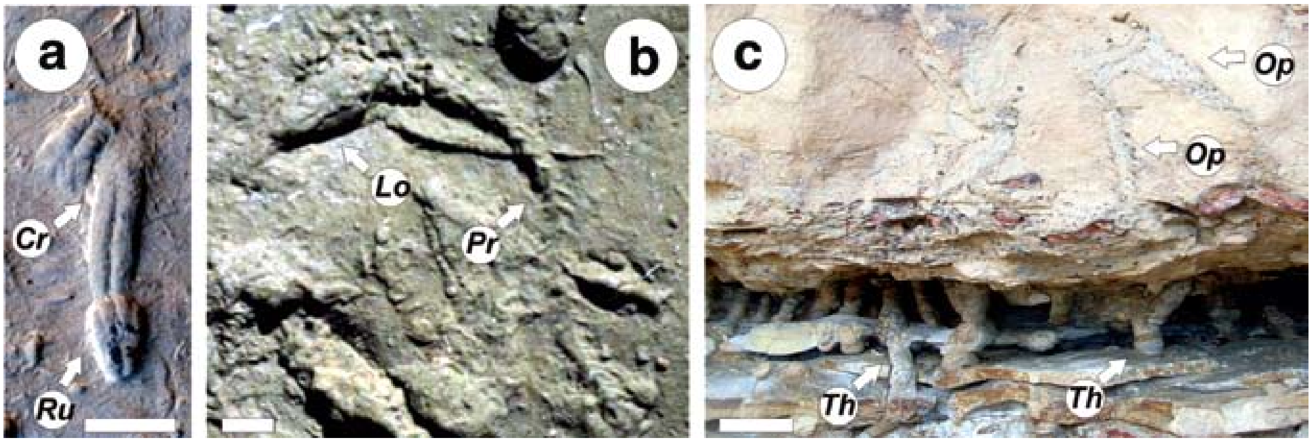


Figure 1.4 Characteristics of trace fossils. The same organism may produce more than one ichnotaxon. (a) Transition between the trilobite locomotion trace *Cruziana* isp. (*Cr*) and the resting trace *Rusophycus* isp. (*Ru*). Upper Carboniferous, Stalnaker Sandstone, roadcut along Kansas Highway 166, United States. Scale bar is 1 cm. See Mángano and Buatois (2004a). (b) Transition between the bivalve locomotion trace *Protovirgularia rugosa* (*Pr*) and the resting trace *Lockeia ornata* (*Lo*). Upper Carboniferous, Stull Shale, Kanwaka Formation, Waverly fossil site, Kansas, United States. Scale bar is1 cm. See Mángano *et al.* (1998). (c) Crustacean galleries showing intergradations between burrows with walls reinforced with pellets in sandy substrates (*Ophiomorpha nodosa*) (*Op*) and burrows with thin lined walls in the underlying more compacted, silty substrates (*Thalassinoides paradoxicus*) (*Th*). Middle Miocene, Socorro Formation, Quebrada El Pauji, northwestern Venezuela. Scale bar is 5 cm.

and Bromley, 2001) (Fig. 1.4b). In addition, associated complex feeding traces have been in some cases referred to the ichnogenus *Lophoctenium* (Ekdale and Bromley, 2001a).

Although common for trails, trackways, and resting traces, this situation is by no means exclusive to this group of biogenic structures. In fact, another common example is that of crustacean burrows (Fürsich, 1973) (Fig. 1.4c). The type of wall in crustacean burrows is largely controlled by substrate grain size and degree of consistency. For example, *Callichirus major* reinforces its burrow wall with pellets in mobile, sandy substrates, and the resulting structure is known as *Ophiomorpha*. However, the same species produces thin burrow linings in more stable sandy or silty sediments, or burrow walls ornamented with bioglyphs in firm, compacted, silty substrates, forming the ichnogenera *Thalassinoides* and *Spongeliomorpha*, respectively. Intergradational forms revealing the transition of one ichnotaxa into another have been called "compound ichnotaxa" (Pickerill, 1994), and are fairly common in the ichnological record (see Section 2.4.1).

In addition to substrate, food supply is another factor that controls burrow morphology. This is illustrated by the amphipod *Corophium volutator*, which is a suspension feeder constructing simple vertical burrows (*Skolithos*) in sandy substrates and a detritus feeder producing U-shaped burrows (*Diplocraterion*) in silty, nutrient-rich sediment (Seilacher, 1953a; Reise, 1985; Bromley, 1990, 1996).

1.2.3 THE SAME ICHNOTAXON MAY BE PRODUCED BY MORE THAN ONE ORGANISM

The same ichnotaxa can be produced by many different animals, revealing behavioral convergence. In most cases, it is simply not possible to establish a one-to-one relationship between producer and biogenic structure. As a general rule, the simpler a trace fossil is, the weaker the link between the biogenic structure and its producer. Simple grazing trails, such as *Helminthoidichnites*, may be produced by nematomorphs, insect larvae, ostracodes, annelids, and many other benthic organisms (Buatois *et al.*, 1998a). The simple vertical burrow *Skolithos* is known to be the product of annelids, phoronids, siphunculids, crustaceans, and probably insects and spiders (Schlirf and Uchman, 2005). The trackway *Diplichnites* records the impressions of multiple undifferentiated locomotory appendages, and has been attributed to many different types of arthropods, including centipedes, millipedes, onicophorans, and trilobites (Buatois *et al.*, 1998b) (Fig. 1.5a). Even burrow systems, such as *Thalassinoides*, which are currently attributed to decapod crustaceans, occur in lower Paleozoic rocks predating the appearance of thalassinideans and callianasids, indicating that other arthropods were probably able to produce similar structures (Carmona *et al.*, 2004).

On the other hand, complex structures can be linked with more confidence to a group of producers. For example, the ichnogenus *Tonganoxichnus* is attributed to apterygote monuran insects based on detailed morphological features and behavioral evidence (Mángano *et al.*, 1997). However, even in this case, a one-to-one link cannot be established because other non-flying insects (e.g. Archaeognatha) are potential producers of *Tonganoxichnus*. Perhaps the closest relationships between trace fossils and their producers can be established with certain insect nests, mostly termites and bees (e.g. Genise, 1997).

Although the precise paleobiological affinity cannot be determined, morphological features may provide enough information on burrowing technique and anatomy to establish a link with a certain group of organisms. Examples of this are represented by *Curvolithus* (turbelarians, gastropods), *Asteriacites* (asteroids, ophiuroids), *Scolicia* (irregular echinoids), *Bichordites* (irregular echinoids), *Protovirgularia* (bivalves), and *Bergaueria* (actinarians, ceriantids, pennatulaceans), among many others. As clearly elaborated by Bromley (1981, 1990, 1996), the practical result of this principle is that biological and ichnotaxonomic classifications should be kept separate.

1.2.4 MULTIPLE ARCHITECTS MAY PRODUCE A SINGLE STRUCTURE

A single structure may reflect the work of more than one producer operating either at more or less the same time or in successive bioturbation events. The first situation typically results from symbiotic or commensalist relationships (see Section 6.7). The

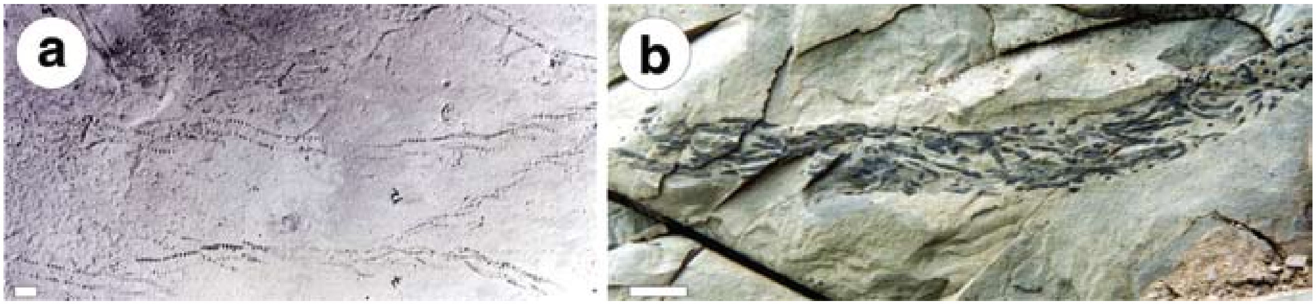


Figure 1.5 Characteristics of trace fossils. (a) The same ichnotaxon may be produced by more than one organism. A wide variety of arthropods, including centipedes, millipedes, onicophorans, and trilobites, are potential producers of *Diplichnites gouldi*. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, United States. See Buatois *et al.* (1998b). (b) Multiple architects may produce a single structure. Concentration of *Chondrites* isp. within "phantom burrows". The high concentration of *Chondrites* helps to delineate the previously emplaced structure that otherwise would have remained undetected. Upper Cretaceous, Horgazu Formation, Covasna Valley, Romania. Scale bars are 1 cm.

standard examples are that of the lobster *Nephrops norvegicus*, the crab *Goneplax rhomboids*, and the fish *Lesueurigobius friessi*, which usually produce independent structures in offshore muds from Scotland, but occasionally construct an interconnected burrow system (Atkinson, 1974). Although this is not uncommon, judging from modern examples, recognition of this type of relationships in the trace-fossil record is extremely problematic. Similar examples are illustrated by burrows constructed by the thalassinidean shrimp *Neaxius acanthus* but also inhabited by the gobiid fish *Austrolethops wardi* (Kneer *et al.*, 2008; Liu *et al.*, 2008). However, in this case the fish apparently does not rework the burrow and, therefore, the resulting structure is essentially the product of the shrimp. The second situation is illustrated by abandoned biogenic structures that are reoccupied by a different organism, which is remarkable common in the trace-fossil record (Fig. 1.5b). A typical example is represented by *Chondrites* and, to a lesser extent, *Phycosiphon*, which may rework the infill of feeding and dwelling burrows, such as *Diplocraterion*, *Cladichnus*, *Gyrolithes*, or *Thalassinoides*, presumably for feeding purposes. This situation is also common in paleosol insect traces (Genise and Laza, 1998; Mikuláš and Genise, 2003). For example, the beetle ichnotaxon *Monesichnus ameghinoi* displays an internal gallery system (*Lazaichnus fistulosus*) probably produced by cleptoparasites (Mikuláš and Genise, 2003). Pickerill (1994) coined the term "composite ichnotaxa" for forms that apparently comprise a single burrow system, but actually result from the interpenetration of individual discrete ichnofossils (see Section 2.4.2), while Mikuláš and Genise (2003) called them "traces within traces".

1.2.5 PRODUCERS ARE COMMONLY SOFT-BODIED ANIMALS THAT ARE RARELY PRESERVED

The body-fossil record is strongly biased towards the groups that have developed hard parts. In contrast, trace fossils commonly record the activities of soft-bodied animals, which make up most of the biomass of a community (Pemberton *et al.*, 1990) (Fig. 1.6a). This principle results from the facts that the trace-fossil record is biased towards the activities of infaunal organisms and that the presence of skeletons is commonly detrimental for infaunal life. Life within the substrate provides protection from environmental stress (e.g. salinity fluctuations, erosion, and desiccation), and biological pressure (e.g. predation). Accordingly, infaunal representatives of many groups of animals, including mollusks, crustaceans, and echinoderms, display a trend to reduce or even eliminate their exoskeleton. For example, efficient burrowers, such as callianassids and upogebids, have significantly reduced calcification of the exoskeleton. In the same vein, deep-infaunal echinoderms have thinner shells than their epifaunal or shallow-infaunal counterparts.

However, examples of the producer preserved in direct association with the biogenic structure have been documented, albeit rarely, in the trace-fossil record. Vertebrate bones preserved inside burrows are related with obrution events (e.g. Voorhies, 1975). The classic example among the invertebrates is that of crustacean claws preserved within *Thalassinoides* burrow systems (Sellwood, 1971; Bromley and Asgaard, 1972a; Mángano and Buatois, 1991). More exceptional are ophiuroids preserved on the resting trace *Asteriacites* (West and Ward, 1990; Mikuláš, 1990) and trilobites on the resting trace *Rusophycus* (Osgood, 1970) (Fig. 1.6b–c). Body fossils of arthropods preserved at the end of their trackway have also been documented. For example, the horseshoe crab *Mesolimulus* is preserved at the end of the trackway *Kouphichnium* in the Jurassic Solnhofen lithographic limestone (Barthel *et al.*, 1990; Seilacher, 2007a).

Figure 1.6 Characteristics of trace fossils. Producers are commonly soft-bodied animals that are rarely preserved. (a) *Bergaueria hemispherica* is produced by burrowing sea anemones. Although these organisms have a remarkably low preservation potential as body fossils, their burrows are common in the fossil record. Lower Cambrian, Gog Group, Lake Moraine, Rocky Mountains, western Canada. See Pemberton and Magwood (1990). (b) *Rusophycus pudicum*. Upper Ordovician, Corryville Formation, Maysville Group, Cincinnati, Ohio, United States. (c) *Flexicalymene meeki* in place associated with the *R. pudicum* specimens shown in (b) One of the unusual cases of producer preserved in connection with the trace fossil. Scale bars are 1 cm. See Osgood (1970).

Because the burrows themselves provide an appropriate microenvironment for body fossil preservation, any shell

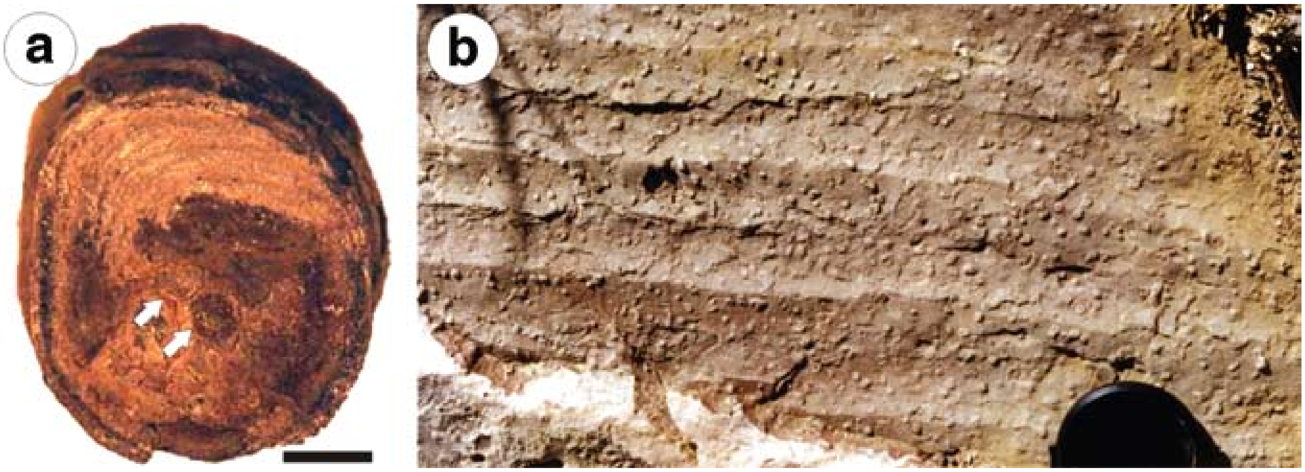


Figure 1.7 Characteristics of trace fossils. Trace fossils are commonly preserved in rock units that are otherwise unfossiliferous. (a) The U-shaped burrow *Tissoa* promotes the formation of minerals that concentrate along tube walls and forms a long axis of conical to cylindrical calcareous concretions. Note the presence of two burrow openings (arrows) indicating a U-shaped morphology. Upper Cretaceous, Hidden Lake Formation, Obelisk Col, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois and López Angriman (1992a). (b) Abundant vertical burrows (*Skolithos linearis*) expressed as circular cross-sections on bedding plane. Lower to Middle Cambrian Campanario Formation, Angosto de Perchel, northwest Argentina. Although trace fossils are abundant in this unit, no body fossils have been recovered with the exception of a few linguliformean brachiopods. See Mángano and Buatois (2004b). Lens cap is 5.5 cm.

that accidentally falls within a burrow may escape destruction by early diagenesis, subsequent bioturbation, and physical reworking, and successfully cross the fossilization barrier (Bromley, 1990, 1996). Repeated storms may lead to accumulation of abundant skeletal material within callianassid burrows producing tubular tempestites (Tedesco and Wanless, 1991). The temptation to establish a genetic link between the burrow system and the preserved body fossils should be resisted at any cost. The standard example here is the delicate preservation of bryozoans trapped inside *Thalassinoides paradoxicus* in chalk (Voigt, 1959, 1974). Another example is the occurrence of the infaunal bivalve *Wilkingia* within *Thalassinoides*-like burrows (Maerz *et al*., 1976).

1.2.6 TRACE FOSSILS ARE COMMONLY PRESERVED IN ROCK UNITS THAT ARE OTHERWISE UNFOSSILIFEROUS

This characteristic derives, at least in part, from the previously outlined fact that trace fossils being produced by soft-bodied faunas have very low preservation potential. In addition, conditions leading to the preservation of trace fossils are remarkably different than those of body fossils. Accordingly, field parties commonly split into two factions, body-fossil paleontologists rushing into mudstone intervals and ichnologists browsing through sandstone and mudstone interfaces. In particular, diagenetic processes that may lead to destruction of body fossils may enhance trace fossils because burrow walls reinforced with mucus act as focus for mineral precipitation.

In some cases, the biogenic structure may promote the formation of diagenetic minerals (see Section 1.3.2). The U-shaped burrow *Tissoa* forms the long axis of conical to cylindrical calcareous concretions due to the formation of minerals that concentrate along tube walls (Frey and Cowles, 1969; Buatois and López Angriman, 1992a) (Fig. 1.7a). Concretionary flint in chalk results from silicification of burrow systems, such as *Thalassinoides*, *Ophiomorpha*, *Zoophycos*, and *Bathichnus* (Bromley and Ekdale, 1984a).

This differential preservation of trace fossils with respect to body fossils is of great importance because it is not uncommon that biogenic structures represent the only biotic evidence in many rock units. For example, thick successions of Cambrian–Ordovician quartzites commonly devoid of body fossils contain abundant trace fossils that allow paleoecosystem reconstructions (e.g. Mángano and Buatois, 2004b) (Fig. 1.7b). In the case of vertebrates, although footprints and bones may be present separately, there are many examples of co-occurrence (e.g. Lockley, 1991).

1.2.7 THE SAME BIOGENIC STRUCTURE MAY BE DIFFERENTIALLY PRESERVED IN VARIOUS SUBSTRATES

The same burrowing technique may lead to apparently disparate biogenic structures if produced under contrasting substrate conditions, both in terms of degree of consistency of the substrate, grain size, and stratal position. The nature of the substrate is essential to determine the feasibility and efficiency of the burrowing technique, and strongly influences the resultant morphology of the trace fossils. The most significant practical consequence of this characteristic is a persistent taxonomic nightmare for ichnologists. This problem is clearly illustrated by the ichnogenus *Nereites* and its multiple preservational variants, such as *Neonereites*, *Scalarituba*, and *Phyllodocites* (see discussion by Uchman, 1995 and Mángano *et al*., 2000). Essentially, *Nereites* consists of a central tunnel enveloped by a zone of reworked sediment, but its preservation is highly dependent on substrate. Chamberlain (1971) demonstrated that single specimens could be preserved as lobes or pustules at the base of sandstone layers (*Neonereites* preservation) or as median furrows with reworked lobes on both sides on top of beds (*Scalarituba*, *Nereites*, or *Phyllodocites* preservation).

Another striking example is that of chevronate locomotion traces of nuculoid bivalves represented by the ichnogenus *Protovirgularia* and its plethora of preservational variants, such as *Walcottia*, *Uchirites*, *Imbrichnus*, and *Chevronichnus* (Rindsberg, 1994; Seilacher and Seilacher, 1994; Mángano *et al.*, 1998, 2002a). The morphology of these locomotion trace fossils is highly controlled by substrate consistency (Fig. 1.8a–c). These ichnotaxa do not represent major behavioral differences; they mainly record changes in the degree of dewatering and other related properties of the sediment. The locomotion mechanism of bivalves is based on rhythmic changes of shape performed by their single muscular foot (Trueman, 1966; Seilacher and Seilacher, 1994). In nuculoid bivalves, which have a bifurcated foot, the repetition of this cycle is recorded by the undertrace, which commonly displays diagnostic chevronate morphology (Seilacher and Seilacher, 1994). The distance between two chevrons represents each sequential set of movements and each chevron indicates the site of anchoring of the foot flaps within the sediment. Sharp, closely spaced chevrons account for short steps, with the animal struggling to advance in stiff, resistant sediment. Longer distances between chevrons may reflect relatively coherent, but less resistant substrates, resulting in lower shell friction, and allowing smoother and easier movement during the protraction phase. Sediment that is too fluid may result in irregular and highly deformed trace-fossil morphologies, recording the difficulties of the foot in obtaining a secure anchorage (Mángano *et al.*, 1998; Carmona *et al.*, 2010).

1.2.8 TRACE FOSSILS COMMONLY HAVE LONG STRATIGRAPHIC RANGES

The large majority of ichnofossils displays long stratigraphic ranges, commonly spanning most, if not all, of the Paleozoic. A smaller number, including mostly very simple forms, has even originated in the Ediacaran (e.g. *Helminthoidichnites* and *Palaeophycus*) (Fig. 1.9a–c). Interestingly, this fact does not seem to indicate a common producer through geological time, but rather the activity of different types of animals involved in the production of a single ichnotaxon through the Phanerozoic. Accordingly, this characteristic reveals behavioral convergence, and is directly linked to the previously discussed principle that states that a single ichnotaxon may be produced by many different animals. Certain behavioral strategies were established relatively earlier in the history of metazoan life and have remained relatively unchanged. Obviously, this characteristic makes trace fossils of limited use in biostratigraphy (see Chapter 13). As with every rule, this one also has its exceptions (Seilacher, 2007b). Some complex structures produced by insect trace fossils have more limited stratigraphic ranges, representing departures to this principle (Genise, 2004). To a lesser extent, the same can be said of biogenic structures produced by micro and macrobioerosion that commonly have narrower stratigraphic ranges than most burrows, trails and trackways (Bromley, 2004; Glaub and Vogel, 2004). In addition, a fair number of ichnotaxa seem to be restricted to the early Cambrian, including *Psammichnites*

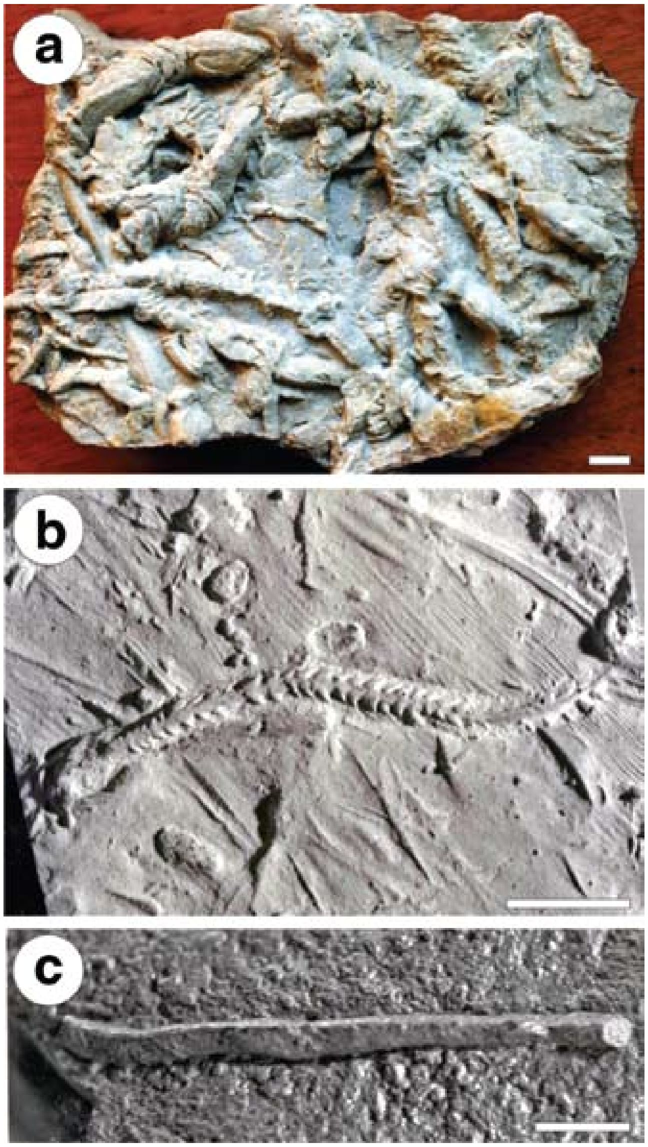


Figure 1.8 Characteristics of trace fossils. The same biogenic structure may be differentially preserved in various substrates. (a) *Imbrichnus wattonensis*. Forest Marble Formation, Jurassic, Forest Marble, Dorset, England. See Hallam (1970). (b) *Walcottia rugosa*. McMillan beds, Ordovician, Cincinnati, Ohio, United States. See Osgood (1970). (c) *Uchirites triangularis*. Guárico Formation, Eocene, Boca de Uchire, Venezuela. See Macsotay (1967). These three forms represent different preservational variants of a chevronate locomotion trace fossil of a cleft-foot bivalve, reflecting various degrees of substrate consistency and corresponding preservation of the chevrons. They are now all included in a single ichnogenus, *Protovirgularia*. Scale bars are 1 cm. See Seilacher and Seilacher (1994) and Mángano *et al.* (1998, 2002a).

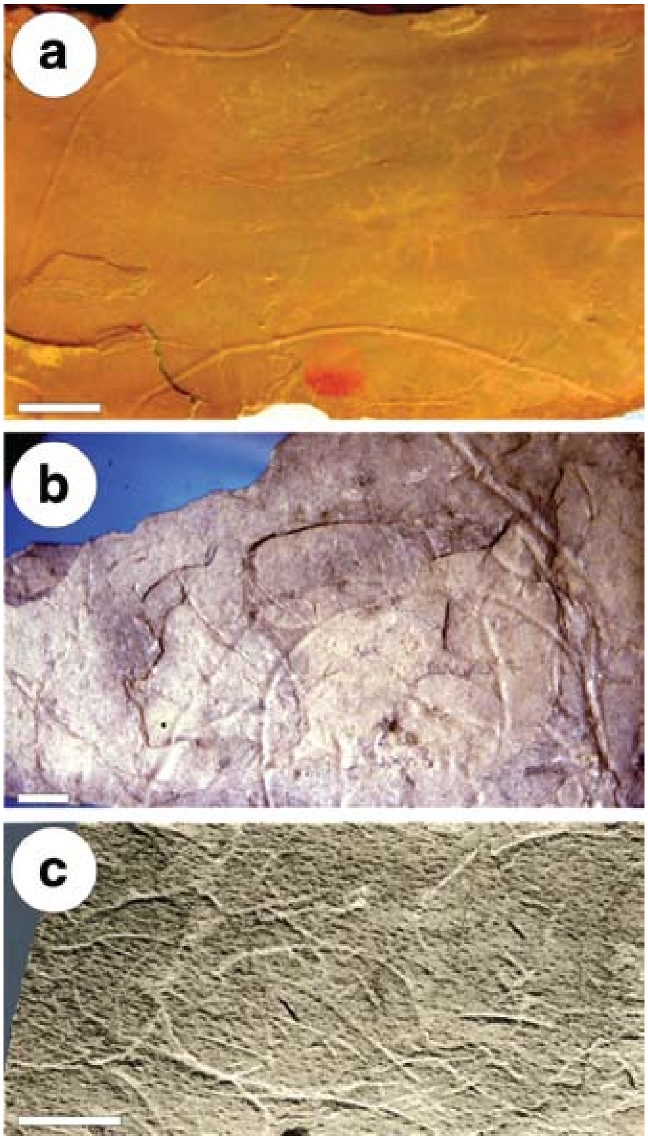


Figure 1.9 Characteristics of trace fossils. Trace fossils commonly have long stratigraphic ranges. *Helminthoidichnites tenuis* (a) Lower Cambrian, Puncoviscana Formation, San Antonio de Los Cobres, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (b) Upper Carboniferous, Agua Colorada Formation, Cantera La Laja, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (c) Lower Cretaceous, La Huérguina Limestone Formation, Las Hoyas fossil site, central Spain. Scale bar is 5 cm. See Buatois *et al.* (2000).

gigas, *Didymaulichnus miettensis*, and several ichnospecies of *Oldhamia* (see Section 13.4).

1.2.9 TRACE FOSSILS COMMONLY HAVE NARROW ENVIRONMENTAL RANGES

Although this characteristic applies more accurately to trace-fossil associations rather than to individual ichnotaxa, it reveals in any case the fact that biogenic structures are strongly controlled by environmental factors and, therefore, they tend to occur preferentially in certain environments of deposition. For example, a number of ichnotaxa are almost exclusively from deep-marine environments, including *Paleodictyon* (Fig. 1.10a), *Helicolithus*, *Spirorhaphe*, *Desmograpton*, *Helminthorhaphe* (Fig. 1.10b), and *Urohelminthoida*. Typical shallow-marine trace fossils include *Psammichnites*, *Curvolithus*, *Daedalus*, and *Arthrophycus*. Another set of trace fossils, such as *Termitichnus*, *Vondrichnus*, *Celliforma*, and *Coprinisphaera*, are exclusive to terrestrial environments. The combination of this characteristic with the fact that trace fossils display long stratigraphic ranges makes them of great importance in paleoecology, allowing comparisons of rocks of different ages formed in similar depositional environments. Certainly, this is at the core of the ichnofacies concept (see Section 4.1).

1.2.10 TRACE FOSSILS ARE RARELY TRANSPORTED

Trace fossils represent the *in-situ* record of biogenic activity. Almost invariably, they have not suffered secondary displacement. Accordingly, trace fossils reveal a more intimate link with the host substrate. This characteristic reveals another of the strengths of trace fossils in paleoecological and paleoenvironmental reconstructions. As with the other principles, some exceptions can be mentioned. First, some trace fossils, most notably borings, can be transported together with the host medium. These include logs bored with *Teredolites* and bioeroded shells and clasts. Second, burrows with strongly reinforced walls are resistant to erosion and reworking, and may be subject to transport. Fragments of crustacean galleries, typically *Ophiomorpha* (Fig. 1.11a–c) and beetle nests, such as *Coprinisphaera*, fall into this category. In particular, the wasp ichnogenus *Chubutolithes* is constructed around plant stems, but subsequently drops to the soil and is reworked by fluvial processes (Genise and Cladera, 2004).

1.3 PRESERVATION OF TRACE FOSSILS

Any trace-fossil description should provide an accurate characterization of preservational aspects. Two main preservational facets can be distinguished: toponomy and physiochemical processes of preservation and alteration (Frey and Pemberton, 1985). Toponomy comprises the description and classification of biogenic structures with respect to their mode of preservation and occurrence. Mode of occurrence is usually defined according to the position of the structure on or within the stratum, or relative to the casting medium. Also included within toponomy are the mechanical processes involved in the fabrication of the structure (stratinomy) and its alteration (taphonomy).

1.3.1 STRATINOMIC CLASSIFICATIONS

Schemes of stratinomic classification (Fig. 1.12) have been proposed by Simpson (1957), Seilacher (1964b), and Martinsson (1970), and are addressed below in chronological order. Summaries and discussions of these classification schemes have been published elsewhere (e.g. Hallam, 1975; Frey and Pemberton, 1985).

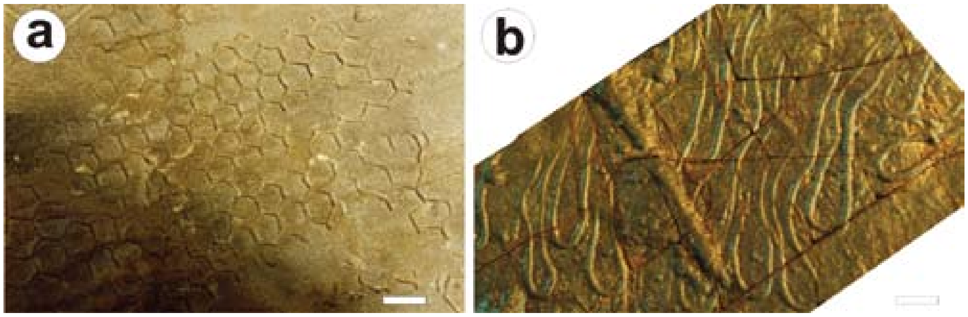


Figure 1.10 Characteristics of trace fossils. Trace fossils commonly have narrow environmental ranges. Some ichnotaxa represent extremely sophisticated feeding strategies that are almost exclusive to deep-marine environments. (a) *Paleodictyon majus.* Zumaya Flysch, Lower Eocene, Guipúzcoa, Spain. See Crimes (1977). (b) *Helminthorhaphe flexuosa*. Lower Eocene, Guárico Formation, Boca de Uchire, Venezuela. See Macsotay (1967). Scale bars are 1 cm.

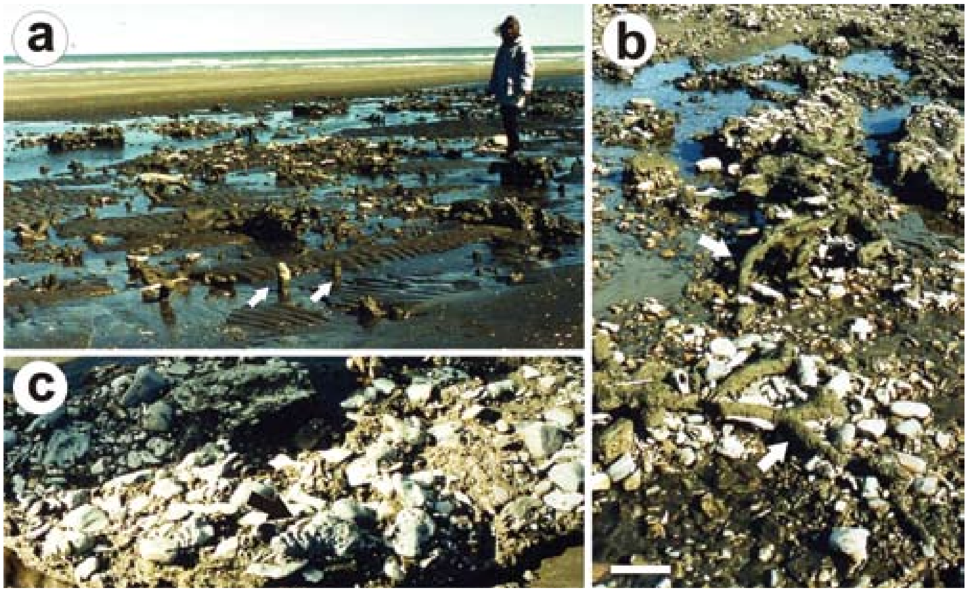


Figure 1.11 Characteristics of trace fossils. Trace fossils are rarely transported. *In situ Ophiomorpha* burrow systems and reworked burrow fragments. Pleistocene, Pehuencó coast, Buenos Aires province, Argentina. (a) General view of *in situ* burrow systems (arrows). (b) Close-up of burrow systems (arrows). Scale bar is 10 cm. (c) Reworked burrow fragments (arrow) in a coastal conglomerate. Lens cap (below arrow) is 5.5 cm.

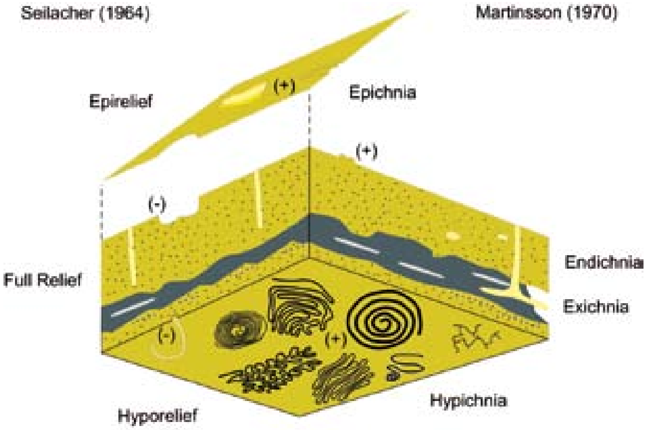


Figure 1.12 Block diagram illustrating the terms used in the stratinomic classifications of Seilacher (1964b) and Martinsson (1970).

SIMPSON'S CLASSIFICATION

Simpson (1957) established four preservational categories: bed-junction, concealed bed-junction, diagenetic, and burial preservations. Bed-junction preservation includes trace fossils preserved in relief at a bed junction. Concealed bed-junction preservation refers to individual burrows that appear to be isolated within an interval of different lithology (Fig. 1.13a). Diagenetic preservation includes ichnofossils preserved as nodule or nodule protuberances formed during early diagenesis (Fig. 1.13b). Burial preservation refers to filled burrows that have been subsequently exhumed by currents winnowing away the associated soft matrix.

SEILACHER'S CLASSIFICATION

Seilacher (1964b) proposed a preservational scheme that comprises two separate sets of terms, descriptive and genetic, which represents a modification of a previous classification (Seilacher, 1953a). Descriptive terms are essentially based on the relationship of the trace fossil to a casting medium, which is usually sandstone. Two main subdivisions, full relief and semirelief, were established. A third category, biodeformational structures, was also defined. Full-relief structures are preserved within the stratum (Fig. 1.13c). Semirelief structures are preserved at lithological interfaces and have been in turn subdivided into epirelief (preserved at the top; Fig. 1.13d–e) or hyporelief (preserved at the base; Fig. 1.13f–g) of the sandstone bed. Additionally, the terms concave (positive) and convex (negative) are used to provide a picture of the trace-fossil relief. Finally, biodeformational

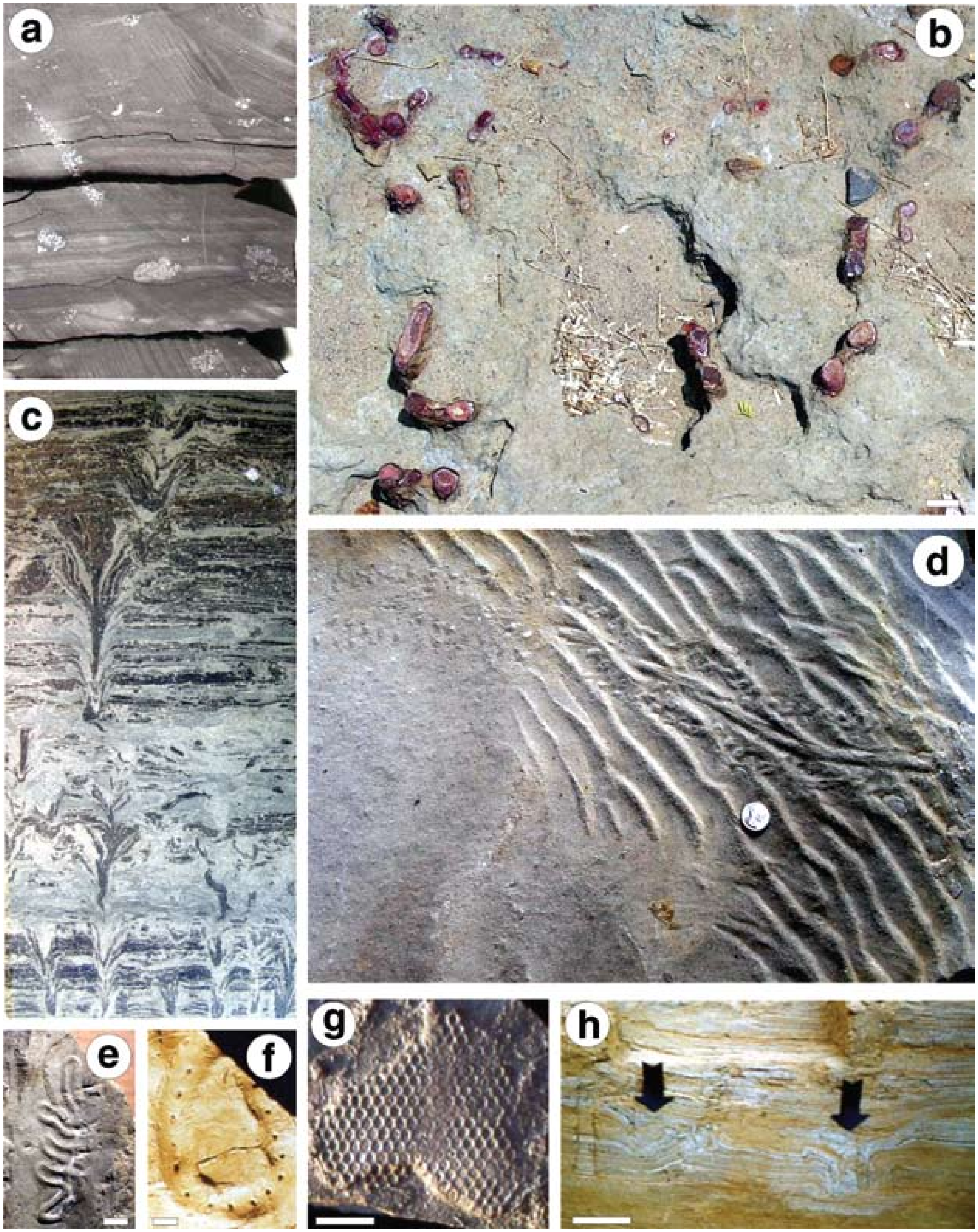


Figure 1.13 Examples of preservational categories. (a) Concealed bed-junction preservation. Firmground *Thalassinoides* filled with coarse-grained sand in prodelta mudstone. Lower Miocene, Tácata Field, Western Venezuela Basin. Core width is 9 cm. See Buatois *et al*. (2008). (b) Diagenetic preservation. Silicified *Diplocraterion parallelum* Middle Miocene, Socorro Formation, Quebrada El Pauji, northwestern Venezuela. Scale bar is 1 cm. (c) Full-relief preservation. *Lingulichnus verticalis* Lower Triassic, Montney Formation, Sturgeon Lake area, west-central Alberta, Canada. Core width is 8 cm. See Zonneveld and Pemberton (2003). (d) Negative epirelief. The arthropod trackway *Protichnites* isp. associated with ripple marks. Upper Cambrian, Cairnside Formation, Postdam Group, slab exhibited at the Fossil Garden at Buisson Point Archaeological Park, Melocheville, Quebec, Canada. Coin is 2.4 cm. (e) Positive epirelief. *Psammichnites implexus* locally preserved along ripple troughs. Upper Carboniferous, Stull Shale, Kanwaka Formation, Waverly fossil site, Kansas, United States. Scale bar is 1 cm. See Mángano *et al*. (2002b). (f) Negative hyporelief. *Psammichnites grumula*. Note well-developed holes (siphon marks) along a median line and prominent levees on both sides of the trace. Upper Carboniferous, Stull Shale, Kanwaka Formation, Waverly fossil site, Kansas, central United States. Scale bar is 1 cm. See Mángano *et al*. (2002b). (g) Positive hyporelief. *Paleodictyon minimum*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Romania. Scale bar is 1 cm. See Buatois *et al.* (2001). (h) Cross-section view of mammoth undertracks (arrows). Mammoth National Park. South Dakota, United States. Scale bar is 10 cm.

structures are not defined with respect to the casting medium, but refer to sediment disturbances of biological origin, such as poorly defined burrow mottling.

Genetic terms refer to the assumed relationship of the trace fossil to the contemporary surface rather than that of the tracemaker. These include exogenic, endogenic, and pseudoexogenic. Exogenic refers to surficial traces covered by sediment that differs from that of the host layer. Endogenic includes those structures actively or passively filled within the host bed. Pseudoexogenic comprises traces formed in a homogeneous medium, but subsequently uncovered by erosion and recast with sand. The terms active and passive can be further added to distinguish between active backfill of the trace fossils from subsequent sedimentation infill. Chamberlain (1971) proposed a slight modification of Seilacher's scheme with the suggestion of replacing the term exogenic by epigenic.

A special case of semirelief preservation has been named cleavage relief and comprises structures seen on cleavage surfaces within intervals of monotonous lithologies (Frey and Pemberton, 1985). This style is commonly associated with preservation of vertebrate and arthropod undertracks (Goldring and Seilacher, 1971; Frey and Pemberton, 1985) (Fig. 1.13h). It has been argued that most fossil trackways are not formed at the sediment surface, but reflect deformation of subsurface laminae during production of the trackway at the surface. This can be typically detected by carefully parting the laminae to reveal vertical repetition of the appendage imprints. Undertrack preservation has been elegantly demonstrated in limulid trackways by Goldring and Seilacher (1971). These authors also detected what was referred to as an undertrack-fallout effect by showing that the most delicate and superficial imprints tend to disappear with sediment depth.

MARTINSSON'S CLASSIFICATION

The classification system proposed by Martinsson (1970) has a lot in common with that of Seilacher (1964b), including the fact that it is also based on the relationship of the trace fossil to a casting medium. Four preservational categories were introduced: epichnia, hypichnia, endichnia, and exichnia. Epichnial preservation comprises structures preserved at the upper surface of the casting strata, while hypichnial preservation includes those preserved at the lower surface of the casting strata. In both epichnial and hypichnial preservations, the terms grooves and ridges are used to denote negative and positive reliefs, respectively. Endichnial preservation refers to structures preserved within the casting medium and exichnial preservation comprises those preserved outside the casting medium.

EVALUATION OF THE CLASSIFICATION SCHEMES

Of these classification systems, those of Seilacher and Martinsson are the ones that have met with most acceptance. Both are very similar and attempt to be comprehensive. Seilacher (1964b) carefully distinguished descriptive and genetic terms. For example, a structure preserved as positive hyporelief may have been formed: (1) as an open burrow system connected to the sediment–water interface that was subsequently filled by sand (e.g. graphoglyptids on turbidite soles); (2) within the sediment along the sand–mud interface (e.g. most specimens of *Cruziana*); or (3) within a homogeneous fine-grained sediment that was subsequently erosionally exhumed and filled by sand. The advantage of Martinsson's scheme relies in its simplicity, but a certain amount of mixing of preservational and genetic aspects in the definition of his terminology represents a problem (Jensen, 1997). Simpson's system is hardly used nowadays, and it is definitely not comprehensive. However, it has been rightly noted that the scheme contains some useful ideas, such as the notion of concealed bed-junction preservation and burial preservation (Frey and Pemberton, 1985). In addition, the classification is not strictly stratinomic because it also takes into consideration diagenetic aspects (see Section 1.3.2) that are overlooked in the other classifications.

1.3.2 PHYSIOCHEMICAL PROCESSES OF PRESERVATION AND ALTERATION

Physiochemical processes of preservation and alteration fall within the realm of diagenesis, and can be quite variable and complex. However, they are still poorly understood although there is an increased recognition of their importance (Simpson, 1957; Frey, 1975; Bromley and Ekdale, 1984a; Frey and Pemberton, 1985; Bromley, 1990, 1996; Schieber, 2002; McIlroy *et al.*, 2003; Pemberton and Gingras, 2005; Needham *et al.*, 2006). Unfortunately, no classification based on diagenetic features is available yet. Early diagenesis is particularly relevant when dealing with trace fossils in carbonates. Organic material and mucus in *Thalassinoides* linings serve as a nucleus for $CaCO_3$ precipitation resulting in the formation of nodular limestones (Fürsich, 1972). Spectacular examples of diagenetically enhanced trace fossils also occur in chalk in the form of flint concretions (e.g. Bromley and Ekdale, 1984a) (see Section 1.2.6). The influence of diagenesis on biogenic structures is also of paramount importance in alkaline lakes (Scott *et al.*, 2007a). These authors evaluated the interplay of diagenesis and animal–sediment interactions, and analyzed the role of efflorescent salt crystallization, substrate wetting and drying, and benthic microbial mats and biofilms. In recent years, different studies have emphasized the links between burrowing and diagenesis (e.g. McIlroy *et al.*, 2003; Pemberton and Gingras, 2005; Needham *et al.*, 2006). In particular, the importance of bioturbation in enhancing permeability in hydrocarbon reservoirs has been stressed (Pemberton and Gingras, 2005).

1.4 ETHOLOGY OF TRACE FOSSILS

Trace fossils are primarily evidence of animal behavior (see Section 1.2.1). Accordingly, understanding the ethological significance of trace fossils lies at the very core of ichnology, and virtually any valuable inference stems from it (Fig. 1.14). It is unsurprising that the ethological classification of trace fossils is one of the most popular in ichnology. This system of classification was proposed

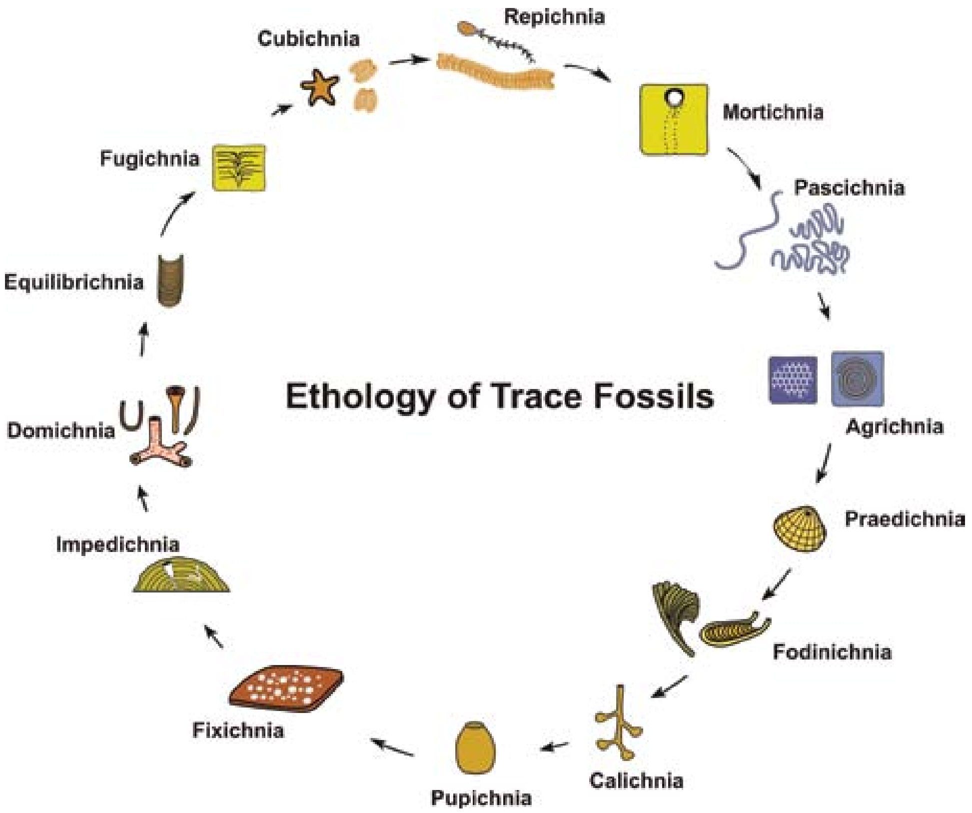


Figure 1.14 Ethological classification of trace fossils. Modified from Bromley (1996).

originally by Seilacher (1953a) and is based on the establishment of a small number of ethological categories. The original system consists of five categories: resting traces (cubichnia), locomotion traces (repichnia), grazing traces (pascichnia), feeding traces (fodinichnia), and dwelling traces (domichnia). These five categories represent the basic building blocks of behavioral interpretations in ichnology. However, refinements have been suggested to take account of additional behaviors. For example, Frey (1973) added a sixth category for escape traces or fugichnia, and Ekdale *et al*. (1984) suggested another one for farming traces and traps or agrichnia. To this list we should add predation traces or praedichnia (Ekdale, 1985) and equilibrium traces or equilibrichnia (Bromley, 1990). In recent years, new ethological categories were added for the work of some terrestrial insects and bioeroders. Nesting traces or calichnia (Genise and Bown, 1994a) and pupation chambers or pupichnia (Genise *et al*., 2007) belong to the first group, while fixation/anchoring traces or fixichnia (Gibert *et al*., 2004) and bioclaustration structures or impedichnia (Tapanila, 2005) fall within the latter. Seilacher (2007a) introduced death traces or mortichnia. Other categories may be considered as subdivisions of the major ones. For example, Genise and Bown (1994a) noted that calichnia may include building traces or aedifichnia, previously proposed by Bown and Ratcliffe (1988). Verde *et al*. (2007) documented aestivation chambers in paleosols, but recommended recognition of further cases to evaluate whether creating a new ethological category is advisable or whether this should be considered a subset of domichnia. In addition, Genise (1995) made the point that substrate selection is an integral part of behavior and introduced xylichnia for wood borings, but placed it as a subcategory of fodinichnia. Unsuccessful attempts at escape have been referred to as taphichnia by Pemberton *et al*. (1992b), but included in fugichnia by Bromley (1996). Needless to say, most trace fossils represent more than one activity and overlap among categories reflects common intergradations. The category polychresichnia was proposed for trace fossils that represent many simultaneous multiple behaviors and uses (Hasiotis, 2003). However, this situation is the rule rather than the exception and, therefore, a discrete ethological category is unnecessary. Excellent summaries of the ethological classification have been published by Frey and Pemberton (1984, 1985), Ekdale (1985), and Bromley (1990, 1996).

1.4.1 RESTING TRACES OR CUBICHNIA

Resting traces are produced by vagile organisms that temporarily dig down, forming shallow depressions, seeking protection from predators or that simply stop their usual activities during quiescent moments. Strictly speaking, few tracemakers actually rest and different subordinate behaviors may be involved (Bromley, 1990, 1996). For example, some resting traces are linked to feeding purposes. Ophiuroids, common producers of *Asteriacites*, dig in the sediment searching for prey and shifting their position at intervals. Resting traces of the ghost crab *Ocypode quadrata* are associated with hydration and respiration (Martin, 2006a). On morphological grounds, resting traces clearly reflect the latero-ventral anatomy of their producers (Fig. 1.15a). As a consequence, resting traces can be ascribed to their

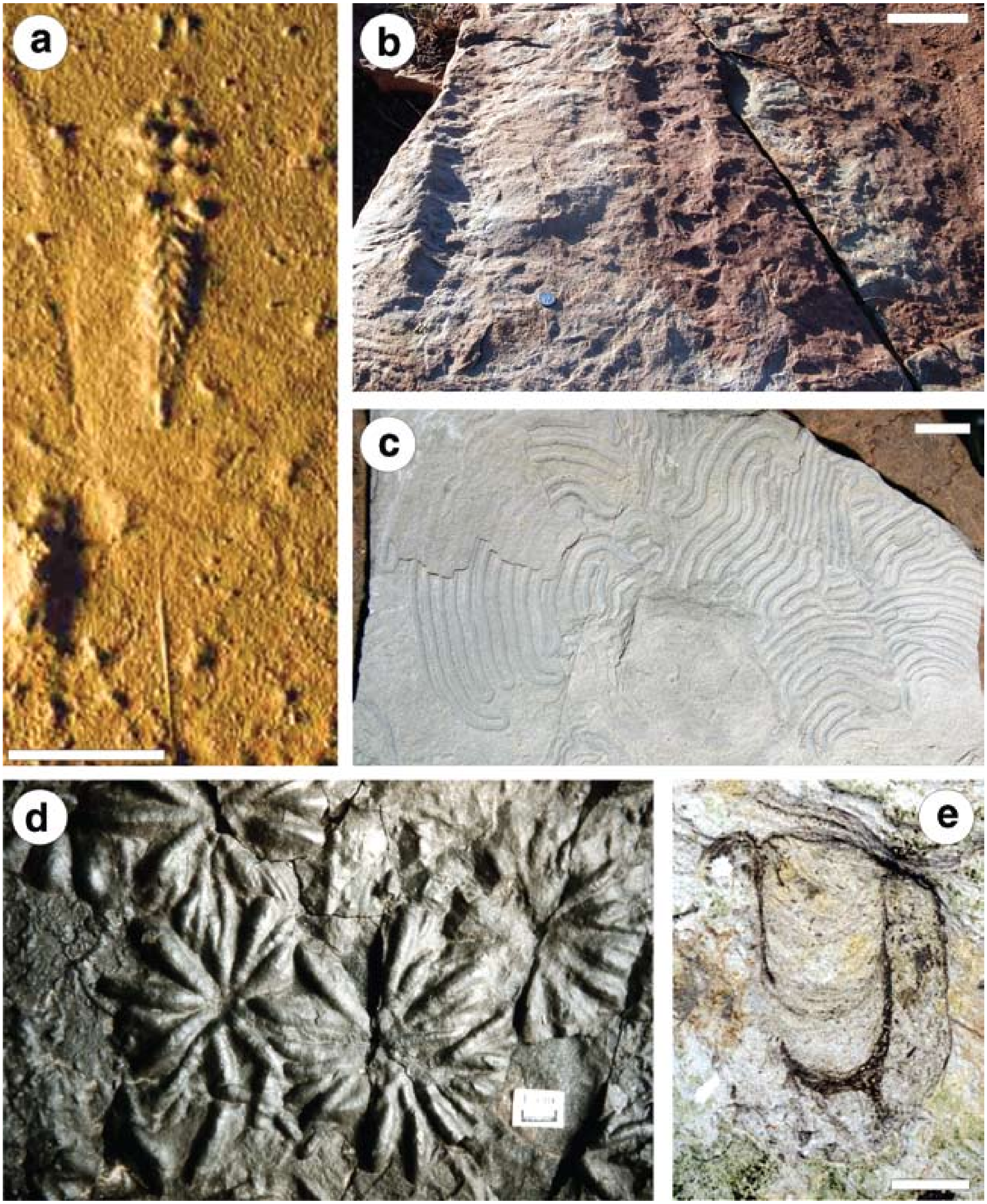


Figure 1.15 Examples of the original ethological categories established by Seilacher (1964b). (a) Resting trace (cubichna) *Tonganoxichnus buildexensis*. Note morphological evidence of the latero-ventral anatomy of its producer, a monuran insect. The anterior region is characterized by the presence of a frontal pair of maxillary palp impressions, followed by a head impression and three pairs of conspicuous thoracic appendage imprints symmetrically opposite along a median axis. The posterior region commonly exhibits numerous delicate chevron-like markings, recording the abdominal appendages, and a thin, straight, terminal extension. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, central United States. See Mángano *et al*. (1997, 2001a). Scale bar is 1 cm. (b) Giant arthropod locomotion trace (repichnia) *Diplichnites cuithensis*. Two rows of imprints produced by the locomotory appendages of a terrestrial myriapod are recorded. Upper Carboniferous, El Cobre Canyon Formation, El Cobre Canyon, New Mexico, southwest United States. See Lucas *et al*. (2005). Scale bar is 10 cm. (c) Grazing trail (pascichnia) *Nereites irregularis*. Note highly specialized guided meanders evidencing efficient covering of the substrate. Paleogene, Rhenodanubian Flysch, Hoflein Wiener Wald, Austria. Scale bar is 1 cm. See Uchman (1999). (d) *Asterichnus* isp., Upper Ordovician, Letná Formation, Chrustenice, Czech Republic. See Prantl (1945) and Mikuláš (1998). Scale bar is 1 cm. (e) The U-shaped dwelling trace (domichnia) *Diplocraterion*. Lower Jurassic, Staithes Sandstone Formation, Staithes Harbour, North Yorkshire Coast, England. See Taylor and Pollard (1999). Scale bar is 1 cm.

makers with a higher degree of certainty than other categories. Although discrete resting traces do occur, intergradations with locomotion traces (e.g. *Rusophycus-Cruziana*) or escape traces (*Lockeia-Protovirgularia wattonensis*) commonly occur. The typical preservation is as positive hyporelief, although negative epireliefs can occur. Examples of resting traces are *Lockeia*, *Tonganoxichnus* (Fig. 1.15a), *Tripartichnus*, *Selenichnites*, *Asteriacites*, *Rusophycus*, *Medousichnus*, *Raaschichnus*, and *Limulicubichnus*. Landing traces or volichnia (Walter, 1983) are best included within cubichnia.

1.4.2 LOCOMOTION TRACES OR REPICHNIA

Locomotion traces result from animals that move from one place to another. The main activity here is displacement of the producer. Other activities, such as feeding, might be involved but they are not reflected by the biogenic structure. As for almost all trace fossils, locomotion traces are typically produced by benthic animals. However, fish swimming close to the sediment–water interface may occasionally touch the bottom leaving locomotion trails (*Undichna*). Because of this, the term "locomotion trace" is preferred to the most widely used "crawling trace". The morphology of the trace fossil is directly related to the locomotion mechanism involved (e.g. locomotory appendages in arthropods and tetrapods, and muscular foot in bivalves). Trackways represent a typical example (Fig. 1.15b), but continuous horizontal trails are also common. Morphologies in this latter case include bilobate traces, simple trails, and chevronate traces. Complex traces suggestive of systematic probing due to feeding activities are excluded. Although less informative of the anatomy of the producers, locomotion traces may shed some light on the type and number of appendages involved in locomotion, as well as on the role of muscles used for displacement. Locomotion traces are invariably preserved as positive hyporelief or negative epireliefs, and are essentially bedding-plane trace fossils formed either at the sediment–water/air interface or along lithological interfaces. Examples include a wide variety of tetrapod and arthropod trackways, such as the ichnogenera *Umfolozia*, *Kouphichnium*, *Diplichnites* (Fig.1.15b), *Permichnium*, *Mirandaichnium*, *Octopodichnus*, and *Paleohelcura*, among many others. Locomotion trails are represented by *Cruziana*, *Gyrochorte*, *Diplopodichnus*, *Didymaulichnus*, and *Protovirgularia*. As indicated by Bromley (1990, 1996), swimming traces (natichnia of Müller, 1962, and Walter, 1983), and running traces (cursichnia of Walter, 1983) are best included under the more general repichnia.

1.4.3 DEATH TRACES OR MORTICHNIA

Death traces reflect the last movements of the makers that are preserved together with their trace fossils. Even post-mortem convulsions may be recorded (Seilacher, 2007a). These are unique cases in which a trace fossil is attributed without any doubt to a producer. They are typically arthropod trackways, such as those of limulids and crustaceans, ending in a body fossil. Less common examples include those of bivalves and gastropods preserved at the end of their burrows and trails, respectively, and tail traces produced by fish. Death traces are almost invariably preserved in anoxic settings as a result of the activity of animals that were transported by turbidity currents into the anoxic zone. With the exception of *Telsonichnus*, which resulted from the final movements of the shrimp *Antrimpos* (Seilacher, 2007a), no formal names have been proposed for death trace fossils. Taxonomic names originally proposed for locomotion structures (e.g. *Kouphichnium*) are commonly used.

1.4.4 GRAZING TRACES OR PASCICHNIA

Grazing traces reflect a combination of locomotion and feeding because the animal searches for food while traveling. They represent the activity of mobile, infaunal deposit feeders or epifaunal detritus- feeding organisms, and typically include forms that are more regular than trails that simply reflect locomotion (Fig. 1.15c). These trails are unbranched and horizontal, varying from simple, straight grooves that may reflect overlapping to, more typically, non-overlapping, curved, circular, and meandering, including tight guided meanders. Trail complexity reveals the degree of sophistication involved in the feeding pattern. In contrast to locomotion and resting traces, anatomic information on the producers of grazing traces is mostly unavailable (although some general morphological information, such as the length of the animal can be readily inferred). As a result, connections between the trace and its producer are difficult to establish. As with locomotion traces, grazing traces are preserved as positive hyporelief or negative epireliefs. They are typical bedding-plane trace fossils formed either at the sediment–water/air interface or along lithological interfaces. Examples of grazing traces are *Gordia*, *Mermia*, *Helminthoidichnites*, *Archaeonassa*, *Psammichnites*, *Helminthopsis*, *Nereites* (Fig. 1.15c), *Bichordites*, and *Scolicia*. *Helminthorhaphe* and *Cosmorhaphe* may belong to this category, although other authors tend to include them in agrichnia.

1.4.5 FEEDING TRACES OR FODINICHNIA

Feeding traces represent combined dwelling and feeding activities. They are typically produced by infaunal deposit feeders that develop an "underground mining" strategy. Morphologies are variable, ranging from simple to extremely complex. Intergradations with dwelling traces are common, and some structures are difficult to place in one category or the other. Common patterns include simple burrows, branched burrow systems, radial structures, and U-shaped tubes. Spreite formation is quite typical. Evidence of active infill (e.g. backfill) by the organism is almost diagnostic. In contrast to the previously described categories, orientation with respect to the bedding plane is highly variable, including horizontal, inclined, and vertical traces. Little, if any, anatomic information is provided by feeding traces. Endichnial preservations are the most common. Examples include *Asterichnus* (Fig. 1.15d), *Asterosoma*, *Arthrophycus*, *Rhizocorallium*, *Treptichnus*, *Dictyodora*, *Lophoctenium*, *Teichichnus*, *Daedalus*, *Syringomorpha*, *Gyrophyllites*, *Dactyloidites*, and *Phycodes*.

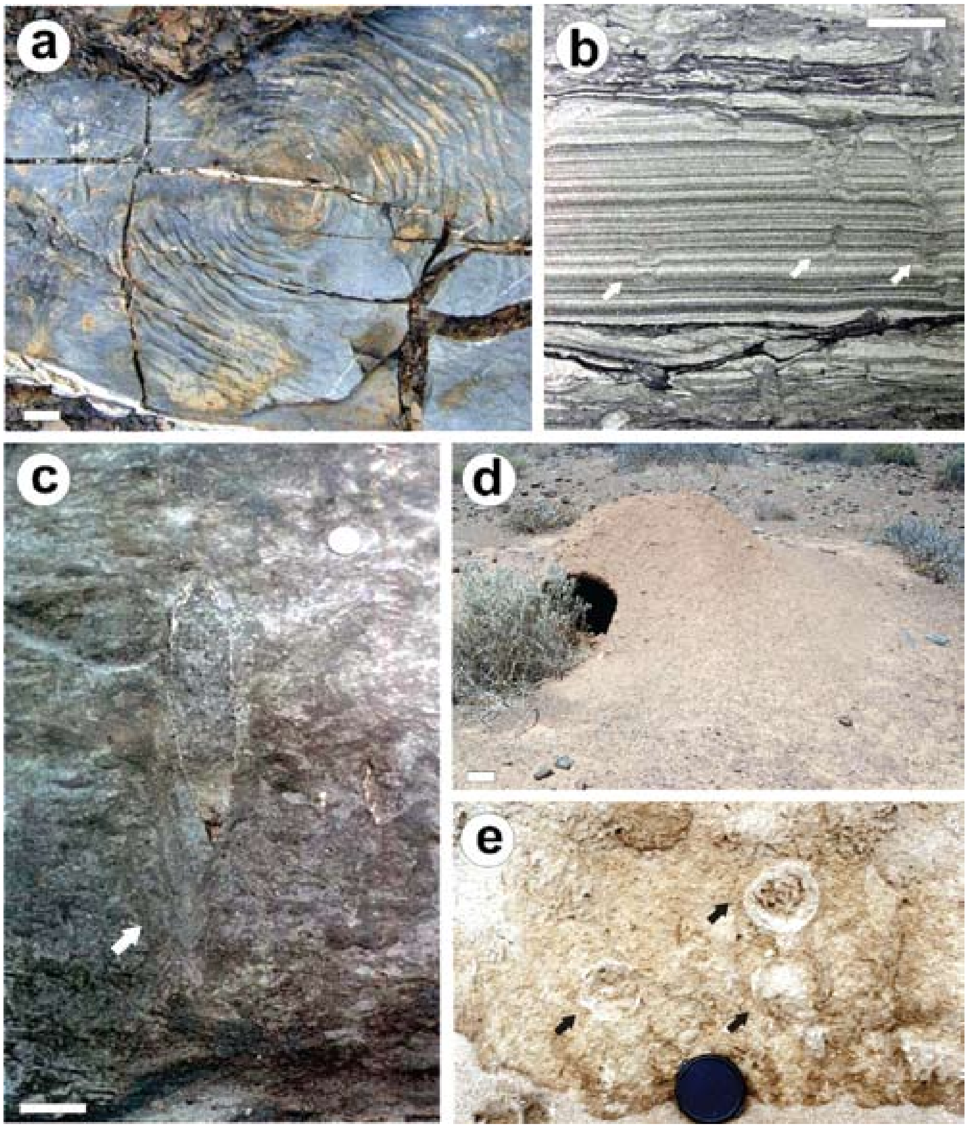


Figure 1.16 Examples of the subsequently added ethological categories. (a) The farming trace (agrichnia) *Spirorhaphe involuta*. Lower Eocene, Guárico Formation, Boca de Uchire, Venezuela. See Macsotay (1967). Scale bar is 1 cm. (b) Escape traces (fugichnia) (arrows) in tempestite. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (c) Equilibrium structure (equilibrichnia) *Scalichnus* (arrow) produced by the bivalve *Atrina* (see body fossil of the producer preserved at the top of the structure). Lower Miocene, Chenque Formation, Caleta Olivia, Patagonia, Argentina. See Carmona *et al.* (2009). Scale bar is 5 cm. (d) Predation trace (praedichnia). Modern termite nest reworked by a myrmecophagous mammal. Matjiesgloof Farm, South Africa. Scale bar is 10 cm. See Fey (2010) (e) The nesting trace (calichnia) *Coprinisphaera ecuadoriensis* (arrows). Pleistocene, Cangagua Formation, Quito, Ecuador. See Laza (2006). Lens cap is 5.5 cm.

1.4.6 DWELLING TRACES OR DOMICHNIA

Dwelling traces comprise permanent domiciles constructed by infaunal organisms, commonly sessile suspension feeders and passive predators. Less commonly, active predators and deposit feeders also construct dwelling traces. Emphasis is on dwelling, but other activities may be involved. The category encompasses not only burrows but also borings in hard substrates. The morphology ranges from simple burrows to U-shaped tubes (Fig. 1.15e) and branched burrow systems. Dwelling traces are typically vertical to oblique, but horizontal burrows may occur. Burrow linings are common, reflecting construction of permanent structures. Burrow diameter tends to be quite constant, reflecting tracemaker width. Dwelling traces are preserved as endichnia. Examples of dwelling traces are *Skolithos*, *Arenicolites*, *Diplocraterion* (Fig. 1.15e), *Ophiomorpha*, *Thalassinoides*, *Monocraterion, Camborygma*, *Lunulichnus*, and *Palaeophycus.*

1.4.7 TRAPS AND FARMING TRACES OR AGRICHNIA

Agrichnia includes complex and extremely regular burrow systems that are referred to as graphoglyptids. These structures represent combined dwelling and feeding activities, and are thought to be produced for bacterial farming or as traps to capture meiofauna or microorganisms (Seilacher, 1977a). Burrow morphologies include branched meanders, spirals (Fig. 1.16a), and nets. These patterns are typical of the deep sea, but have been compared with modern spirals formed in intertidal areas by the polychaete *Paraonis fulgens* for trapping diatoms (Röder, 1971; Papentin and Röder, 1975; Seilacher, 1977a; Minter *et al.*, 2006). However, some graphoglyptids display multiple exits and side branches that suggest bacterial farming rather than trapping (Seilacher, 1977a). The burrows are maintained as open tunnels in hemipelagic mud, very close to the sediment–water interface and, therefore, no active infill occurs. They are subsequently excavated by turbidity currents and

Box 1.2 The ethology of *Zoophycos*

Zoophycos is one of the most complex trace fossils (Fig. 1.17a–h). Several constructional models have been proposed to account for its intricate morphology and its ethological significance. Hardly a year passes without a new paper on *Zoophycos*. Richard Bromley (1991) elegantly summarized the different available models for *Zoophycos*. Because of the large morphological variability of Ordovician to Recent *Zoophycos*, it is likely that there is no single universal "correct" model and, instead, models should be applied on a case-by-case basis. It is even possible that the *Zoophycos* animal displays a behavioral plasticity that allows for shifts in feeding strategies and trophic types if necessary.

Strip-mine model: This model implies a deposit-feeding strategy for the *Zoophycos* producer. In this model, the spreite is the result of sediment feeding and waste disposal occurring simultaneously. This is a low-cost system based on minimal sediment transport. However, the discovery by Nobuhiro Kotake that the *Zoophycos* producer introduces sediment from the sediment–water interface in the form of excreted pellets militates against the strip-mine, deposit-feeding model.

Detritus-feeding model: A detritus-feeding strategy is supported by the downward conveyance of sediment involved in *Zoophycos*. However, this is definitely a high-cost system and its viability remains unclear.

Refuse-dump model: This model attempts to reconcile the two apparently contradictory facts that the *Zoophycos*-infilling material is derived from a higher level and that the spreite is suggestive of a deposit-feeding strategy. Solving this contradiction requires that the preconstructed cavity is the result of deposit feeding and that the resulting material is conveyed upwards, while sediment from the surface is conveyed downwards to maintain the narrow form of the tube. This model is consistent with the generally accepted deep-tier nature of *Zoophycos*. However, as in the previous model, this is a high-cost system.

Cache model: Evidence from marine benthic ecology suggests that the flux of food supply varies periodically and, as a result, some organisms squirrel away food to be used later. The cache model implies that the *Zoophycos* producer feeds at the surface, but also conveys organic material downwards, using the burrow as a storage place for times of reduced food supply. This model is consistent with both the well-accepted downward convection and the deep-tier nature of *Zoophycos*.

Gardening model: This model adds another level of complexity to *Zoophycos* behavior. It has been noted that the thin burrow-fill laminae have a large interface with the surrounding sediment, and that a long marginal tube runs around the perimeter of the spreite. According to the gardening model, the *Zoophycos* animal uses the surface sediment as a carrier of microbes and cultivates bacteria within the marginal tube. This model is consistent with the overall complexity of the burrow.

References: Seilacher (1967a, 2007a); Simpson (1970); Wetzel and Werner (1981); Kotake (1989, 1991, 1994, 1997); Bromley (1991); M.F. Miller (1991); Ekdale and Lewis (1991a); Wetzel (1992); Gaillard and Olivero (1993); Fu and Werner (1995); Olivero and Gaillard (1996, 2007); Bromley *et al.* (1999); Miller and d'Alberto (2001); Bromley and Hanken (2003); Löwemark and Schäffer (2003); Knaust (2004a, 2008); Löwemark *et al.* (2006, 2007).

cast by the turbidite sand. Accordingly, graphoglyptids are preserved as a positive hyporelief at the base of turbidite sandstones. Examples of agrichnia are *Spirorhaphe* (Fig. 1.16a), *Belorhaphe*, *Helicolithus*, *Urohelminthoida*, *Paleomeandron*, *Desmograpton*, *Paleodictyon*, *Megagrapton*, and *Protopaleodictyon*. It has been suggested that some deeper branching burrow systems may be included in agrichnia, such as *Chondrites* (Seilacher, 1990a; Fu, 1991; Bromley, 1996) and *Pragichnus* (Mikuláš, 1997). In addition, farming has been suggested as the feeding strategy involved in the helically coiled spreiten burrow *Zoophycos* (Fu and Werner, 1995) (Box 1.2), and the sinusoidal crustacean burrow system *Sinusichnus* (Gibert, 1996; Buatois *et al.*, 2009a).

1.4.8 ESCAPE TRACES OR FUGICHNIA

Escape traces include structures formed in response to rapid changes in sedimentation, typically event deposition. Animals are forced to rapidly readjust their burrows to avoid burial. Lateral escape from predators may be included in this category (Bromley, 1990, 1996). The polychaete *Scolelepis squamata* forms sinusoidal trails similar to *Cochlichnus* to escape from predators (Behrends and Michaelis, 1977). This latter group of escape traces is difficult, if not impossible, to recognize in the fossil record. In any case, typical escape structures are revealed by the vertical repetition of dwelling traces, commonly forming not only cone-in-cone morphologies (Fig. 1.16b) but also U-in-U traces. Burrow walls are poorly defined and unlined, reflecting rapid sediment reworking. These structures are invariably preserved as endichnial structures. Bivalves and sea anemones usually produce escape traces. Because their morphology is so simple, it is common practice among ichnologists not to give formal ichnotaxonomic treatment to escape traces (e.g. Hanken *et al.*, 2001). As noted by several authors, care should be exercised to avoid confusing escape traces with physical collapse features (Frey and Pemberton, 1985; Buck and Goldring, 2003).

1.4.9 EQUILIBRIUM TRACES OR EQUILIBRICHNIA

Equilibrium traces encompass structures formed in substrates affected by progressive aggradation and degradation. In contrast to escape traces, equilibrichnia comprises more gradual adjustments under background sedimentation reflecting the fact that infaunal organisms live at a certain depth with respect to the sediment–water interface. Displacements include upward

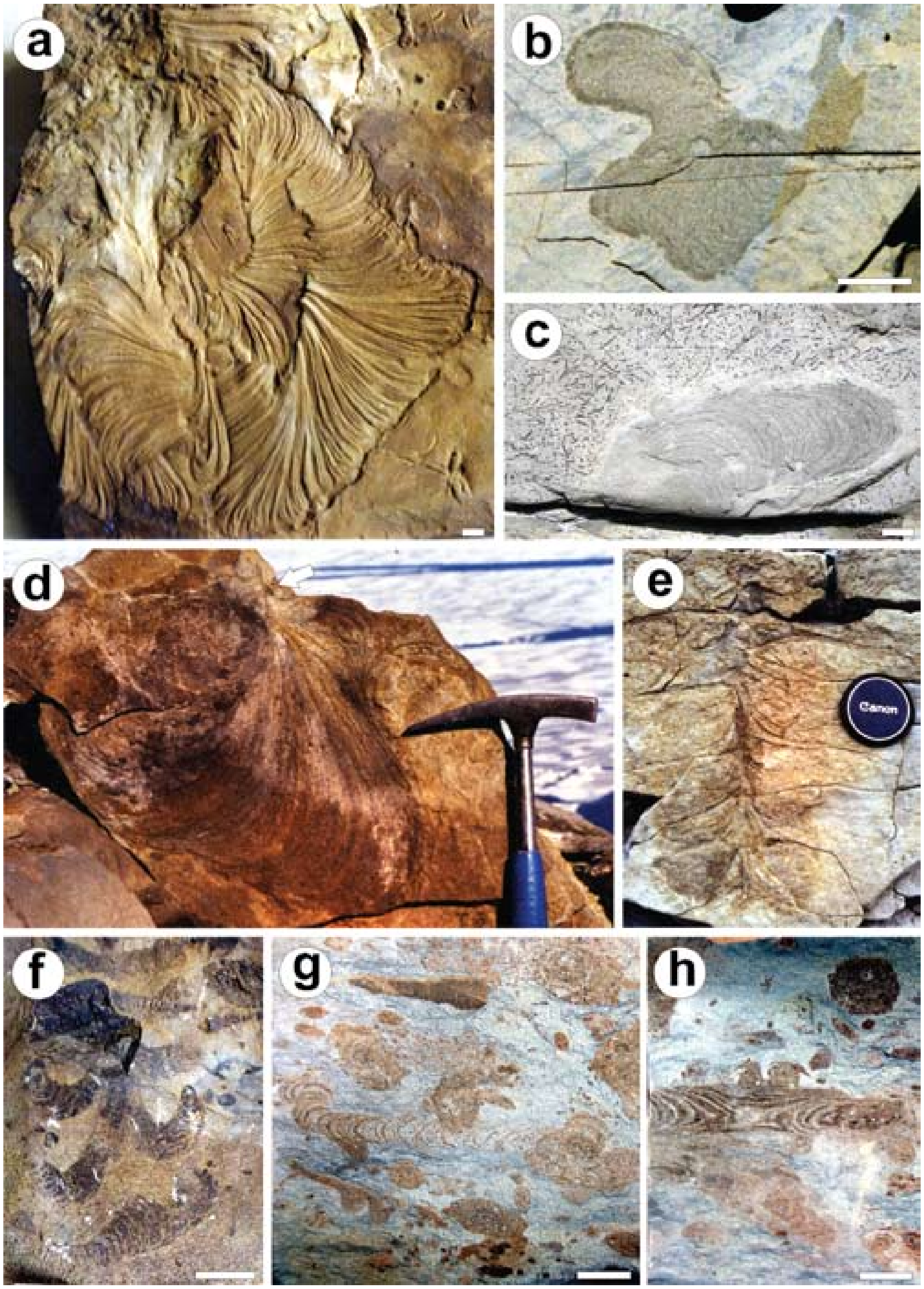


Figure 1.17 Morphological variability and different expressions of *Zoophycos*. (a) Bedding-plane view of a large specimen showing a complex spiral form and lobes with well-developed primary lamellae. Middle Ordovician, Tabuk Group, northern Saudi Arabia. Scale bar is 1 cm. (b) Bedding-plane view of a small specimen showing a complex spiral form and lobes with well-developed marginal tube. Upper Cretaceous, Amden Beds, Fäneren area, Switzerland. Scale bar is 1 cm. See Wetzel (2003). (c) Bedding-plane view of a large specimen showing a simple planar form and lobes with well-developed primary lamellae. Upper Cretaceous, Siliceous Marl, Rzyki, Outer Carpathians, Poland. Scale bar is 1 cm. See Uchman and Gieszkowski (2008a). (d) Bedding-plane view of a large specimen showing a complex spiral form and lobes with well-developed primary lamellae. Note horizontal section of axial shaft (arrow). Upper Cretaceous, Rabot Formation, Rabot Point, James Ross Island, Antarctica. Length of hammer is 33.5 cm. See Buatois *et al.* (1993). (e) Cross-section view of specimen showing axial shaft and successive lobes. Upper Cretaceous, Rabot Formation, Rabot Point, James Ross Island, Antarctica. Lens cap is 5.5 cm. See Buatois *et al.* (1993). (f) Cross-section view of specimen showing successive lobes. Lower Cretaceous, Kotick Point Formation, Kotick Point, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois and Mángano (1992). (g) Cross-section view of specimen in core showing lamina consisting of alternating dark- and light-colored menisci. Lower Cretaceous, Muderong Shale Formation, Pluto Field, Carnavon Basin, offshore Northwestern Australia. Scale bar is 1 cm. (h) Cross-section view of specimen in core showing change in the orientation of the backfilled. Lower Cretaceous, Muderong Shale Formation, Pluto Field, Carnavon Basin, offshore Northwestern Australia. Scale bar is 1 cm.

movement as a response to aggradation and downward burrowing during substrate degradation. Under a rapid increase in sedimentation rate, equilibrium traces grade into escape traces. Vertically oriented, spreite U- or V-shaped burrows represent the typical morphology and are preserved as endichnia structures. The classical example is the vividly named *Diplocraterion yoyo* (Goldring, 1962). *Rosselia socialis*, a vertical fusiform burrow attributed to terebellid polychaetes, is commonly stacked suggesting an equilibrium behavior (Nara, 2002). The bivalve *Panopea* generates equilibrium structures that have been included in the ichnogenus *Scalichnus* (Hanken *et al.*, 2001). The bivalve *Atrina* also produces spectacular equilibrium/adjustment structures by cutting and regenerating its byssum (Carmona *et al.*, 2008) (Fig. 1.16c).

1.4.10 PREDATION TRACES OR PRAEDICHNIA

This category reflects predatory activities. The most common cases are those of borings in hard substrates, such as shells or, less commonly, bones. Round drill holes, gnawings and the chipped margins observed in gastropod and bivalve shells represent typical morphologies. Examples include *Oichnus* and different types of bites and durophagous scars. Predatory holes have also been recorded in the Ediacaran tubular shell *Cloudina* (Bengtsön and Yue, 1992; Hua *et al.*, 2003). Walker and Behrens-Yamada (1993) have even documented structures due to failed predation by crabs in empty gastropod shells. Interestingly, predation by trilobites on worms has been suggested based on ichnological evidence (Bergström, 1973; Jensen, 1990; Brandt *et al.*, 1995). In particular, Jensen (1990) documented examples where the axis of the trilobite trace fossil *Rusophycus dispar* is nearly parallel to the worm burrows. Also, the worm burrows closely follow the curvature of the *Rusophycus dispar* trace and are commonly in contact with only one of its lobes, suggesting active predation. Kramer *et al.* (1995) described trackways of scorpions or spiders (*Octopodichnus*) and insects (*Permichnium*) that abruptly terminate against pelicosaur trackways (*Laoporus*), suggesting predation on arthropods. Modern examples include termite nests that are reworked by myrmecophagous mammals, such as aardvarks and aardwolves (Taylor and Skinner, 2000) (Fig. 1.16d).

1.4.11 NESTING TRACES OR CALICHNIA

Calichnia comprises nests constructed or excavated by the adult insects for breeding purposes (Fig. 1.16e). Insect larvae are confined to cells or chambers that are provisioned by the adults. Nesting traces require specific substrate conditions, particularly with respect to humidity (Genise and Bown, 1994a; Genise *et al.*, 2000). Excessive moisture inside cells leads to the decay of provisions, which are attacked by fungi and other saprobic organisms, whereas insufficient moisture results in the dehydration of larvae, which are not protected by a water-resistant cuticle like adults. Included in calichnia are beetle nests, such as *Coprinisphaera* (Fig. 1.16e) and *Quirogaichnus*, and bee cells (*Celliforma*).

1.4.12 PUPATION CHAMBERS OR PUPICHNIA

Pupichnia consists of structures produced by insects, which mostly live freely in soils or in vegetation, for their protection during pupation (Genise *et al.*, 2007). The same individual that produces the structure, later emerges from it, although in a different developmental stage. Examples include *Fictovichnus*, *Pallichnus*, and *Rebuffoichnus*.

1.4.13 FIXATION/ANCHORING TRACES OR FIXICHNIA

Fixichnia comprises superficial structures formed on hard substrate by sessile epilithic organisms to provide attachment. Two main groups of fixichnia are recognized: those formed by the anchoring of an organism by means of soft parts and those produced by the fixation of its skeleton (Gibert *et al.*, 2004). Examples of fixichnia include *Centrichnus*, *Podichnus*, *Renichnus*, *Stellichnus*, and *Leptichnus*.

1.4.14 BIOCLAUSTRATION STRUCTURES OR IMPEDICHNIA

This category includes structures that record two distinct behaviors during the construction of a cavity in skeletal material (Tapanila, 2005). The resulting structure, referred to as embedment by Bromley (1970) and bioclaustration by Tapanila (2005), is produced by the activity of the endosymbiont that inhibits skeletal accretion of the host and by the host, which alters skeletal growth to accommodate the infesting organism. The bioclaustration structure also serves as a domicile for the endosymbiont. Examples of impedichnia are *Helicosalpinx*, *Tremichnus*, *Chaetosalpinx*, *Hicetes*, *Klemmatoica*, and *Eodiorygma*.

1.4.15 DISCUSSION: COMPLEX TRACES AND EXTENDED ORGANISMS

Undoubtedly, the ethological classification has been extremely successful. As noted by Frey and Pemberton (1985), the classification is intentionally restricted to a small number of categories and proliferation of new ones is not advisable, unless they are well founded. In any case, the more recent additions are valuable because they document behaviors that were not represented in the original Seilacherian scheme. As noted by Genise and Bown (1994a), the fact that the original categories were based almost exclusively on marine ichnotaxa should result in some changes when dealing with behavior peculiar to terrestrial trace fossils.

More recently, some authors suggested that complex trace fossils, such as *Zoophycos*, *Paleodictyon*, and *Phymatoderma*, cannot be accommodated in the traditional classification scheme (Miller, 1998, 2002, 2003). The underlying idea is that these structures have been occupied for long intervals of time and seem to record some sort of active control of the habitat by the tracemaker. In particular, Miller and Vokes (1998) attempted to categorize trace fossils under two main groups: incidental or those that record a single or dominant behavioral activity and deliberate or those that represent restructuring of habitats, modulation of disturbances, and control of food resources. Incidental structures are typically simple, while deliberate structures are complex. These authors advocated a fabricational analysis of trace fossils that involved evaluation of construction, operation, and maintenance of burrow systems. This approach may be framed within the recent view of trace fossils as extended organisms (Turner, 2000, 2003) or the notion of animals as ecosystem engineers (Jones *et al.*, 1994). Although the application of this perspective to the fossil record remains to be tested more extensively, it provides a more active role for the tracemakers rather than a simple passive response to the prevailing environmental conditions (see Section 6.6).

2 Taxonomy of trace fossils

In the final analysis, it is the morphology of the trace as an expression of animal behaviour that is the basis of the name.

Richard Bromley
Trace Fossils: Biology, Taphonomy and Applications (1996)

As ichnologists we must admit that the introduction and discussion of different ichnotaxonomic philosophies reminds us of the inherent subjectivity in any scientific endeavor. Ostensibly the ICZN should constrain such subjective interpretation and bring order to the field. In practice this is difficult, and a certain degree of chaos and ambiguity still reigns. Nonetheless the science progresses, and names, however reliable or controversial, are used for descriptions and dialog between ichnologists.

Martin Lockley
"A tale of two ichnologies: the different goal and potential of invertebrate and vertebrate
(Tetrapod) ichnotaxonomy and how they relate to ichnofacies analysis" (2007)

Although it is not uncommon to find expressions of doubt about the need to use a formal taxonomy to classify trace fossils, ichnotaxonomic classification is an unavoidable companion to preservational and ethological schemes. If a formal name is available, simple descriptors (e.g. vertical burrows and meniscate traces) should be avoided. The ichnotaxonomic classification, albeit imperfect, provides the best common ground on which to base more theoretical elaborations and practical applications (Buatois *et al.*, 2002a). In any case, in modern ichnology contrasting philosophical perspectives have been adopted to classify trace fossils. However, exchange of ideas during and after the 1998, 2002, 2006, and 2010. Workshops on Ichnotaxonomy have resulted in a growing consensus among practicing ichnologists (Bertling *et al.*, 2006). In this chapter, we turn our attention into the theoretical and practical aspects involved in classifying trace fossils from a taxonomic standpoint. We first address some philosophical problems involved in this approach. Then, we focus on a detailed review of the different ichnotaxobases currently in use and the problems associated with compound and composite trace fossils. Subsequent to that, we move on to some recent ideas and proposals with respect to the uses of hierarchies in trace-fossil taxonomy and the peculiarities of vertebrate ichnotaxonomy. Finally, we review some practical aspects involved in the recognition of trace fossils in both outcrops and cores.

2.1 APPROACH AND PHILOSOPHY

As in the case of body-fossil taxonomists, the lumpers and the splitters represent two opposing ways of weighting trace-fossil morphology (Pickerill, 1994). Lumpers tend to cluster all existing forms in a few essential ichnogenera and splitters find visible morphological differences significant enough to create a plethora of new forms. From a philosophical perspective, lumpers are certainly more inferential and splitters are more empirical. Lumpers tend to favor behavior over morphology, trying to define the basic ethology that relates a group of structures, while splitters remain reluctant to make invisible links among apparently dissimilar forms, tending to adopt morphology at face value. This confrontation is a revisitation of the old debate about the roles of observation and theory in science. In our view, it is impossible to adopt a strictly descriptive procedure to name ichnotaxa. Understanding of the behavioral significance, which implies different degrees of interpretation, is necessary. Although there should be a conscious effort to focus on significant morphological details, there is no such a thing as a purely morphological classification. The ichnotaxonomic classification is permeated by our understanding of the ethology.

We fully agree with Bromley (1996, p. 166) that "in the final analysis, it is the morphology of the trace as an expression of animal behaviour that is the basis of the name". To decipher the behavior of the tracemaker, however, may be quite a difficult task. Very frequently, morphology in itself is considered sufficient to define new ichnotaxa, although its ethological meaning is hardly understood. Some morphological features can be objective in the sense of being observable and easily recognizable, and they may still not deserve any consideration at any ichnotaxonomic level. A drastic difference in morphology may actually provide evidence of extrinsic controls, such as the degree of substrate consolidation, rather than behavioral determinants (see Section 6.1.2). As noted by MacNaughton and Pickerill (1995), taphonomy may negatively impact on ichnotaxonomic precision. As quality of preservation decreases, ichnotaxonomic identifications become less reliable. In most cases, taphonomic overprint may artificially increase trace-fossil diversity, although poor preservation may occasionally induce lumping. These authors introduced the notion of taphoseries to refer to ichnotaxa that could potentially be mistaken for each other (see also MacNaughton and Pickerill, 2003). Only morphological characters that are known to reflect significant behavioral traits should be considered (see Section 2.3).

Because ichnofossils are commonly preserved *in situ*, the relationship established between burrowing organisms and their host substrate is so intimate that both components cannot be studied in isolation. The degree of connection between biogenic structures and the substrate is such that even strict taxonomic studies of trace fossils should not be done without a proper analysis of the associated substrate and the idiosyncrasies of trace-fossil taphonomy. An accurate understanding of the environmental conditions under which a trace fossil is created should illuminate our understanding of the biogenic structure, even if those factors are not formally considered in the nomenclature of trace fossils (Goldring *et al.*, 1997). When this guideline is not followed, ichnologists are forced to deal with a large number of poorly defined ichnotaxa whose actual relevance is doubtful. In contrast to standard body-fossil taxonomy, ichnotaxonomy cannot be performed on purely observable morphological grounds. While morphology is observed, behavior must be inferred. The degree of behavioral inference varies with each particular case. For example, in the simplest case, there is almost a continuum from the morphological observation of clearly preserved ventral anatomic features to the interpretation of a trace as a resting structure (e.g. Mángano *et al.*, 1997). However, analysis of most trace fossils requires a larger inferential jump, involving knowledge of a complex array of biological, taphonomic, and environmental determinants.

Advantages of a dual nomenclature (i.e. two separate names for biotaxa and ichnotaxa) as well as the risks involved in the biotaxonomic identification of the tracemaker have been stressed by Bromley (1990, 1996) and Bertling *et al.* (2006). Attempts to avoid this approach (e.g. Dzik, 2005) create a large number of problems and give the false impression that a particular trace fossil can be directly linked to a producer [e.g. *Treptichnus* (*Mankyodes*) *rectangularis* invariably to priapulids]. In most cases behavioral convergence rules out establishing a one-to-one relationship between a producer and a trace fossil (see Section 1.2.3). The idea of replacing ichnotaxonomic names with vernacular names, such as “a trail of a worm on the sediment surface” (Dzik, 2005, p. 519) is impractical and represents a step backwards in ichnological practice and communicability. Besides, one is tempted to ask “Was the trail actually produced by a worm?” and “Was it really produced *on* the sediment surface?” In soft substrates, some arthropods can leave a smooth trail undistinguishable from a worm trail (Mángano *et al.*, 1996a; Davis *et al.*, 2007). In addition, very few trace fossils actually represent the work of an animal moving on the sediment surface (i.e. epigenic); most of them record infaunal activities (i.e. endogenic).

Another complication results from the inclusion of the actual taxonomic identification of the tracemaker as an essential component of naming trace fossils (e.g. Hasiotis and Bown, 1992). In the same vein, introduction of an environmentally based ichnotaxonomy is problematic at best (Hasiotis and Bown, 1992; Hasiotis, 2002). As noted by Buatois *et al.* (1997a), if biological or sedimentological criteria are applied to ichnotaxonomy, it will be virtually impossible to escape from circular reasoning when using trace fossils as an aid to interpret ancient depositional environments. If *Isopodichnus* is named simply because it is present in continental red beds, it is tricky to use its occurrence as an evidence of continental deposition. The establishment of parallel ichnotaxonomic systems for marine, transitional, and continental ichnology proposed by Hasiotis and Bown (1992, p. 71) creates further problems. It is hard to provide a rationale that supports the idea of the same crustacean burrow receiving different names in brackish and fully marine settings. If we restrict *Ophiomorpha* for fully marine environments, which name do we have to use for the same decapod burrow emplaced in the landward side of the barrier island facing the brackish-water lagoon? Such a taxonomic system undercuts the information potential of trace fossils in sedimentology, stratigraphy, and paleoecology (Buatois *et al.*, 1997a).

Maintaining the dual nomenclature certainly does not imply that biology does not play a significant role in trace-fossil taxonomy. We strongly advocate a more active role for biology in ichnotaxonomy. Biology provides the “blood” that enlightens the functional-morphology analysis of trace fossils. Although the detailed biology of the producers may remain unknown, understanding the bauplan and biological affinities of the tracemakers is essential. Constructional possibilities are determined by intrinsic biological factors and, therefore, should be helpful in evaluating the relative significance of behavioral traits as reflected by trace-fossil morphology (Mángano *et al.*, 2002a). In this sense, the biology of the tracemaker ends up playing a role, albeit indirect, in trace-fossil taxonomy. An adequate ethological interpretation of a morphological feature is impossible without this biological framework.

2.2 SOME PROBLEMS AND PRACTICAL GUIDELINES

The problems that the practicing ichnologists should face result both from historical contingencies, and the intrinsic nature of ichnofossils. Among the historic factors, a large number of ichnotaxa, some of those of widespread use, were introduced during the nineteenth century when trace fossils were still regarded either as animal or plant body fossils (the so-called Age of Fucoids; Osgood, 1975). In accordance, the original diagnosis and descriptions of some of the most representative ichnotaxa include a plethora of zoological and botanical terms to name the morphological elements of these biogenic structures (D’Alessandro and Bromley, 1987; Bromley, 1990, 1996). Another historical peculiarity derives from the fact that the 1964 edition of the International Code of Zoological Nomenclature (ICZN) established that trace-fossil names defined after 1930 should be accompanied by a statement on the identification of the tracemakers. Because fulfilling that requisite was virtually impossible, in practice, post-1930 ichnotaxa became unavailable marking the beginning of what has been referred to as the “Dark Age of Ichnotaxonomy” (Bromley, 1990, 1996). Fortunately, most ichnologists decided to keep a reasonable degree of order and treated valid and invalid ichnotaxa in the same way (Häntzschel, 1975). The requirement of identifying the producer was subsequently eliminated and trace fossils are now bounded by the ICZN.

In addition, ichnotaxa have been introduced frequently in a rather chaotic and careless way. Some ichnotaxa have been poorly diagnosed or illustrated, based on scarce or fragmentary material, or insufficiently compared with similar forms. Taxonomic revisions are extremely useful, but usually cannot keep pace with newly introduced forms. Proliferation of new ichnotaxa based on superfluous features, characteristics of uncertain ethological significance, and poorly preserved or scarce specimens should be avoided. As noted by Bertling *et al*. (2006), trackways are particularly problematic because they are commonly represented by blurred or morphologically deviating undertracks or overtracks. Accordingly, only complete tracks should be used as a basis for establishing an ichnotaxon (see also Minter *et al*., 2007a).

If possible, ichnotaxa should be classified at ichnospecific level to avoid losing potential information (Pemberton and Frey, 1982). However, in some cases, the quality of preservation precludes ichnospecific assignments. In other cases, confusion persists with respect to which criteria should be adopted to classify certain ichnogenera at ichnospecific level (e.g. *Zoophycos*). Open nomenclature (i.e. the use of "cf.", "aff.", and "?") may be used in some cases (Bertling *et al*., 2006). Detailed procedures for the establishment of new ichnotaxa were outlined by Pickerill (1994).

The fact that trace fossils have their own peculiarities that mark significant departures with respect to body fossils (see Section 1.2) further complicates trace-fossil taxonomy. It is fair to say that ichnotaxonomy has all of the problems of body-fossil taxonomy plus their own. The ICZN established that only fossil specimens should be named, and this rule certainly prevents ichnologists dealing with a plethora of ichnotaxa based on recent examples that only have very minor chances of being preserved in the fossil record. One of the underlying reasons is that it is commonly assumed that modern traces can be assigned to their producers on a case-by-case basis. However, continuous attempts to capture the elusive *Paleodictyon* producer demonstrate that this is not always the case (Rona *et al*., 2009). Identification and collection of modern traces, particularly those produced in unconsolidated substrates, are commonly much more difficult than with fossil material. Trace fossils are usually enhanced by diagenetic processes that assist in their recognition (Magwood, 1992). Most important, many biogenic structures are in fact cumulative structures, which consist of both abandoned and active components (Bromley and Frey, 1974). Casts of modern cumulative structures only reflect the morphology of the open components that are actively occupied by the producer, resulting in a simpler pattern than the actual overall architecture (Frey, 1975; Frey and Seilacher, 1980; Magwood, 1992).

However, this ICZN regulation has its problems. Unlike body fossils, the boundary between recent and fossil traces may be, on occasion, quite uncertain (Bromley, 1990, 1996; Bertling *et al*., 2006). For example, ambiguous situations result from the uncertain status of modern borings (which may be considered fossils as soon as their producers die) and from modern burrows excavated in Pleistocene sediments (Bertling *et al*., 2006). The fact that some modern traces are identical to well-established trace fossils has led some ichnologists to refer them to the corresponding ichnotaxa (e.g. Ekdale, 1980; Wetzel, 1984; Gaillard, 1988). Some authors prefer to follow the code and name the producer in connection with the biogenic structure (e.g. burrows of *Upogebia pugittensis*) (Rindsberg, 1990a), while others opt for using the prefix "incipient" before the ichnotaxon (e.g. incipient *Thalassinoides*) (Bromley and Fürsich, 1980). In short, although discrepancies exist with respect to dealing with modern biogenic structures, there is general agreement that ichnotaxa should not be constructed on the basis modern material (Bromley, 1990, 1996; Magwood, 1992; Pickerill, 1994; Bertling *et al*., 2006).

Another distinction, which may be occasionally problematic, is that between body fossils and trace fossils. For example, bivalve internal moulds (*steinkerns*) may be associated with the resting trace *Lockeia*. In other cases, ornamented bivalve resting traces resembling body fossils are connected to the locomotion trace *Protovirgularia*. However, careful examination of the chevron orientation in *Protovirgularia* indicates that the animal exited the resting structure (e.g. Mángano *et al*., 1998). Albeit similar to body fossils, these structures should be regarded as trace fossils. Distinction between plug-shaped burrows and body fossils of ceriantid or actinarian anemones has been historically problematic particularly with Ediacaran specimens (Jensen, 2003; Seilacher *et al*., 2005). In particular, the ichnogenera *Bergaueria* may be difficult to distinguish from the body fossils *Beltanellifomis* and *Beltanelloides* (e.g. Crimes and Germs, 1982; Fedonkin, 1985; Crimes, 1992; Crimes and Fedonkin, 1996; Jensen, 2003); and the ring-like structure *Intrites* has alternately been regarded as a trace fossil and a body fossil (Fedonkin, 1985; Crimes, 1994; Gehling *et al*., 2000; Jensen, 2003).

2.3 ICHNOTAXOBASES

Bromley (1990, 1996) noted that very little has been written on the characters that should be used to classify trace fossils. In an attempt to shed light on these issues, he introduced the concept of ichnotaxobases. An ichnotaxobase is a distinctive morphological feature of a trace fossil that displays significant and readily detectable variability and, therefore, is commonly used in ichnotaxonomic classifications (Bromley, 1990, 1996; Buatois *et al*., 2002a). Both requirements should be met. Morphological variability should reflect behavioral functions, therefore illuminating our ethological interpretation of a trace fossil. Additionally, an ichnotaxobase should be easily detectable in the sense of allowing uncontroversial identification. Five main ichnotaxobases (general form, wall and lining, branching, fill, and presence or absence of spreite) are discussed here. It should be noted, however, that each of these ichnotaxobases cannot be applied to every group of trace fossils. Arthropod trackways, insect nests, and vertebrate burrows or trackways, commonly pose their own problems to the ichnotaxonomist. For example, Laza (2006) illustrated the significance of the presence and position of the small egg chamber with respect to the large provision chamber in the taxonomy of dung-beetle nests.

In theory, those features that relate to major behavioral aspects should be used to differentiate ichnogenera, while those of lower significance should be applied for ichnospecies (Fürsich, 1974; Pemberton and Frey, 1982; Bromley, 1990, 1996; Bertling *et al*., 2006). In practice, to determine which characters are of main significance is not always straightforward. Characters that are rejected as useful ichnotaxobases are size, producer, type of passive fill, substrate consistency, geological age, geographic location, facies-environment, and any preservational aspect (Magwood, 1992; Pickerill, 1994; Bertling *et al*., 2006). The role of substrate as an ichnotaxobase remains controversial (see Section 2.7). Bertling *et al*. (2006) suggested keeping separate trace fossils formed in lithic, woody, and soft substrates regardless of morphological similarity, but at the same time cautioned against naming a new ichnotaxon based solely on a difference in substrate (see also Carmona *et al*., 2007). Taphonomy also plays a major role because, unfortunately, potentially useful ichnotaxobases may, in some cases, have lower preservation potential.

2.3.1 GENERAL FORM

The general form of a trace fossil represents its basic morphological plan and includes configuration, orientation, and position with respect to stratification (Pickerill, 1994) (Fig. 2.1a–c). Configuration is determined by the spatial arrangements of the trace components and reveals what is usually visualized, at first sight, as a whole (*gestalt*). Examples of descriptors for configuration are hexagonal networks (*Paleodictyon*), meandering traces displaying two orders of meanders (*Cosmorhaphe*), and simple sinusoidal trails (*Cochlichnus*). In these examples, ichnogeneric classification is based essentially on their distinctive configuration. Orientation (e.g. vertical, inclined, or horizontal), and position with respect to stratification or toponomy (e.g. positive hyporeliefs and negative epireliefs; see Section 1.3.1) are also first-order ichnotaxobases that help to classify biogenic structures at the ichnogeneric level. For example, *Rhizocorallium* and *Diplocraterion* share the same configuration (i.e. U-shaped burrows), but differ in their orientation, predominantly horizontal for the former and vertical for the latter. Other structures are essentially similar with respect to their basic configuration and orientation, but differ in stratal position. Examples are some horizontal bilobate trails, such as *Didymaulichnus* (positive hyporelief) and *Gyrochorte* (positive epirelief). In this case, stratal position reflects a completely different mode of construction. Although size may influence our perception of a structure, it should not be considered as a first-rank character, and is certainly a weak ichnotaxobase. However, size has been used in some cases to differentiate ichnospecies substantiated by significant statistical analysis, as illustrated with *Paleodictyon* (Uchman, 1995). Ontogenetic variations should be carefully evaluated (Pickerill, 1994). Bertling *et al.* (2006) expressed their reluctance to use size at the ichnospecies rank, and totally reject it at higher ranks.

2.3.2 WALL AND LINING

Bioturbation results in changes in the sediment and formation of burrow mottlings and discrete structures with different degrees of definition, depending on their function and substrate consistency. For example, a trace that serves as a semipermanent domicile implies certain constructional traits (e.g. burrow lining) that are not present in a trace that reflects a simple incursion through the sediment by a vagile organism (intrusion *sensu* Bromley, 1990, 1996). In particular, details on burrow walls can reveal significant information on trophic type, burrowing technique, and biological affinity (Bromley, 1990, 1996; Ekdale and Gibert, 2010). However, some aspects of the burrow wall lack ichnotaxonomic significance. Although diagenetic haloes may be rather spectacular, they are related to the diagenetic history of the structure rather than animal behavior (Bromley, 1990, 1996). In contrast, more subtle constructional features of burrow walls serve as ichnotaxobases.

Two main components are represented in a wall, internal lining and external deformation in the host sediment (Bromley, 1990, 1996). This author recognized seven main types of walls based on linings, ornamentation, and manipulation of sediment by the organism (Box 2.1): unlined walls (Fig. 2.2a), dust films

Figure 2.1 Examples of general form, illustrating combinations of configuration, orientation, and preservation (a) *Helminthorhaphe* isp., horizontal guided meanders preserved as positive hyporelief. Eocene, Hecho Group, Huesca, Spanish Pyrenees. See Uchman (2001). (b) *Gyrochorte* isp, horizontal biblobate trail preserved as positive epirelief. Upper Cretaceous, Kennilworth Member, Blackhawk Formation, south entrance to Tusher Canyon, Book Cliffs, Utah, United States. (c) *Gyrolithes* isp., Lower Miocene, contact between the Lower Freshwater Molasse and the Upper Marine Molasse, Kobel, St. Gallen area, Switzerland. See Heer (1865) and Wetzel *et al.* (2010). Scale bars are 1 cm.

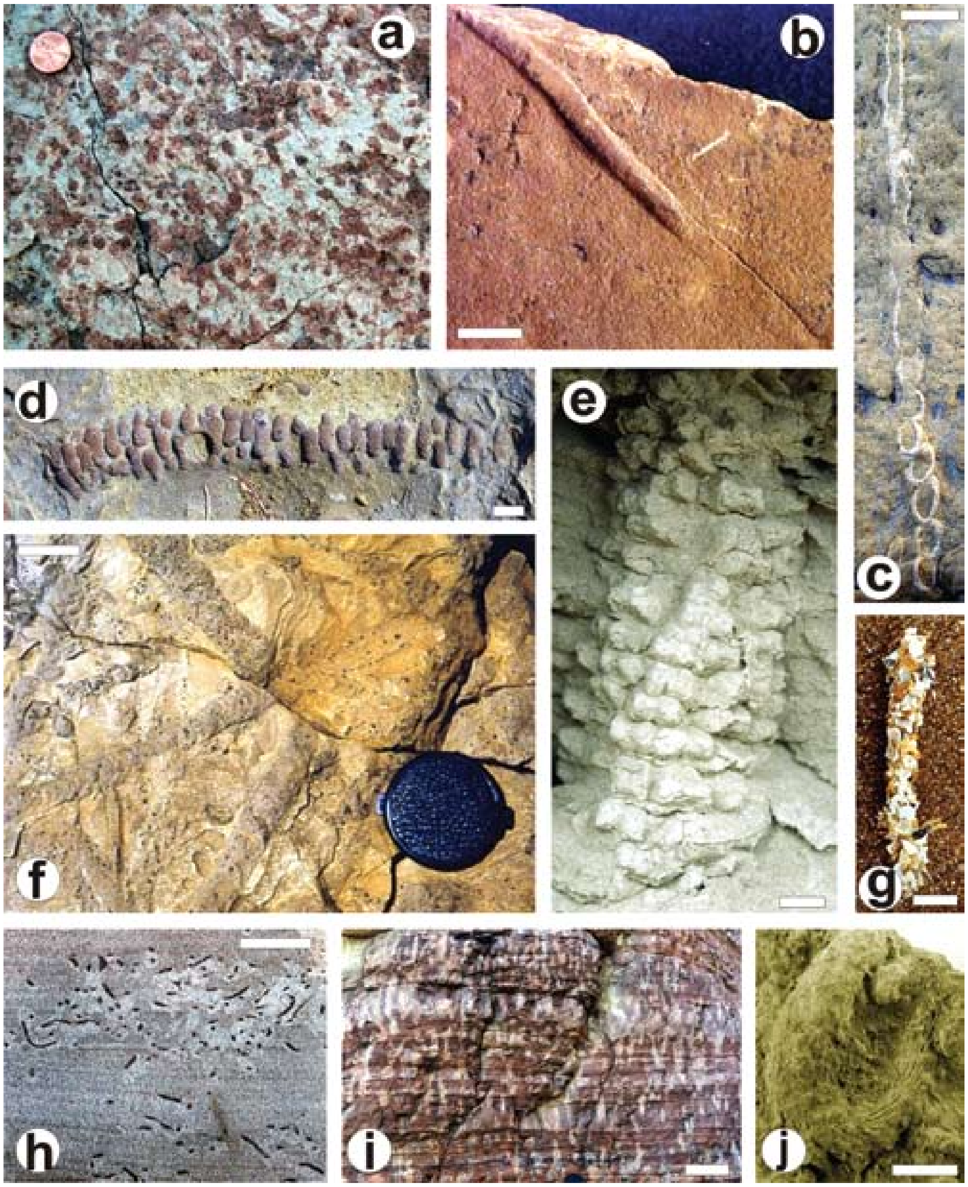


Figure 2.2 Types of walls. (a) Unlined wall in *Planolites montanus*. Upper Carboniferous, El Cobre Canyon Formation, El Cobre Canyon, New Mexico, United States. Coin is 1.9 cm. (b) Thin dust film in *Palaeophycus tubularis*. Permian, De la Cuesta Formation, Los Colorados de Patquía, La Rioja Province, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (2004a). (c) Thick dust film in *Schaubcylindrichnus coronus*. Upper Cretaceous, Panther Tongue Member, Star Point Formation, Kennilworth Wash, Book Cliffs, Utah, United States. Scale bar is 1 cm. (d) Constructional lining with pellets arranged in transverse rows forming relatively continuous rings or annulations in *Ophiomorpha annulata*. Upper Miocene to Lower Pliocene, La Vela Formation, Quebrada el Muaco, La Vela de Coro, northwestern Venezuela. Scale bar is 1 cm. (e) Constructional lining with bilobate pellets in *Ophiomorpha borneensis*. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Chubut Province, Patagonia, southern Argentina. Scale bar is 1 cm. See Scasso and Bellosi (2004). (f) Constructional lining with orbitoid forams. Middle Eocene, Punta Carnero Formation, Airport, Margarita Island, Venezuela. Lens cap is 5.5 cm. (g) Constructional lining with shell material in a modern *Diopatra cuprea*. Gower Peninsula, Wales. Scale bar is 1 cm. (h) Zoned fill characterized by a pale mantle surrounding a dark core in *Phycosiphon incertum*. Lower Jurassic, Plover Formation, Sunrise–Troubadour Field, East Timor Sea, northern Australia. Scale bar is 1 cm. (i) Diagenetic oxidation haloes in *Skolithos linearis* forming a pipe rock. Lower to Middle Cambrian, Campanario Formation, Mesón Group, Maimará, northwest Argentina. Scale bar is 10 cm. See Mángano and Buatois (2004b). (j) Wall ornament of *Fuersichnus striatus* characterized by a powerful bioglyph. Upper Cretaceous, Hidden Lake Formation, Brandy Bay, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois (1995).

(Fig. 2.2b–c), constructional linings (Fig. 2.2d–g), zoned fills (Fig. 2.2h), wall compaction, diagenetic haloes (Fig. 2.2i), and wall ornament (Fig. 2.2j). Bioglyphs, engravings in the ornamented walls of burrows or borings, result from various activities of the tracemaker, including scratching, drilling, plucking, gnawing, poking, and etching (Ekdale and Gibert, 2010). Bertling *et al*. (2006) noted that surface features (sculpture) usually play a secondary role, and are diagnostic mostly at the ichnospecific level. However, surface features and micromorphological characters may be of higher ichnotaxonomic significance in insect nests (Genise and Hazeldine, 1998; Cosarinsky, 2003; Genise, 2004).

2.3.3 BRANCHING

Presence and type of branching are commonly first-rank ichnotaxobases. Three main types of branching are recognized: secondary successive, primary successive, and simultaneous (Bromley and Frey, 1974; D'Alessandro and Bromley, 1987; Bromley, 1990, 1996). The so-called "false branching" simply consists of overlap between two specimens giving the false impression of branching. Secondary successive branching results from an animal that revisits a previously formed structure (Fig. 2.3a). Primary successive branching is a cumulative structure formed by successive probings and implies a series of movements by the producer, such as rotating and moving back and forth

Box 2.1 Types of wall

Seven main types of walls are commonly recognized:

- Unlined walls: The burrow fill abuts against the enclosing sediment at a clean discontinuity surface (Fig. 2.2a). Examples: *Planolites*, *Taenidium.*
- Dust films: The burrow is lined with mucus, introducing dust that adheres on the wall. Linings may be thin (Fig. 2.2b) to thick (Fig. 2.2c). Examples: *Palaeophycus, Schaubcylindrichnus*.
- Constructional linings: The burrow wall is constructed with sediment and special grains. Building materials include sediment pellets of various shapes (Fig. 2.2d–e) and shell fragments (Fig. 2.2f–g). Examples: *Ophiomorpha, Diopatrichnus*.
- Zoned fills: The apparent burrow lining is in fact the outermost layer of a concentrically zoned fill resulting from deposit feeding (Fig. 2.2h). Examples: *Ancorichnus*, *Phycosiphon*.
- Wall compaction: The wall is bounded by an external zone showing disturbance as a result of burrowing.
- Diagenetic haloes: The burrow wall has been affected by special diagenesis, enhancing visibility of the structure (Fig. 2.2i). Examples: *Bathichnus*, some specimens of *Thalassinoides* and *Skolithos*.
- Wall ornament: Walls are characterized by bioglyphs (Fig. 2.2j). Examples: *Spongeliomorpha*, *Scoyenia*.

Reference: Bromley (1990, 1996).

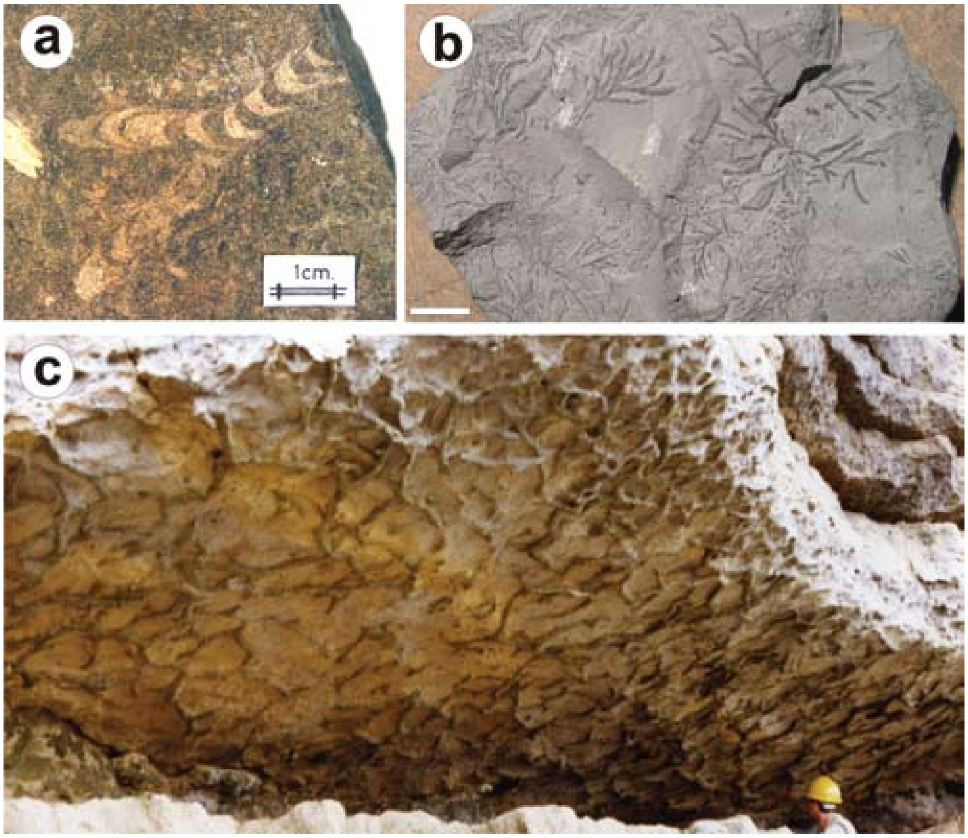


Figure 2.3 Types of branching (a) Secondary successive branching. *Taenidium* isp. Upper Cretaceous, Santa Marta Formation, Santa Marta Cove, James Ross Island, Antarctica. Scale bar is 1 cm. See Scasso *et al.* (1991). (b) Primary successive branching. *Chondrites arbuscula*. Upper Cretaceous, Rhenodanubian Flysch, Voralpen, Austria. Scale bar is 1 cm. See Uchman (1999). (c) Simultaneous branching. Burrow systems assigned to the ichnospecies *Thalassinoides suevicus*. Upper Jurassic, Coralline Oolite Formation, Filey Brigg, North Yorkshire Coast, England. Person for a scale on the lower right. See Fürsich (1972).

(Fig. 2.3b). Simultaneous branching is represented by open passages in permanent or semipermanent domiciles, such as in galleries constructed by crustaceans (Fig. 2.3c).

2.3.4 FILL

Fills can be classified into two main categories: passive and active (Box 2.2). Such distinction, and the type of active fill are first-rank ichnotaxobases because they reveal information on trophic types and feeding strategies. On the other hand, the type of passive fill may provide sedimentological and sequence-stratigraphical information (see Section 12.2) rather than ethology and, therefore, should not be used as an ichnotaxobase (Bromley, 1990, 1996).

Passive fill results from material entering the burrow gravitationally, and mostly characterizes the dwelling structures of suspension feeders and predators. Different types of passive

Box 2.2 Types of burrow fill

Passive and active fill are the two major categories of burrow fill. While passive fill enters the burrow gravitationally, active fill is emplaced by the burrower. In turn, these two major categories are subdivided into many other types.

- Passive massive fill similar to the host sediment: Material from the host sediment is introduced gravitationally into the burrow (Fig. 2.4a). It is a common type of burrow fill in open gallery systems. Example: *Palaeophycus*.
- Passive massive fill contrasting with the host sediment: Material from an overlying layer, typically coarser-grained, is introduced gravitationally into the burrow (Fig. 2.4b). This is also known as bed-junction preservation (Simpson, 1957) (see Section 1.3.1). It is typical of open burrows formed at discontinuity surfaces. Example: Firmground *Thalassinoides*.
- Passive laminated fills: Lamination results from sedimentation within the burrow (Fig. 2.4c). An example of passive laminated fills is tubular tidalites, which consist of rhythmically bedded alternating layers of fine-grained and coarse-grained laminae deposited within open burrows resulting from tidal action (Gingras, 2008). Examples: *Thalassinoides, Ophiomorpha*.
- Draught fill canals: Laminated fill in open burrows having a narrow entrance (Seilacher, 1968) (Fig. 2.4d). The narrow draught canal may be confused with a burrow itself reworking the fill of the larger. Example: *Thalassinoides.*
- Irregularly concentric fills: Intermediate between passive and active because the structure results from gravitation, and sediment manipulation by the animal (Goldring, 1996).
- Active massive fill: Structureless fill typically contrasting with the host sediment, resulting from mechanical manipulation or ingestion (Fig. 2.4e). It may be pelleted. Examples: *Planolites, Macaronichnus*.
- Active meniscate fill: Fill forming a characteristic structure, commonly packed as backfill meniscae, resulting from mechanic manipulation or ingestion (Fig. 2.4f). Examples: *Scolicia, Taenidium*.
- Active concentric fill: (both simple or multiple): Burrow fill formed by concentric alternating layers of contrasting material (Fig. 2.4g). Examples: *Rosselia*, *Cylindrichnus*, *Asterosoma.*

Reference: Bromley (1990, 1996).

fills are recognized, including massive fills similar to the host sediment (Fig. 2.4a), massive fills contrasting with the host sediment (Fig. 2.4b), laminated fills (Fig. 2.4c), and draught fill canals (Fig. 2.4d) (Seilacher, 1968; Bromley, 1990, 1996; Goldring, 1996; Buatois *et al*., 2002a). Irregularly concentric fills are intermediate between passive and active because the structure results from gravitation and sediment manipulation by the animal (Goldring, 1996).

Active fill implies active manipulation of material by the animal, and commonly results in lithological contrasts between the trace and the host sediment. Most commonly, active fill is produced by deposit and detritus feeders. Different types of active infill include massive fill (Fig. 2.4e), meniscate fill (resulting from mechanic manipulation or ingestion) (Fig. 2.4f), and concentric (both simple or multiple) (Fig. 2.4g).

2.3.5 SPREITE

Spreite refers to a lamination that results from closely spaced successive tunnel walls formed by the lateral shifting of a burrow (Bromley, 1990, 1996). Presence of spreite reveals either the ability of an animal to adjust its burrow as a response to instability at the sediment–water interface or to actively mine in search for food (Figs. 2.5, 2.6a–b, and 2.7). Its presence is useful as an ichnogeneric ichnotaxobase. The classic example is the distinction between the U-shaped burrows *Diplocraterion* (with spreite) (Fig. 2.6a) and *Arenicolites* (without spreite) (Fig. 2.6b).

Two types of spreite are recognized, protrusive and retrusive. Protrusive spreite is formed due to distalward movements (i.e. away from the apertures), while retrusive spreite is produced by proximalward movements (i.e. toward the apertures) (Bromley, 1990, 1996) (Fig. 2.5). Careful analysis of the spreite may be useful in ichnotaxonomy of feeding structures (Fig. 2.7) both at ichnogeneric (e.g. *Lophoctenium*, *Zoophycos*, *Teichichnus*, *Phycosiphon*, and *Oldhamia*) and ichnospecific (*Oldhamia alata* and *O. geniculata*) levels. However, the type of spreite is of no use at all for the ichnotaxonomy of equilibrium traces. In this latter case, a retrusive spreite reflects upward burrow migration as a response to increased sedimentation rate, while a protrusive spreite records downward burrow migration resulting from decreased sedimentation or slight erosion. Although of use for paleoenvironmental reconstructions (Goldring, 1964), its value in ichnotaxonomy is limited in this situation (Bromley, 1990, 1996).

2.4 COMPOUND AND COMPOSITE TRACE FOSSILS

2.4.1 COMPOUND TRACE FOSSILS

Another peculiarity of trace-fossil taxonomy is the presence of compound and composite trace fossils (Pickerill, 1994; Pickerill and Narbonne, 1995). Compound trace fossils result from the changing behavior of a single producer, and can represent two different situations: successive or simultaneous formation (Bertling *et al*., 2006) (Fig. 2.8). More commonly, the tracemaker behaves in distinct ways in chronological order, comprising intergradations of one ichnotaxon into another one either at ichnogeneric or ichnospecific level (see Section 1.2.2). The typical example is the transition between locomotion and resting

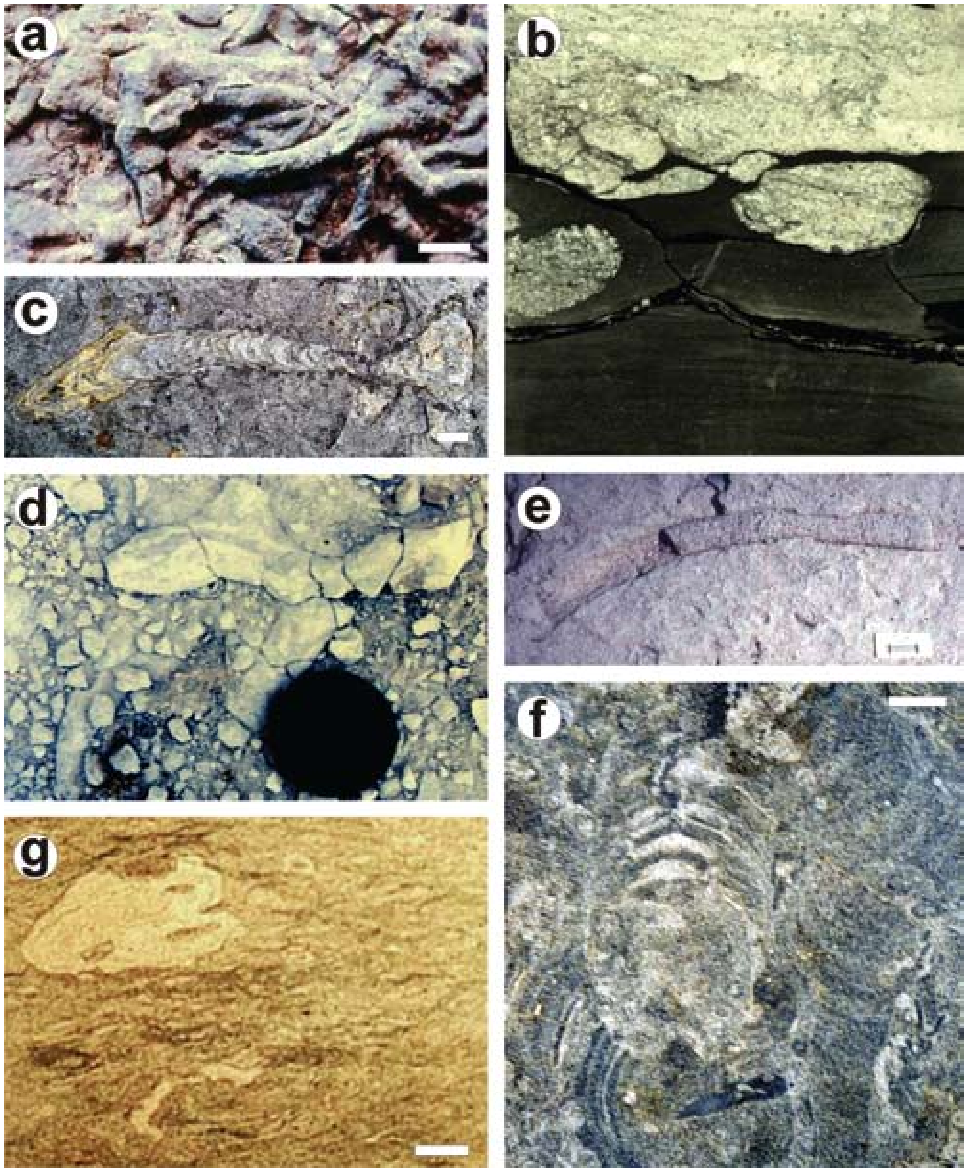


Figure 2.4 Different types of burrow fills. (a) Passive massive fill similar to the host sediment in *Palaeophycus tubularis*. Upper Cambrian, Pico de Halcón Member, Santa Rosita Formation, Quebrada del Salto Alto, Purmamarca, northwest Argentina. Scale bar is 1 cm. See Mángano *et al.* (1996b). (b) Passive massive fill contrasting with the host sediment in firmground *Thalassinoides*. Contact between the Upper Cretaceous Burguita Formation and the Middle Eocene Gobernador Formation, Caipe Field, Barinas Basin, western Venezuela. Core width is 8 cm. (c) Passive laminated fill in *Ophiomorpha nodosa*. Cretaceous, Quiriquina Formation, Cocholgüe, Chile. Scale bar is 1 cm. See Buatois and Encinas (2011). (d) *Thalassinoides suevicus* with draught fill canal Upper Cretaceous, Gramame Formation, Poty Quarry, northeast of Olinda, northeast Brazil. Lens cap is 5.5 cm. (e) Active massive fill illustrated by *Planolites beverleyensis*. Upper Carboniferous, Malanzán Formation, Cuestita de la Herradura, La Rioja Province, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (1995a). (f) Active meniscate fill resulting from ingestion in *Scolicia* isp Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, southern Argentina. Scale bar is 1 cm. See Carmona *et al.* (2008). (g) Active multiple concentric fill in *Asterosoma* isp. Lower Miocene, Oficina Formation, Oritupano field, Eastern Venezuela Basin. Scale bar is 1 cm.

traces, such as trilobite locomotion traces (*Cruziana*) and resting traces (*Rusophycus*) (Crimes, 1970a; Mángano *et al*., 1996b), and bivalve locomotion traces (*Protovirgularia*) and resting traces (*Lockeia*) (Mángano *et al*., 1998). Other ethological categories may be involved, such as transitions between the echinoid grazing trace *Scolicia* and its resting counterpart *Cardioichnus* (Smith and Crimes, 1983) (Fig. 2.8). In other instances, intergradations may occur within an ethological category as illustrated by crustacean dwelling burrows, such as *Ophiomorpha*, *Thalassinoides*, and *Gyrolithes* (Bromley and Frey, 1974; Muñiz *et al*., 1995). Typical examples at ichnospecific and ichnosubspecies levels are shown by transitions between trilobite trace fossils, such as *C. rugosa furcifera* and *C. rugosa rugosa*.

Bertling *et al*. (2006) noted that these compound structures pose two problems in ichnotaxonomy if methods of biological taxonomy are applied: (1) an exceptional intergradation of ichnotaxa that are normally found separately would imply synonymization in all other occurrences, leading to invalidation of at least one established ichnotaxon, and (2) if the constituents of a normally compound ichnotaxon are found separately, they would have to be named differently, as they form discrete trace fossils. However, following procedures of biological taxonomy is not advisable here. The standard practice with compound specimens is to name the whole structure for its predominant component, taking careful note of the intergradations (Pickerill, 1994; Pickerill and Narbonne, 1995).

Another situation results when the producer may simultaneously behave in various distinct ways. For example, Bromley *et al*. (2003) documented the trace fossil of a bivalve that used its foot to dig into the substrate and its siphons to collect food. A collective name, *Hillichnus*, was given in this case (Fig. 2.8). Most of these simultaneously produced compound trace fossils are complex trace fossils (*sensu* Miller, 1998, 2002, 2003) (see Section 1.4.15). However, not all complex trace fossils are

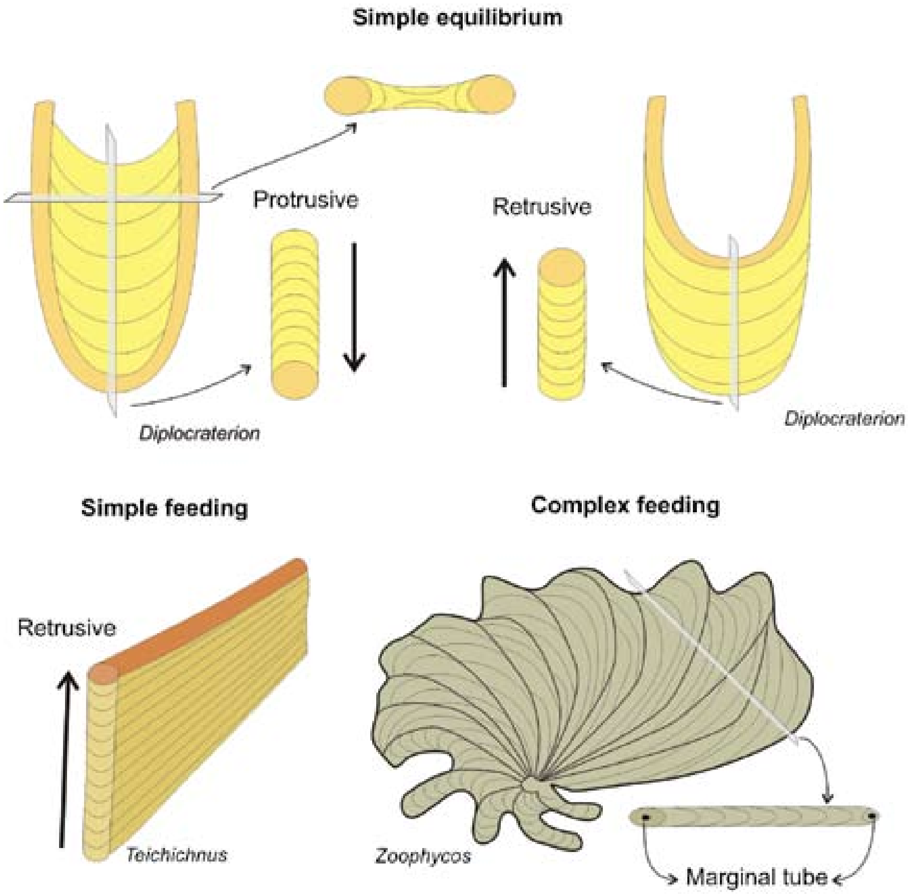


Figure 2.5 Types of spreite. In equilibrium structures the spreite reveals the ability of an animal to adjust its burrow as a response to instability at the sediment–water interface, while in feeding structures the spreite reflects an organism actively mining in search for food.

Figure 2.6 Use of spreite to differentiate U-shaped trace fossils. (a) Spreite in *Diplocraterion parallelum*. Lower Cambrian, Dividalen Group, Imobekken, northern Norway. See Bromley and Hanken (1991). (b) Absence of spreite in *Arenicolites*. Lower to Middle Cambrian, Hanneh Member, Burj Formation, Dead Sea, Jordan. Scale bars are 1 cm.

compound structures, because although more than one behavior is involved, discrete components cannot be identified, and some behaviors may not be strictly simultaneous. Bertling *et al*. (2006) stated that if these compound superstructures mirror a recurrent pattern of behavior, then they deserve their own name, as illustrated by *Hillichnus*.

2.4.2 COMPOSITE TRACE FOSSILS

Composite trace fossils apparently comprise a single system, but actually result from the interpenetration of discrete ichnotaxa (Pickerill, 1994; Pickerill and Narbonne, 1995) (see Section 1.2.4) (Fig. 2.8). A typical example is a structure that was referred to as *Mixoteichichnus* by Müller (1966), but that, in fact, consists of a specimen of *Teichichnus* intersected by *Planolites* (Pemberton and Frey, 1982). Common examples are discrete feeding or dwelling traces (e.g. *Thalassinoides*, *Diplocraterion*, *Gyrolithes*, and *Cladichnus*) that are reworked by *Chondrites* or *Phycosiphon* (e.g. Bromley and Frey, 1974; Ekdale and Bromley, 1991; Buatois and Mángano, 1992) (Fig. 2.8). In some cases, a high concentration of trace fossils reworking a burrow helps to delineate the previously emplaced structure ("phantom"

Figure 2.7 Feeding spreite in long specimens of *Rhizocorallium irregulare*. Upper Jurassic, Lastres Formation, cliffs west of Playa de España, Quintes, Villaviciosa, Asturias, northern Spain. Scale bar is 5 cm.

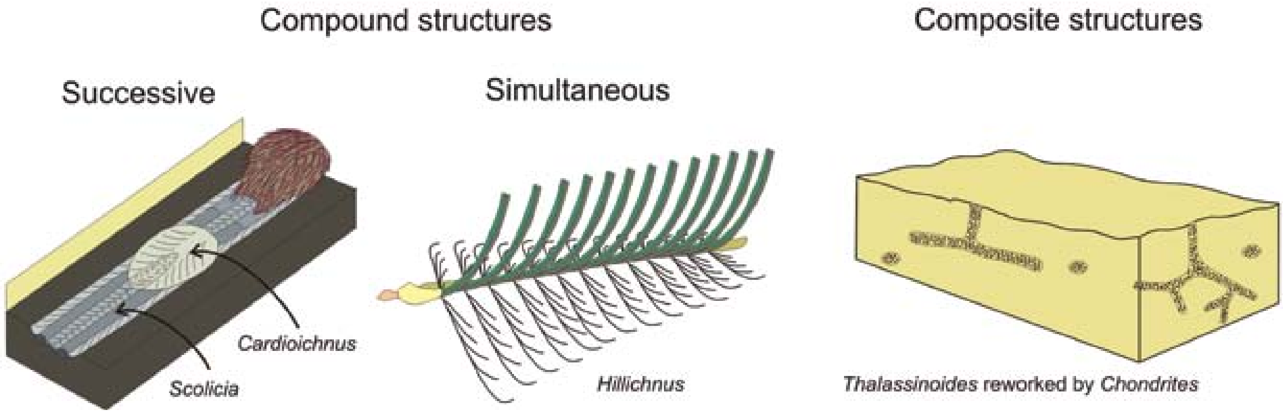


Figure 2.8. Examples of compound (successive and simultaneous) and composite trace fossils.

burrow) that otherwise would have remained undetected. Wood fragments with *Teredolites* enclosing sand-lined tubes produced by sabellariid polychaetes represent another example (Miller, 1996). The feeding trace *Piscichnus* excavated by rays, and reworked by polychaetes (producers of *Macaronichnus*) also illustrates a composite structure (Kotake, 2007). In the realm of paleosol insect trace fossils, composite structures seem to be very common as illustrated by beetle nests (*Monesichnus ameghinoi*) that have been reworked by cleptoparasites, which in turn produced open galleries (Genise and Laza, 1998). Composite structures should not be named as a whole. Rather, discrete components should be named separately (Pickerill, 1994; Pickerill and Narbonne, 1995; Bertling *et al.*, 2006).

2.5 HIERARCHIES IN ICHNOTAXONOMY

Although trace fossils are different from body fossils, the classical binominal scheme has been adopted. In contrast to body fossils, however, the terms ichnogenera (ichnogen. or igen.) and ichnospecies (ichnosp. or isp.) are used to make clear that the entity is a trace fossil rather than a body fossil. Traditionally ichnologists have treated trace fossils at these two main hierarchical levels. However, in recent years, it has become increasingly clear that additional categories may be of use (Buatois *et al.*, 2002a) and a growing consensus is building in support of their importance (Bertling *et al.*, 2006). In fact, ichnofamilies are formally accepted by ICZN (1999, Art. 10.3), and some have been proposed since the end of the nineteenth century (e.g. Chondriteae, Rhizocorallidae, and Arenicolitidae) based on morphology, albeit with limited ethological insights (e.g. Schimper and Schenk, 1890; Fuchs 1895, 1909). More recently, new ichnofamilies have been suggested (e.g. Walter, 1983; Fu, 1991; Seilacher and Seilacher, 1994; Genise, 2000, 2004).

Bromley (1996) noted that three main criteria have been used to group trace fossils in ichnofamilies: a common producer at high taxonomic level (e.g. Pelecypodichnia), morphological similarities based on anatomy of the producers (e.g. Multipodichnia), and functional similarities based on morphology (e.g. Alectoruridae). The present consensus is that ichnofamilies should be based on trace-fossil morphology, not on the biology of the potential producer (Bertling *et al.*, 2006). As indicated by Buatois *et al.* (2002a), the present challenge is to define ichnofamilies based on a common set of morphological traits of functional significance that allow links to be established among trace fossils related on constructional grounds, regardless of phylogenetic relationships (Buatois *et al.*, 2002a). Bertling *et al.* (2006) noted that many of the morphological groups of flysch ichnotaxa recognized by Książkiewicz (1977) and Uchman (1995, 1998) could be formalized as ichnofamilies.

On the other side of the taxonomic spectrum, ichnosubgenera and ichnosubspecies are allowed in trace-fossil taxonomy, but have been rarely used, particularly the former (Rindsberg 1990a). However, ichnosubspecies have been occasionally employed, and may be advisable in certain cases. For example, Mángano and Buatois (2003a) treated the components of the so-called *Cruziana rugosa* group as ichnosubspecies (*C. rugosa rugosa*, *C. rugosa furcifera*, and *C. rugosa goldfussi*), following a suggestion by Seilacher (1996). They noted that although these ichnotaxa are morphologically distinct, they are best regarded as ethological variations at the ichnosubspecies level rather than at the ichnospecies level. This scheme reflects more adequately the fact that differences among these ichnosubspecies are less significant than those between them and other *Cruziana* ichnospecies (e.g. *C. semiplicata*). Ichnosubspecies have been also suggested for some *Arthrophycus* ichnospecies (Seilacher, 2000).

2.6 VERTEBRATE ICHNOTAXONOMY

The relationship between vertebrate and invertebrate ichnology is one of the present hot topics in ichnology (e.g. Melchor and Genise, 2004a, b; Hunt and Lucas, 2007; Lockley, 2007; Lucas, 2007; Minter *et al.*, 2007a). Central to this debate is the idea of unity or disunity of ichnology with respect to concepts and methods. In practical terms, invertebrate and vertebrate ichnology developed independently, to a large extent (Lockley, 2007). Ichnology textbooks tend to cover either one topic or the other, and only rarely (e.g. Ichnia 2004 and 2008) vertebrate and invertebrate ichnologists gather together in the same scientific meetings. One of the central issues is how to keep a balance between unification of the ichnological field on one side, while giving enough room for diversity of approaches on the other. While some authors favor "one ichnology" (e.g. Melchor and Genise, 2004a, b), others regard this as a nice, but impractical, idea (Lockley, 2007).

Ichnotaxonomic problems are at the core of this topic. Hunt and Lucas (2007) noted that invertebrate ichnologists mostly use an ethological approach, while vertebrate ichnologists favor a biotaxonomic approach. In other words, the focus of invertebrate ichnology is in classifying biogenic structures based on the ethological significance of their morphology, while vertebrate ichnologists attempt to relate traces to their producers. The word "mostly" in this context means that these two approaches work essentially as end members with some groups of trace fossils occupying an intermediate position (e.g. arthropod trackways and insect traces in paleosols). However, Minter *et al.* (2007a) noted that the field of vertebrate ichnology also uses an ethological approach because the same ichnotaxonomic name should not be assigned to a burrow and a trackway produced by the same vertebrate, or to a resting trace and a trackway also sharing the producer. In this regard, at least theoretically, vertebrate and invertebrate ichnology do not seem to be so far apart. More controversial gray zones include trackways produced by the same animal, but reflecting a change in speed. In any case, this is also a contentious issue with arthropod trackways (e.g. Braddy, 1995), so it is a problem inherent to trackways not strictly to vertebrate traces.

However, in practical terms the problem persists because the vast majority of vertebrate traces identified in the fossil record are trackways and, therefore, locomotion is the main behavior involved. Lockley (2007) specifically raised the question of whether it is reasonable to apply the same conventions and expectations of invertebrate ichnotaxonomy to vertebrates. The morphology of a footprint is determined not only by the structure of the foot of the producer but also by foot–substrate interaction, the latter resulting in extramorphological variation (Lucas, 2007). Haubold (1996) proposed the name phantom taxa for tetrapod footprint taxa based on such extramorphological variation, while Lucas (2001) suggested the name taphotaxon for a taxon based on distinctive morphological features that result from taphonomic processes, noting that this situation is more common with trace fossils than with body fossils. There is consensus among vertebrate ichnologists that extramorphological features should not be used in ichnotaxonomy, and it has been argued that this may be a problem with most taxa defined at ichnospecific level (Lucas, 2007). Assuming that the vast proportion of vertebrate trace fossils record locomotion, it is hard to see how a completely morpho-ethological system can be applied in practice to vertebrate ichnotaxonomy.

Carrano and Wilson (2001) summarized the main methods employed by vertebrate ichnologists to relate tracks to their producers. These authors noted that the three main approaches that have been employed are phenetic correlation, coincidence correlation, and synapomorphy-based correlation. Phenetic correlation is the standard method, and is based on the similarity between the track and the foot skeleton. Coincidence correlation uses information other than morphology (e.g. geological age, geographic provenance, or local faunal composition) to establish the link between track and producer. Synapomorphy-based correlation applies cladistic methods to classify trackways assigning ichnotaxa to biological taxa using shared derived characters. Although Carrano and Wilson (2001) favored this latter approach, Lucas (2007) raised some doubts about the benefits of applying synapomorphy-based correlation instead of the more standard phenetic correlation. Coincidence correlation, although useful in the search of potential tracemakers, should not be used as a taxonomic criterion because it may lead to circular reasoning (see Section 2.1). The challenge in vertebrate ichnotaxonomy seems to be to formulate ichnotaxobases based on morphology, which allows the establishment of ichnotaxa at different hierarchical levels avoiding circular reasoning.

2.7 THE UNCERTAINTY PRINCIPLE IN ICHNOTAXONOMY

Since its original formulation by Werner Heisenberg, physicists have been forced to deal with the uncertainty principle, which establishes that certain pairs of physical properties of an electron, such as position and momentum, cannot simultaneously be known. Perhaps ichnologists may be allowed to play with an analogy in ichnotaxonomy. No matter how hard we try, it seems that we cannot establish an ichnotaxonomic system that simultaneously fulfills the following requirements: (1) internal consistency and (2) applicability. The search for internal consistency is desirable, but occasionally the system may lose applicability if consistency is pushed too far.

There is general consensus that ichnotaxonomic classifications should be based on intrinsic properties of trace fossils that are of enough ethological significance. Accordingly, extrinsic parameters, such as stratigraphic age, facies, or geographic location, play no direct role. However, this sharp boundary gets blurred when substrate is addressed. It seems that substrate in itself cannot be considered an ichnotaxobase because of its extrinsic character, although it is the behavior that results from the influence of substrate that is at play. In any case, substrate plays an indirect role in naming trace fossils, essentially in the same way that the biology of the producer influences behavior (see Section 2.1). Regardless of this, substrate has been historically considered significant enough to form the basis on which ichnotaxa are established; vertical burrows in sediment are called *Skolithos* while vertical borings in lithified substrates are called *Trypanites*. These problems were raised by Ekdale and Bromley (2001b) when defining the ichnospecies *Gastrochaenolites oelandicus* because some of their specimens seem to be borings and some burrows. Carmona *et al.* (2007) noted that Miocene specimens of *Gastrochaenolites ornatus* formed in firmgrounds were identical to *G. ornatus* produced in hardgrounds. Accordingly, these authors concluded that using substrate as an ichnotaxobase in this case would be artificial and misleading. Substrate may qualify as a high-rank ichnotaxobase when morphology reflects distinct ways of organism–substrate interactions, but when the same organism is able to excavate and bore, and the excavation technique is identical to the mechanical perforation technique, the validity of the substrate vanishes (Carmona *et al.*, 2007).

There is widespread agreement that general form is a high-rank ichnotaxobase. Accordingly, some authors (Fürsich, 1973; Schlirf, 2000) have suggested that general form should be used to classify crustacean burrow systems, such as *Ophiomorpha*, *Thalassinoides*, and *Spongeliomorpha*, ichnogenera that at present are distinguished on the basis of the nature of burrow wall, a character of lesser significance. If this view is adopted, then the ichnogenera *Thalassinoides* and *Ophiomorpha* should become junior synonyms of *Spongeliomorpha*, which is the oldest available name. It is undeniable that this approach aims for internal consistency in ichnotaxonomy. However, it has been met with little acceptance (e.g. Bromley and Frey, 1974; Bromley, 1990, 1996; Carmona and Buatois, 2003). Besides other possible reasons to keep the three ichnogenera, reluctance to abandon *Thalassinoides* and *Ophiomorpha*, two ichnotaxa firmly entrenched in the literature and of widespread recognition in outcrop and cores, undoubtedly plays a huge role.

2.8 CLASSIFICATION OF TRACE FOSSILS IN OUTCROPS AND CORES

Outcrops and cores are two very different realms and comparison of ichnological information may represent a challenge (Bromley, 1990, 1996). However, in the same way that sedimentological observations in outcrops should be integrated with core data in order to produce more accurate depositional models, subsurface and surface ichnological information should be evaluated using similar criteria and ichnotaxonomic standards. With an increasing recognition that ichnological information is of paramount importance in petroleum exploration and reservoir characterization, studies addressing trace fossils in cores have become common practice, and a series of atlases has been published (e.g. Chamberlain, 1978; Pemberton *et al.*, 1992c, 2001; Gérard and Bromley, 2008). Commonly, trace fossils in cores are classified at ichnogeneric level (e.g. Ekdale, 1977). However, in many other cases ichnospecific assessments are possible when dealing with ichnogenera whose ichnospecies are classified according to features that are easy to detect in cores, such as the type of burrow wall in some ichnospecies of *Ophiomorpha* (Bromley, 1990, 1996).

The fact that ichnologists working with cores have to deal with narrow two-dimensional views represents a departure with respect to the study of trace fossils in outcrops. As noted by Gerard and Bromley (2008), the probability of a single burrow being detected is related to its orientation, its size, and the core diameter. Some of these peculiarities pose a problem, but others may represent an advantage. Some ichnotaxa that are easily identified in outcrops may be impossible to recognize in cores. Biogenic structures preserved in semirelief, such as graphoglyptids, locomotion traces (e.g. trackways), and shallow grazing trails, fall into this category. These structures are revealed along bedding planes in outcrops. On the other hand, full relief ichnofossils, such as endichnial feeding and dwelling traces, are easy to visualize in cores. Furthermore, cores commonly reveal subtle details of burrow boundaries that may be overlooked in outcrops, as illustrated by haloes in *Phycosiphon*. The lack of weathering in cores is particularly helpful to examine biogenic structures in mudstone. In outcrops, where sandstone interbeds are absent in fine-grained successions, it is often difficult to evaluate the ichnological content. On the other hand, discrete structures emplaced in mudstone are easily detected in cores.

Besides their classification in cores, paleoenvironmental interpretation of trace fossils is enhanced by the amount of additional information available in subsurface. For example, biofacies data (e.g. foraminiferans, palynofossils, and calcareous nanoplankton) from regularly selected core intervals are currently available, as well as geochemical and petrophysical information. These additional datasets can be employed to integrate ichnological information with other lines of evidence, promoting more robust depositional models. Also, where core recovery is good, one is able to examine relatively continuous intervals. Unfortunately, some oil companies tend to take cores only from the reservoir interval (sandstone and carbonate) and associated mudstone facies, whose characterization would be essential to understand depositional conditions and paleoenvironments, cannot be examined.

Finally, in many cases cores represent the only available information. This is the case with modern offshore areas (e.g. Ekdale, 1978, 1979; Wetzel, 1983, 1984), and some rock units that are only known from the subsurface (e.g. Buatois *et al.*, 1999, 2002b). In recent years, subsurface information also become available through the study of borehole images and various core-imaging techniques. Ichnological data can also be evaluated from borehole images, albeit with a lower level of resolution than in cores (e.g. Salimullah and Stow, 1995; Bockelie *et al.*, 1998; Gerard and Bromley, 2008). Calibration of these images is highly recommended, as elegantly illustrated by Gerard and Bromley (2008). Also, scanner-imaging techniques may help to visualize the three-dimensional morphology of trace fossils in cores (Gerard and Bromley, 2008).

3 Paleobiology of trace fossils

> This success stems mainly from the intimate connection of ichnology with sedimentology and the importance of both fields for paleoenvironmental and basin analysis, which becomes more and more important in petroleum exploration. This useful connection, however, also had its price. In the hand of biogeologists, trace fossils easily lose their significance as unique biological documents.
>
> Dolf Seilacher
> *Trace Fossil Analysis* (2007)

> One of the triumphs of the palaeobiological approach to palaeontology is the insight functional morphology has given us about the life activities of long dead organisms.
>
> Richard Bambach, Andrew Bush, and Douglas Erwin
> "Autecology and the filling of ecospace: key metazoan radiations" (2007)

Although the significance of trace fossils in paleoenvironmental reconstructions is responsible for the rapid development of ichnology, we should not forget that ichnofossils are produced by living organisms and, as such, the biological nature of trace fossils is at the core of any study on animal–substrate interactions. In this chapter, we analyze the paleobiological facet of trace fossils. In order to do so, we revise concepts from benthic ecology and paleoecology. First, we explore the concept of modes of life, addressing feeding strategy, position in relation to the substrate–water interface, and level of motility. Second, we elaborate on the different modes that organisms have to interact with and, in particular, penetrate into the substrate. Third, we look at basic locomotion and burrowing mechanisms from a historical perspective, revisiting the pioneering work of Schäfer and the synthesis by Trueman. We exemplify all these mechanisms with examples form the trace-fossil record. Finally, we close this chapter by introducing the new paradigm of movement ecology and its potential implications in ichnological studies.

3.1 MODES OF LIFE

Animals burrow in order to solve four basic problems: respiration, feeding, reproduction, and protection (Bromley, 1990, 1996; Mángano and Buatois, 1999a). The diverse modes of life in the living world reflect viable strategies to deal with these problems. Mode of life includes feeding strategy, position in relation to the substrate–water interface, and level of motility (Bambach *et al*., 2007; Bush *et al*., 2007). These modes of life reveal all possible combinations of ecological parameters, allowing a multidimensional analysis of theoretical ecospace. The combination of these elements results in 216 potential modes of life. In practice, only 92 of these modes of life are recorded as utilized (Bambach *et al*., 2007).

3.1.1 FEEDING STRATEGY

Food is an essential requirement for life and, according to their structural possibilities, each invertebrate group has developed a repertoire of feeding mechanisms and strategies in order to get the necessary nutrients from the surrounding environment. The questions what does an animal eat, where is this food resource located in relation to the animal life-site, and how common is this resource (availability) determine the specific adaptations for food acquisition (Mángano and Buatois, 1999a). Trace fossils provide valuable information on trophic types and feeding strategies.

Marine biologists have recognized incredibly diverse and ingenious ways of feeding. However, their perspective is quite different from that of a paleobiologist or an ichnologist. Biologists are largely focused on particular characteristics, such as food particle size, and less attention is paid to what, where, and how something is eaten (Crame, 1990). In other cases, exquisite details about a peculiar behavior have been observed by marine ecologists, but very little of that behavior is recorded in the sediment and has preservation potential. From a paleobiological and ichnological standpoint, the signal left in the substrate is a simplified version of the behavior involved, and can be interpreted in terms of a few major trophic types and feeding strategies. Trophic categories can be broadly defined as groups of organisms that feed, in general, in the same fashion (Walker and Bambach, 1974; Bambach, 1983; Bambach *et al*., 2007). In other words, a certain source of food is exploited in a similar manner. Although the classification commonly adopted by ichnologists (e.g. Bromley, 1990, 1996) is mostly based on marine invertebrates, it can be modified to include feeding strategies in terrestrial environments. Trophic types are based on the type of food, source location in relation to the sediment–water interface, and the general feeding mechanism involved.

There are five major feeding categories: suspension feeding, detritus feeding (also known as surface deposit feeding), deposit feeding (also known as mining), grazing, and predation (Bambach *et al*., 2007). However, other unconventional categories, such as trapping, farming, photo- and chemosymbiosis, and parasitism have also been recognized. In particular, parasitism is discussed in the context of animal–animal interactions (see Section 6.7). In addition, some organisms are able to

Box 3.1 *Tasselia ordamensis*, a complex deposit-detritus feeding-gardening structure of maldanid polychaetes

Studies involving three-dimensional CT scan and X-ray analyses of incipient *Tasselia* recovered from shallow- to deep-water settings off the coast of Africa and deep-water sediments from eastern Canada revealed its complex internal structure, and provide strong evidence to support a maldanid polychaete origin. However, the ethological meaning of this peculiar structure has remained elusive until recently. Based on the detailed analysis of over 400 exquisitely preserved specimens of *Tasselia ordamensis* from the Upper Cretaceous to Cenozoic marine deposits of Tierra del Fuego and Antarctica, a new feeding strategy has been proposed. This trace fossil, unquestionably related to maldanid worms, illustrates the complex feeding strategies developed by representatives of this polychaete group. *Tasselia ordamensis* is a pear-shaped structure characterized by an axial thickly lined tube surrounded by vertically stacked sediment disks and continuing downward into a basal chamber (Fig. 3.1). Composition, geometry, and the cross-cutting relationships of internal elements reveal the existence of two domains within each sediment disk: the outer and the inner burrow-fill domains. The outer domain contrasts with the host rock in grain size and composition of particles, consisting of a fine-grained, micritic matrix enriched in microfossils, such as radiolarians, calcispherules, and diatoms, and tiny plant debris. The internal structure of the outer domain consists of radially arranged, subhorizontal to oblique petal-like elements. Coarse particles (e.g. microfossils) are re-oriented parallel to the petaloid elements. The boundary between the outer-fill domain and the host rock is sharp, but no particle orientation is visible. The inner-fill domain has a higher concentration of coarser particles than the outer burrow-fill domain. Its internal structure consists of short, subvertical and strongly arched petaloid elements, which are confined to the sediment disk. The boundary between the outer- and the inner-fill domain is also sharp with clear evidence of the inner-fill-domain laminae cross-cutting the outer-fill domain. *Tasselia ordamensis* has been traditionally interpreted as a retrusive domichnion/equilibrium structure produced by suspension-feeding or microcarnivore organisms. However, detailed analysis of the internal structure of *Tasselia* clearly indicates that it is constructed protrusively (i.e. in a downward direction), and that is most likely a complex structure resulting from the deposit feeding, detritus feeding and microbial-gardening activities of maldanid polychaetes. The outer-fill domain, mostly formed of fine-grained particles, suggests a deposit-feeding mode with ingested particles passing through the gut of the producer up to the surface (i.e. upward advection), and non-ingested particles (large size particles, medium and coarse-grained sand) remaining in the basal chamber or on the central part forming part of the inner fill domain. Microfossils and plant debris within the outer-fill domain are clearly oriented. They may have been collected at the surface and placed within the petaloid elements (i.e. downward advention), documenting the role of detritus feeding. Densely packed microfossils and plant debris in discrete levels within the structure most likely reflect pulsed delivery of organic matter to the seafloor, followed by rapid subduction and redistribution by the tracemaker (detritus-feeding mode). After excavation and deposit-detritus feeding resulting in the formation of a burrow fill disk, a new feeding chamber is excavated below. The old feeding chamber is now situated above, and functions as "culturing compartment". The distinct structure of the inner domain results from reworking of particles stored in previous feeding chambers. Therefore, *Tasselia ordamensis* illustrates the feeding plasticity of maldanid polychaetes, producing complex structures, resulting from a combination of deposit-detritus feeding and gardening activities, and most likely as a response to fluctuating food supply.

References: Olivero and López-Cabrera (2010).

switch feeding strategies. For example, some suspension- and surface-deposit feeding bivalves are able to switch mechanisms facultatively (Skilleter and Peterson, 1994). Combined feeding strategies may result in complex trace fossils, as in the case of the ichnogenus *Hillichnus*, which has been attributed to a combination of deposit feeding and chemosymbiosis with sulfide-oxidizing bacteria (Bromley *et al*., 2003). Behavioral plasticity in terms of feeding strategies is also common in decapod crustaceans and polychaetes (Box 3.1).

Suspension feeders capture suspended particles from the water column, and are commonly sessile forms that do not move around to get the necessary nutrients. Filter feeding is a subdivision of suspension feeding, in which an organic filtration mechanism is involved in food acquisition (Walker and Bambach, 1974). In the trace-fossil record, suspension feeding is revealed by simple (e.g. *Skolithos*) or U-shaped (*Diplocraterion*) vertical burrows with lined walls preserved in clean sandy substrates. In modern environments, these structures are produced by polychaetes, sabellariids, spionids, and phoronids, among other organisms (Alpert, 1974; Gingras *et al*., 2008a). Suspension-feeding strategies have been envisaged for some simple horizontal burrows, such as *Palaeophycus*, which is thought to have been produced by a wide variety of organisms, including polychaetes (Pemberton and Frey, 1982).

Various devices and adaptations have been developed by suspension feeders to attain the appropriate position in the water column for trapping particles. Some suspension-feeding brittle stars (ophiuroids) can coil their arms and hence are well-adapted for clinging onto corals and other elevated structures. Other ophiuroids (e.g. the basket star) display delicate branching arms that form a mucus-trapping basket directed towards the current (Barnes and Hughes, 1999). The ophiuroid trace fossil *Asteriacites aberensis* is characterized by long rays frequently oriented parallel to the inferred paleocurrent (Crimes and Crossley,

Figure 3.1 *Tasselia ordamensis*, a complex trace fossil attributed to the detritus- and deposit-feeding, and gardening activities of maldanid polychaetes. Visible internal structural elements are the axial, lined tube, the stacked sediment disks, the outer and inner fill domains, and the terminal chamber. Upper Eocene-Lower Oligocene, Punta Gruesa Beds, Punta Gruesa, Tierra del Fuego, southern Patagonia, Argentina. Scale bar is 5 cm. See Olivero and López-Cabrera (2010).

1991), suggesting a suspension-feeding trophic type (Mángano *et al*., 1999). Preferential orientation with respect to the predominant current (i.e. rheotaxis) by clusters of resting traces has been commonly invoked to infer suspension feeding. Examples include *Rusophycus* in freshwater environments attributed to notostracan crustaceans (Bromley and Asgaard, 1972b) and in marine environments presumably produced by trilobites (Pickerill, 1995).

Some suspension-feeding body plans, such as those of sponges and cnidarians, include chambers or an internal cavity lined with tissue, whose cells, by means of cilia, seta, flagella, or amoeboid pseudopodia, capture particles trapped within the cavity. This strategy is illustrated by the clionid sponge-boring *Entobia* (Bromley, 1970). Brachiopods exhibit a more complex design, in which anatomical structures are particularly adapted for filtering. In particular, the lophophore with ciliated filaments performs three interrelated functions as a pump, a sieve, and a respiratory organ. Although it is a well-established dogma that brachiopods are sessile epifaunal organisms, modern lingulide brachiopods live within a vertical to inclined, mucus-lined burrow; the anterior part of the shell at or slightly projecting from the water–sediment interface and anchored, via a flexible pedicle, into the substrate (Emig *et al*., 1978; Savazzi, 1991). As documented by Zonneveld and Pemberton (2003), the dwelling trace fossil *Lingulichnus* illustrates a wide range of behaviors, including stationary suspension feeding, escaping from burial, and reburrowing after erosional exhumation, all behaviors known in extant lingulide.

Suspension-feeding bivalves display complex gill morphologies, which are used for both respiration and particle collection from the mantle cavity. A set of morphological features, such as a streamlined shape, deep pallial sinus, marginal posterior gape, and absence of prominent shell ornamentation characterize suspension-feeding bivalves (Stanley, 1970). The presence of a deep pallial sinus is related unequivocally to posterior siphons. The posterior gape signals the existence of a long siphon that cannot be withdrawn entirely into the shell, forcing the animal to be confined permanently in a deep burrow safe from the hazards of the shallower tiers. This type of siphon is almost invariably linked to a suspension-feeding strategy. The ichnospecies *Lockeia siliquaria* has been interpreted as the basal part of a dwelling structure of suspension-feeding bivalves (Mángano *et al*., 1998). A similar interpretation can be made for freshwater bivalve traces because almost all lacustrine representatives are suspension feeders (White and Miller, 2008). Another example of trace fossils produced by a suspension-feeding bivalve is represented by the occurrence of *Panopea faujasi* within its equilibrium structure *Scalichnus phiale* (Hanken *et al*., 2001).

Detritus feeders or surface deposit feeders capture loose particles on the depositional interface, which is rich in organic matter (Bromley, 1990, 1996; Bambach *et al*., 2007). Both vagile organisms that move around in search of food and sessile animals that explore around their burrows are represented. Non-specialized grazing trails (e.g. *Mermia* and *Gordia*) in freshwater environments have been attributed to detritus-feeders, most likely insect larvae (Buatois and Mángano, 1993a). Snails in both marine and freshwater environments graze on organic matter and algal material at the sediment surface, producing structures akin to the ichnogenus *Archaeonassa*. Tellinid bivalves are common surface deposit feeders living below the sediment–water interface and using the inhalant siphon to collect particles at the surface. These structures are well documented in modern tidal flats (e.g. Schäfer, 1972). However, the only trace fossil attributed to tellinid bivalves, the ichnogenus *Hillichnus*, is remarkably complex and has not been regarded as reflecting a *Macoma*-like detritus feeding strategy (Bromley *et al*., 2003). Surface deposit feeding is also adopted by various worms, such as some terebellids, maldanids, and glycerids (Gingras *et al*., 2008a). Concentrically filled burrows assigned to the ichnogenus *Rosselia* have been attributed to detritus-feeding terebellid polychaetes (Nara, 1995, 2002).

Deposit feeders or miners ingest organic matter within the substrate to recover buried food. Because most of the sediment is composed of inorganic mineral grains (even organic-rich sediment can be 95% inorganic in matter) animals may wander through the sediment in search of organic food particles or construct complex and more permanent burrows to systematically mine the sediment. Because the surface and uppermost parts of the substrate are richer in nutritious particles, they are heavily populated by deposit feeders (Bromley, 1990, 1996). Deposit feeders can be selective (i.e. those that only extract nutritious grains from the sediment) or non-selective (i.e. those that engulf the sediment uncritically and digest what they can from it). Most infaunal organisms (i.e. endobenthos) are deposit feeders that rework the sediment to get nutritious particles producing biogenic reworking (Bromley, 1990, 1996). In many cases, the morphology and nature of the infill of trace fossils record unquestionable support for a deposit-feeding habit of the tracemaker. For example, an actively infilled burrow (i.e. a fill that has been subject to biological processing, passing through the animal's gut) commonly contrasts in organic content or grain size with the host rock (e.g. *Planolites*), or is packed as backfilled menisci (e.g. *Taenidium*, *Scolicia*).

Marine benthic ecology and neoichnological studies indicate that deposit feeding is a widely represented feeding strategy among many vermiform organisms. Various polychaetes, such as terebellids, maldanids, glycerids, and opheliids, feed within the sediment (Gingras *et al*., 2008a). The latter are known to produce the ichnogenus *Macaronichnus* (Clifton and Thompson, 1978; Pemberton *et al*., 2001). In continental settings, oligochaetes and various annelids, such as tubificids and lumbriculids, are typical deposit feeders (White and Miller, 2008). Protobranch bivalves and many echinoids are also well-known deposit feeders with an extensive representation in the ichnological record. Combined locomotion and feeding activities of protobranch bivalves are represented by the chevronate trace fossil *Protovirgularia* (Seilacher and Seilacher, 1994; Mángano *et al*., 1998; Carmona *et al*., 2010). Structures attributed to spatangoid echinoids are illustrated by the backfilled ichnogenera *Scolicia* and *Bichordites* (Bromley and Asgaard, 1975; Smith and Crimes 1983; Bromley *et al*., 1995).

Some complex gallery systems produced by decapod crustaceans reveal adaptations for deposit feeding (Ekdale, 1992). According to Gingras *et al*. (2008a), some thalassinid shrimps construct tiered boxworks and networks using the vertical shaft to maintain a connection to the sediment–water interface and the basal network for deposit feeding.

A number of biogenic structures known from the fossil record have been attributed to deposit feeders based on design, although the actual affinities of the producer remain unknown in the absence of modern analogues. Examples include ichnogenera from the ichnofamily Arthrophycidae, such as *Arthrophycus* and *Phycodes* (see Section 13.3), as well as other feeding burrows, such as *Halopoa*, *Phycosiphon*, and *Heimdallia*, among many others (Seilacher, 2007b).

A deposit-feeding trophic type has been inferred for extinct organisms based on combined ichnological and functional morphological evidence. One of the most remarkable examples is trilobites, which are regarded for the most part as deposit feeders, although some may have developed other feeding strategies, such as scavenging, predation, and suspension feeding (Seilacher, 1985; Jensen, 1990; Whittington, 1992; Fortey and Owens, 1999). Deposit feeding is suggested on morphological grounds, such as the absence of mandibles and chelate appendages, and the presence of multiple undifferentiated biramous limbs. The so-called trunk-limb feeding mechanism involves the rhythmical inward motion of the endopodites (inner branch of the limb), which convey the gathered particles to the mouth through the intercoxae food groove (Seilacher, 1985; Clarkson, 1992; Levi-Setti, 1993). Some features, such as the presence of a spinose coxae and the backfacing mouth at the rear of the hypostome, suggest that larger size particles were probably squeezed and shredded along the intercoxae groove and subsequently pushed forward to the mouth (Whittington, 1992). The abundance of cruzianids in lower Paleozoic rocks also provides a strong evidence for deposit feeding. These structures not only involved high-energy requirements inconsistent with simple locomotion, but also, in some cases, display scribbling or circling patterns best explained by food searching (e.g. Seilacher, 1970; Fortey and Seilacher, 1997; Mángano and Buatois, 2003a; Neto de Carvalho, 2006). Functional morphological analysis of the trace fossils *Cruziana* and *Rusophycus* has provided valuable information to elucidate the mechanics involved in trilobite deposit feeding (Seilacher 1970, 1985) (see Section 3.3.1). Bilobate trails are also produced by various other invertebrates, many of which are deposit feeders, such as isopods, which move through sediment to extract organic matter (Hauck *et al*., 2008; Gingras *et al*., 2008a).

Grazers are basically herbivores who scrape or nibble plants, algae, or even microbial material from the depositional surface, or chew or rasp larger plants or seaweeds (Mángano and Buatois, 1999a). Ecologists tend to link the feeding strategy of grazing to the development of grasslands, mammals being the archetypal grazers (Owen, 1980; see also Thomasson and Voorhies, 1990). In the sea, limpets, sea urchins, and fishes are well-established grazers on hard substrates. In modern coral reefs, grazing fish are major determinants of the benthic community structure (Bellwood and Wainwright, 2006). Reef structures have been related to the activities of grazers throughout the Phanerozoic, the most marked change being in the Cenozoic when diverse grazing fishes accompanied by some groups of invertebrates, such as deep-grazing limpets and sea urchins, resulted in a drastic increase in grazing pressure (Bellwood and Wainwright, 2006). The use of the term "grazing" in ichnology may be somewhat misleading. In ichnology, the strategy of "grazing" refers to a combination of feeding and locomotion being recorded by the ethological category pascichnia (see Section 1.4.4). Archetypal grazing structures commonly reflect that the animal is feeding while moving on or within the substrate, so from a trophic-type perspective detritus- or deposit-feeding, and, less commonly, true grazing may be involved. In soft marine substrates, grazers commonly eat some superficial organic detritus, so this category is actually transitional to detritus feeding. Organisms that feed on large particles of dead animals found at the sediment–water interface are referred to as scavengers. As particle size decreases, this category also grades into detritus feeders. On the other hand, some carnivores may eat dead, undecayed animals and, therefore, scavengers may grade into predators (Walker and Bambach, 1974). Although grazers, detritus feeders, and scavengers are not easily differentiated in terms of their trace-fossil record, in some contexts, it is possible to point to a grazing trophic type. For example, Ediacaran simple trails, some of the first metazoan structures, are best interpreted as the product of grazers on microbial mats (Seilacher, 1999; Buatois and Mángano, 2003a) (see Section 14.1.2). The trace fossil *Radulichnus*, a rasping structure, is a typical example of grazing feeding strategy in the ichnological record. In Carboniferous tidal flats, grazing trails may be directly associated with fossil leaves and other plant material (see Section 8.1.2).

Terrestrial arthropods feed on living and dead plants using multiple strategies, including piercing-and-sucking, chewing, galling, scraping, and boring. While there are few primary decomposers in marine food chains and webs, primary decomposers are essential elements of terrestrial ecosystems, giving rise to a second food chain. Woody, supporting tissues, which form the bulk of vegetation, only become available as food once they are dead. Arthropod adaptations to consume plant material are documented in the fossil record not only by the study of arthropod body fossils but also by the trace-fossil record of plant–arthropod interactions (Labandeira, 1998, 2007) (see Section 14.2.7).

Predators, also known as carnivores, get their food by capturing prey that is capable of resistance (Bambach *et al.*, 2007; Bush *et al.*, 2007). They represent the highest levels of the food chain. Predators can be passive or active, according to whether they wait in a fixed position for prey or they actively pursue it. Passive predation is illustrated by some polychaetes, sea anemones, and other anemone-like anthozoans (Ceriantharia). Some tube-dwelling worms are typically carnivores, they use the tube as a protective retreat and extend from the opening to seize passing prey. Vertical burrows, such as *Skolithos*, are commonly attributed to suspension feeders, but passive predation cannot be disregarded. Sea anemones live attached to corals, shells, or hide in rock crevices, and some burrow in sand or mud. They prey on various invertebrates, such as bivalves and crustaceans, swept by currents or waves, and some large species are even able to capture fish. The prey is paralyzed by nematocysts, caught by the tentacles, and carried to the mouth (Barnes and Hughes, 1999). Plug-shaped burrows (e.g. *Conostichus*, *Bergaueria*, *Conichnus*) are typically attributed to anthozoan cnidarians, including sea anemones (Actinaria) and tube anemones (Ceriantharia) (Pemberton *et al.*, 1988; Bromley, 1990, 1996). Most recent anthozoans are microcarnivores, however, and the distinction between passive predation and suspension feeding based on morphology of biogenic structures is difficult.

Active predation is the main mode of predation. This strategy is illustrated by many invertebrates and all vertebrate predators. In terms of biomass, predators are commonly underepresented in the fossil record, but they have played a critical role in shaping long-term trends in adaptation (Vermeij, 1987). Several phases are involved in predation, namely, search, capture, penetration, ingestion, digestion, and defecation (Bishop, 1975). Direct evidence of predation in the fossil record includes trace fossils of penetration and ingestion of preys, and digestive contents and fecal products of predators (Mángano and Buatois, 1999a) (see Section 1.4.10). Bites or crush marks on the prey exoskeleton result from pre-ingestive breakage, and circular and parabolic bore holes are produced by drilling. Crustaceans have developed various techniques to kill their prey, including peeling (i.e. piece by piece breakage), crushing between the claws, or pounding their prey with expanded segments of their maxillipeds (Brett, 1990). Drilling is a specialized mode of predation, as illustrated by many marine mollusks (Brett, 1990). Circular drilling holes (ichnogenus *Oichnus*) are well known in the trace-fossil record, and may be produced by a number of organisms, including carnivorous gastropods and octopodid cephalopods (Bromley, 1981, 1994).

Evidence of predators *in situ* on prey is fascinating, but extremely uncommon. Sublethal predation scars and biogenically induced broken fragments of trilobites provide evidence of trilobites being preyed upon (Babcock and Robinson, 1989; Babcock, 1993; Pratt, 1998). Moreover, right–left behavioral asymmetry recorded by predation scars, preferentially on the right side, indicates the existence of predators with a lateralized nervous systems since at least the Early Cambrian (Babcock and Robinson, 1989). Ichnological evidence of predation by trilobites has been suggested by Jensen (1990), who documented the recurrent association of the trilobite resting trace *Rusophycus dispar* and worm trace fossils. This author noted that the trilobites consistently positioned themselves so that only the legs of one side were in contact with the worm burrow, suggesting a capture technique in which the legs of one side were flexed around the prey, squeezing it against the spinose inner part of the coxae. Although, this predation interpretation has been questioned by Rydell *et al.* (2001), further case studies documenting ichnological evidence of predation by trilobites have been published (e.g. Brandt *et al.*, 1995; English and Babcock, 2007).

Ingested prey within the gut and gastric contents is another source of information, mostly restricted to fossil deposits of exceptional preservation (e.g. Viohl, 1990; Habersetzer *et al.*, 1994; Zhu *et al.*, 2004). Coprolites, however, are a more widespread evidence of diet, being found both in fossil lagerstätten (Vannier and Chen, 2005) and in terrestrial red beds (Hunt *et al*, 1994, 1998). Although the nature of coprolites was recognized very early by William Buckland (Pemberton and Frey, 1991), only recently has their potential in paleoecology and biostratigraphy started to be explored. Coprolites and gut contents provide crucial data to reconstruct ancient trophic webs (Richter and Baszio, 2001; Richter and Wedmann, 2005; Habgood *et al.*, 2003; Vannier and Chen, 2005).

Trapping, farming (also referred to as gardening), photosymbiosis, and chemosymbiosis are unconventional feeding categories (Mángano and Buatois, 1999; Bambach *et al.*, 2007). Trapping is the passive capture of migrating meiofauna or other microrganisms within spiral or complex structures (see Section 1.4.7). A typical example of trapping is represented by the paraonid polychaete *Paraonis fulgens*, which produces spiral burrows within intertidal sediment (Röder, 1971; Risk and Tunnicliffe, 1978). This polychaete selectively feeds upon diatoms as indicated by analysis of its gut contents and by its small size (Röder, 1971; Levin *et al.*, 1999). The spiral burrows are used as traps to capture diatoms as they migrate vertically within the sediment. The gaps between the whorls are interpreted as an area from which new diatoms can move into the trap, and so repeated visits can yield additional food (Röder, 1971). Although these intertidal biogenic structures have very low preservation potential, they have recently been described from the fossil record (Minter *et al.*, 2006).

Farming is a feeding adaptation that involves the culturing of suitable bacteria or fungi to provide food (Seilacher, 1977a) (see Section 1.4.7). Both farming and trapping can be inferred from complex, regular architectural patterns of biogenic sedimentary structures that are difficult to explain in terms of deposit feeding and are illustrated by the ethological category agrichnia (see Section 1.4.7). Complex three-dimensional network designs with secondary undulations, side branching, and anastomoses are commonly suspected to represent trapping or farming structures (Seilacher, 1977a). Examples include the ichnogenera *Paleodictyon*, *Protopaleodictyon*, *Acanthorhaphe*, *Desmograpton*, and *Urohelminthoida*, among many others. In particular, the ichnogenus *Spirorhaphe* has been modeled on the *Paraonis* spiral trap. Although commonly overlooked, these feeding adaptations may be the cornerstone of some sophisticated food chains. These specialized strategies are developed in response to depleted food conditions and absence of sunlight, and are typical of base-of-slope environments (see Sections 9.2 and 9.3).

Photosymbiosis and chemosymbiosis are feeding adaptations, which, until recently, have been overlooked in the paleontological literature. Photosymbiosis has been recognized in corals and several recent bizarre bivalves (e.g. *Tridacna*, *Corculum*) (Seilacher, 1990a). Chemosymbiosis involves animal endosymbiosis with chemoautotrophic bacteria. This adaptation has been extensively studied in relation to deep-sea vents, where chemosymbiotic bacteria allow the development of real oases of life in an otherwise life-depleted setting (Grassle, 1985). Chemoautotrophs use different inorganic sources (e.g. hydrogen sulfide, elemental sulfur, ammonia, ferrous iron, hydrogen) to produce energy. For example, sulfuricant bacteria occur within the soft tissue of the host (e.g. gills, mantle) where they are able to oxidize vent-derived H_2S in the presence of sufficient oxygen. Other reactions used by bacteria to obtain chemical energy are hydrogen oxidation and methane production. Chemosymbiosis is also an effective strategy in other environments such as anoxic muds (e.g. anoxic fjords, seagrass meadows, mangrove swamps) where oxygen and hydrogen sulfide are found in close proximity. In these environments, recent amphisiphonate lucinids (e.g. *Thyasira*, *Codakia*) are known to host chemoautotrophic bacteria in their gills. Chemosymbiosis is an unusual mode of nutrition that requires physiological adaptations and protection from the toxic surrounding environment. The recent bivalve *Solemya* has its gills packed with bacteria and its gut is reduced or absent (Yonge, 1936). These modifications in the soft parts, however, are not reflected by the shell morphology, which is largely unaffected (Seilacher, 1990a).

In the fossil record, photo- and chemosymbiosis have been inferred based on morphological and behavioral adaptations, and are well represented in some invertebrate groups, such as bivalves (Seilacher, 1990a). While photosymbiosis does not involve a particular interaction with the substrate and, accordingly, has not been documented from the trace-fossil record, some ichnofossils have been related to chemosymbiosis. Many odd burrows, such as the ichnospecies *Solemyatuba ypsilon*, have been interpreted as specialized chemosymbiotic designs, and modeled based on analysis of the bivalve *Solemya*. *Solemyatuba ypsilon* displays a basic U-shaped design that allows burrow ventilation and oxygen intake and a downward blind extension, presumably used for pumping hydrogen sulfide from the surrounding sediment (Seilacher, 1990a). The ichnogenus *Chondrites*, whose branching design cannot be satisfactory explained as the work of a deposit feeder, may actually represent "sulfide wells" constructed by the activity of a chemosymbiotic worm-like animal (Seilacher, 1990a; Fu, 1991).

3.1.2 POSITION WITH RESPECT TO THE SUBSTRATE–WATER INTERFACE

The position in relation to the substrate–water interface or tiering is a central concept in ichnology (see Section 5.1). It identifies the setting where an animal lives and, as such, it is intimately related to its feeding type. Six basic situations can be recognized (Bambach *et al.*, 2007; Bush *et al.*, 2007). These are pelagic (living in the water column as either plankton or nekton), erect (benthic, extending into the water mass), epifaunal or surficial (living on the surface, not extending significantly upwards), semi-infaunal (partly infaunal, partly exposed to the water column), shallow infaunal (living in the upper 5 cm of the substrate), and deep infaunal (living below the upper 5 cm of the substrate). The 5-cm boundary reflects approximately a depth above which organisms are challenged by disturbance rather than maintaining contact with the sediment–water interface and below which these difficulties are reversed in severity (Bush *et al.*, 2007). In any case, this boundary may be highly variable as it is highly dependent on several parameters, such as hydrodynamic energy (see Section 6.1.1) and depth of the redox discontinuity surface (see Section 6.1.3).

All the latter five categories include organisms living on and/or within the substrate, and are regarded as benthic (Walker and Miller, 1992). The terms epibenthic (= epifaunal, living at the sediment–water interface) and endobenthic (i.e. living within the sediment) are widely used in ichnology. Although occasionally some nektonic organisms may be revealed in the trace-fossil record (e.g. the fish trail *Undichna*), ichnology deals essentially with the activities of benthic organisms. In ichnological studies a more detailed subdivision of the infaunal ecospace is attainable because a finer-grained zonation can be obtained by careful study of tiering of biogenic structures that are produced not only by animals with hard parts but mostly by soft-bodied organisms (see Section 5.1).

3.1.3 LEVEL OF MOTILITY

The level of motility is the capability of an animal to move under its own power (Bambach *et al.*, 2002). Motility level is essential in ecological reconstructions because it determines an animal's range of physical activities (Bush *et al.*, 2007). It has been subdivided into six main categories: freely fast (regularly moving, unencumbered); freely slow (regularly moving, intimate contact maintained with substrate); facultative unattached (moving only when necessary, free-lying); facultative attached (moving only when necessary, attached); non-motile unattached (not capable of self-propulsion, free-lying), and non-motile attached (not capable of self-propulsion, attached) (Bambach *et al.*, 2007; Bush *et al.*, 2007).

Motility level is reflected by the basic ichnological categories of sessile and vagile used in ichnoguild characterization (see Section 5.4). However, not all the categories established based on body-fossil analysis are recorded in the ichnological realm.

Tracemakers are for the most part motile animals, either fully or facultatively motile. The only exception is attachment structures (e.g. *Podichnus*). In this case, the brachiopod tracemaker is a non-motile attached organism. Overall, those fully motile in intimate contact with the substrate are the most effective burrowers. Those motile animals that are less encumbered and that move by pressing the substrate with their appendages (e.g. many epibenthic arthropods) are less effective burrowers or do not burrow at all, but may produce trackways under appropriate substrate conditions. Facultatively motile animals can move to escape a threat or to reposition if affected by environmental disturbance (Bush *et al.*, 2007), therefore producing biogenic structures (e.g. escape traces).

3.2 MODES OF INTERACTION WITH THE SUBSTRATE

There are several classifications that account for the many ways that animals interact with the substrate (e.g. Hanor and Marshall, 1971; Bromley, 1990, 1996; François *et al.*, 1997; Solan and Wigham, 2005). Each of these schemes emphasizes different aspects, but to a certain extent equivalencies between the different frameworks can be proposed.

Bromley (1990, 1996) defined four main types of interactions between infaunal animals and the substrate: intrusion, compression, excavation, and backfilling (Fig. 3.2a–k). These categories are based on increasingly more complex animal–sediment

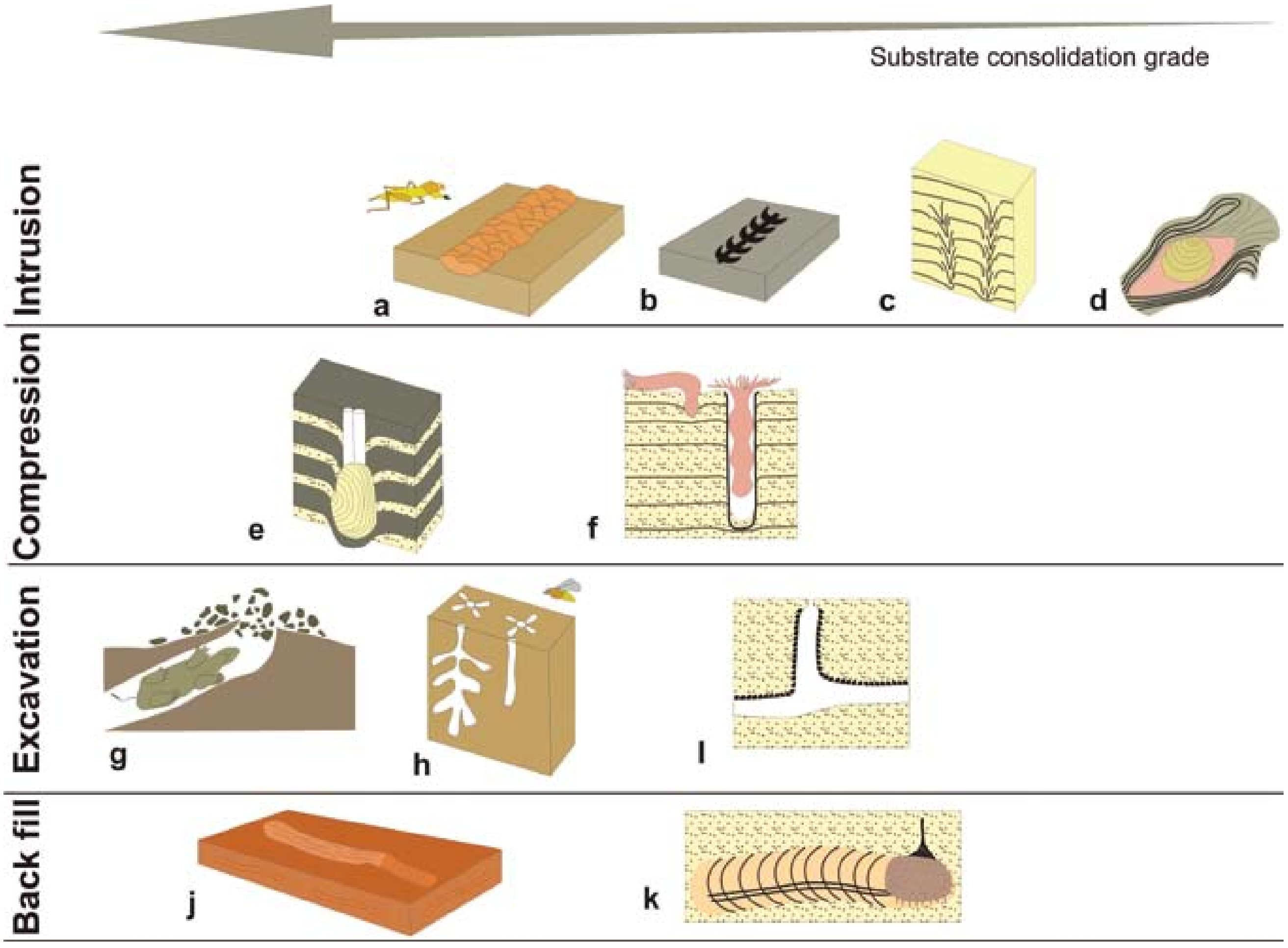


Figure 3.2 Some classic trace fossils interpreted within the categories of animal–substrate interactions of Bromley (1990, 1996). Note the relation with substrate consolidation. (a–d) Intrusions may form under a wide range of sediment consistencies from soupy to firm. (a) Shallow insect tunnel produced in a stiff sediment (stabilization may be related to sediment dewatering and/or microbial binding). (b) Bivalve trace in softgrounds. (c) Escape structures typically record intrusions in soft-to-soupy substrates. (d) Carnivore gastropods may intrude into soft-to-soupy sediment in search of prey producing biodeformational structures. (e–f) Compression structures are typically formed in partially dewatered sediment with enough shear strength. Compression action re-orients sediment particles at the structure boundary. Mucus can be used to bind the sediment grains. (e) Bivalve burrow. (f) Sea-anemone burrow. (g–l) Excavations can be formed in a wide range of consistencies, but are commonly not effective in soupy substrates. (g) Many mammals are well-adapted for excavating in firm terrestrial settings. (h) Excavation is the most common type of construction by insects in soils. (i) In soft sediments, excavations require reinforcement of the burrow boundary by a construction wall. (j–k) Backfilling is an efficient way of advancing through sediment while feeding, the loosened grains ahead being transported backwards via digestion or mechanical transport, and packed in a meniscus structure. Backfills can be found in soft to firm substrates. (j) Striated and meniscate burrow. (k) Irregular echinoid burrow.

interactions, namely the sediment is simply displaced, pushed aside and reorganized, manipulated and transported somewhere or digested and redeposited during burrowing. He noted that this approach is essentially from an ichnological standpoint.

During intrusion an animal simply displaces sediment temporarily with its body (Bromley, 1990, 1996) (Fig. 3.2a–d). As the animal moves on, the medium closes behind (i.e. no cavity is left open). In soupy or soft sediments, this burrowing strategy results typically in biodeformational structures rather than permanent and distinct burrows. This mode of interaction is also adopted by many different organisms producing escape traces (see Section 1.4.8). According to Bromley (1990, 1996), intrusion is also accomplished by some terrestrial vertebrates (e.g. moles, some reptiles) and insects (e.g. crickets and beetles), when they move close to the sediment surface. In this case, the uncompacted roof sediment is simply moved up and, in many cases, the structure collapses behind the animal. However, if these structures are produced at a slightly deeper level within a firmer substrate, a compression structure rather than an ephemeral intrusion will be produced.

Compression records the activity of an infaunal organism that forces a passage through the sediment by pressing material aside and compacting it (Fig. 3.2e–f). This mode of interaction typically results in relatively permanent and distinct burrows. The burrow boundary is typically smooth and only exceptionally ornamented (e.g. *Lockeia ornata*). Hydrodynamic deformation of the body (or part of the body) may result in compression on the boundary if sediment consistency is appropriate. In marine environments, this mode is adopted by bivalves, cnidarians, and many worms that move using a hydraulic mechanism through a firm substrate. Bivalve resting structures (e.g. *Lockeia*) and cnidarian resting and dwelling structures (e.g. *Bergaueria*, *Conostichus*) are examples, while in continental environments, tunnels made by earthworms and many vertebrates (e.g. rodents) are produced by compression.

Excavation is the most efficient way to deal with somewhat compacted sediment (Fig. 3.2g–i). The animal loosens the sediment ahead and relocates the material elsewhere, typically onto the substrate surface. Crustaceans use a basket formed by their anterior appendages to transport sediment outside the burrow, while fish use their mouths (Bromley 1990, 1996). Crustaceans may also use mucus and their anterior appendages to produce construction pellets that are pressed into the boundary of the structure to form a reinforced wall (e.g. *Ophiomorpha*). In some cases, part of the sediment may be ingested and the feces deposited outside the burrow, into the wall, or stored somewhere within the structure. In terrestrial settings, this burrowing strategy is commonly adopted by many fossorial mammals and insects.

Backfill consists of active manipulation by the animal in which sediment ahead is loosened, transported backwards around or through the body and redeposited behind as the organism moves forward (Fig. 3.2j–k). In the case of sediment being moved around the body, the sediment is mechanically manipulated, while sediment transported through the body of the organism involves ingestion and excretion. Burrow fill may be either meniscate, showing alternation of layers of different grain size (e.g. *Taenidium*), or homogeneous (e.g. *Planolites*) (see Box 2.2). Backfill is typically employed by worms, but it is also common in arthropods and irregular echinoids. Although some insects are able to backfill their structures by mechanical manipulation (Smith *et al.*, 2008a), they do not ingest and excrete sediment (Bromley *et al.*, 2007).

The ichnological classification by Bromley (1990, 1996) can be easily related to the approach of Hanor and Marshall (1971), who identified four mechanisms by which organisms can induce mass transport: turbulent diffusion, shear, advection, and molecular diffusion. More than one of these mechanisms may be involved in the generation of a biogenic structure. The first three mechanisms correlate well with distinctive categories in Bromley's scheme, the fourth one involves chemical reactions, inducing mixing on a molecular level and can be favored by any of the three types of physical transport processes.

Turbulent diffusion (also known as eddy diffusion) is produced when an organism moves through sediment generating turbulent stirring. This may occur around the margin of the animal and within its digestive tract in the case of deposit feeders. Turbulent diffusion takes place during intrusion in soupy substrates and commonly produces biodeformational structures (Bromley, 1990, 1996).

Shear takes place if the movement generates a laminar flow of sediment that predominates over turbulence. Some structures may display a central core of turbulent disturbance surrounded by a region of shear at the boundary of the structure. Shear is involved at the boundary of structures generated by compression *sensu* Bromley (1990, 1996). Internally, within the organism, shear is involved during mastication and digestion where solid grains are crushed and ground (Hanor and Marshall, 1971).

Advection refers to the bulk transport of a component, and may involve downward, upward, and axial movements. Burrows filled by sediment collapse or passive infill of open galleries involved downward advection. Many compression structures left open are infilled by collapse and downward advection. Upward advection is involved when an organism excavates a burrow and transports sediment up to the sediment–water interface. Some worms select what they eat, indigestible material is advected through the worm and excreted at the other end. Conveyor burrowers, such as maldanid worms in marine environments and earthworms in terrestrial settings, provide excellent examples of selective advection. If the organism ingests sediment at one end and excretes it out at the other or transports it mechanically along the structure, we are dealing with axial advection. This type of mass transport is recorded in backfill *sensu* Bromley (1990, 1996).

Sediment particle redistribution by the activities of benthic invertebrates and the evaluation of the bioturbation capacity of extant assemblages have received considerable attention by marine ecologists (e.g. Rhoads, 1974; Snelgrove and Butman, 1994; Pearson, 2001; Solan *et al.*, 2004a, b). However, many of the resulting models and classification schemes may be of limited application in paleoichnology as the identity of the tracemaker is in most cases a fundamental incognita. However, Solan and Whigam (2005) modified a previous classification by François *et al*. (1997), which provides a mechanistic understanding of biogenically induced mixing irrespective of the species identity that can be applied more generally. Seven basic modes of bioturbation are recognized: epifaunal bioturbators, surficial modifiers, biodiffusive bioturbators, gallery biodiffuse bioturbators, upward conveyors, downward conveyors, and regenerators. Some of these categories (e.g. upward conveyors and downward conveyors) closely match the basic mechanisms of Hanor and Marshall (1971) and categories of Bromley (1990, 1996), but others deserve further comments and clarification. Epifaunal bioturbators refer to organisms whose activities occur predominantly above the sediment–water interface, and therefore have a negligible contribution to vertical particle transport, but may contribute to lateral heterogeneity by redistribution of fine particles over very short distances along the surface. In contrast, the surficial modifiers of this scheme are actually very shallow-tier bioturbators that inhabit the uppermost 1–2 cm of the sediment, and generate more disturbance than the epifaunal bioturbators. Biodiffusive bioturbators move particles through every level of the sediment profile resulting in a down gradient vertical transport of particles analogous to molecular and eddy diffusion. Gallery biodiffusive bioturbators account for rapid transport of particles from the upper regions of the sediment to the lower limit of burrow penetration. Regenerators excavate holes and transfer sediment from depth to the surface where it is removed by physical processes, such as currents; and is replaced by surficial sediment and burrow collapse material; this is analogous to the typical excavations described by Bromley (1990, 1996) involving upward advection of material during excavation followed by passive infill by downward advection. Solan and Whigam (2005) also explored the interactions between biogenic reworking and microbial activity, emphasizing the necessity of including the microbial component in our understanding of animal–sediment interactions at different scales.

3.3 LOCOMOTION AND BURROWING MECHANISMS

We can approach to the problem of animal–substrate interactions analyzing the many ways in which animals move on and through the substrate. In order to decipher the ethological meaning of a biogenic structure, it is essential to have an understanding of the locomotion and burrowing mechanisms available to the different groups of benthic organisms. Movement is a fundamental characteristic of life, driven by processes that act across a wide variety of spatial and temporal scales (Nathan *et al*., 2008). Constrains on movement are both intrinsic (i.e. morpho-structural and behavioral) and extrinsic (environmental). The locomotion and burrowing techniques employed by different groups of invertebrates have been analyzed using different frameworks based on experimental work and observation of extant species (e.g. Trueman and Ansell, 1969; Trueman, 1975; Ott *et al*., 1976), a combination of modern and body-fossil material (e.g. Savazzi, 1982) or reconstructed based on the analysis of biogenic structures both, modern and ancient (e.g. Seilacher, 1953b; Yochelson and Fedonkin, 1993; Mángano *et al*., 1999). In recent decades, biomechanics and analysis of muscle-skeletal form and function have made a major contribution to our understanding of vertebrate locomotion and feeding strategies, in particular, in extinct groups such as dinosaurs and South American mammals (e.g. Vizcaíno and Fariña, 1999; Vizcaíno *et al*., 2001; Vizcaíno and De Iuliis, 2003; Sellers and Manning, 2007; Manning, 2008; Manning *et al*., 2009; Falkingham *et al*. 2009).

In invertebrates, only a handful of studies have dealt with the issue of defining general categories of locomotion and burrowing mechanisms (e.g. Schäfer, 1972; Trueman, 1975; Carney, 1981). There are essentially three ways of looking at this problem. One is an exhaustive documentation of the multiple modes of moving on and through the substrate (Schäfer, 1972). Another possibility is to focus on a reduced number of functional morphological traits (i.e. intrinsic constraints) that allow an organism to move (Carney, 1981). Finally, it is possible to distil a few archetypal mechanisms that can account for the locomotion and burrowing capabilities of invertebrates (Trueman, 1975).

3.3.1 MULTIPLE MODES OF LOCOMOTION: THE EMPIRICIST APPROACH

In a pioneer study on the tidal flats of the Wadden Sea, Schäfer (1962, 1972) identified 12 mechanisms of locomotion in marine invertebrates: amoeboid, ciliar, undulatory, peristaltic, glide-crawling, push-and-pull-crawling, bolting, multiple circular shoveling, pacing, drilling, chimney climbing, and jumping. Although this list is based on extant species, with some adjustments, it can be extrapolated to understand the production of a wide variety of biogenic structures in the fossil record. Although a monumental effort, this classification does not attempt to be comprehensive. As the focus of this classification is providing an analogical link to interpret biogenic structures in the fossil record, locomotion mechanisms of nektonic invertebrates (e.g. jet propulsion) were excluded from this classification (see Trueman, 1975). In practice, many organisms may employ a combination of more than one mechanism.

Schäfer's studies were performed within the framework of the so-called actuopaleontology, a research field that involves the study of marine benthic ecology from a perspective that incorporates a strong paleobiological interest (see Cadée and Goldring, 2007, for a historical study). His empirical approach, based on decades of meticulous observations in modern tidal flats, remains a classic in marine neoichnology.

The breadth of this classification is impressive, from both organism and substrate standpoints. It aims to cover protozoans to vertebrates, and softgrounds to hardgrounds.

Amoeboid locomotion is characterized by the flowing of the body. It is performed by protozoans lacking a shell or rigid pellicle. The mechanism is based on the formation of pseudopodia as a result of local expansion of the protoplasm, ectoplasm, or plasma gel of the protozoan. Locomotion structures produced by amoeboid protozoans in soft tidal-flat mud can be more conspicuous than their producers. In the case of foraminiferans, the plasma body is enclosed by a rigid shell and locomotion is due to rhizopodia extending out of the shell. Schäfer (1962, 1972) noted that little empirical support was available, but suggested that foraminiferan traces may consist of narrow and deep furrows in mud; this has been recently corroborated based on observations of the deep-sea floor (Matz *et al.*, 2008).

Another mechanism used by very small organisms is ciliary locomotion. In this type of locomotion cilia project beyond the surface of the cell membrane and generate a beat that commonly consists of a movement within a single plane. Because the plane of the ciliary beat is diagonal to the longitudinal axis of the body, small ciliate organisms rotate during locomotion. Forward locomotion is achieved via coordination of cilia by a metachronal rhythm, in which a wave of simultaneously beating groups of cilia moves from the anterior to the posterior end of the organism. Although a ciliary epithelium is common in many multicellular animals, ciliary locomotion is only effective in small organisms, protozoans, small metazoans, and larvae. Ciliary locomotion is common in meio- and microfauna inhabiting the uppermost layers of oxygenated sediment. Most of the structures produced are not persistent, although ciliary movement is responsible for the grain dislocation and displacement involved in cryptobioturbation. Some gastropods moving on hard substrates use ciliary movement to complement to glide-crawling (Trueman, 1975).

In undulatory movement, propulsion is achieved by sine waves that propagate along the body, typically in a single plane. The most common type of undulatory motion involves waves traveling from head to tail as the organism moves forward, but backward motion can be achieved by reversing the direction of wave motion from tail to head. The active contraction on one side of the body is responsible for the passive stretching of the opposite side. The wavelength is constant at a given time, although it may change from time to time. This locomotion mechanism is employed by different groups of organisms, such as nematodes, nemertines, errant annelids, cephalocordates (lancelets), fish, limbless lizards, and snakes (although a more complex variant: lateral undulation), moving in a wide variety of substrates, from completely dry (e.g. thixotropic sand) to fluid (i.e. soupy substrate). Undulatory movement is not exclusive to benthic animals, but is also employed by nektonic fish. This wide array of organisms shares a basic morphology consisting of an elongate body, but does not require the presence of an internal cavity (e.g. coelom). To move efficiently within the substrate, undulation can be used in combination with other mechanisms. For example, the polychaete *Nereis*, shoots its proboscis forward (bolting) while the posterior part undulates, helped by the use of large parapodia that act as walking legs (pacing) beating a backstroke on the convex side and a forward stroke on the concave side (Schäfer, 1972). In short, nereids can propel themselves through the sediment using a combination of three locomotory mechanisms: bolting, undulating, and pacing. If the sediment is soupy, some animals can essentially "swim" through it using pure undulations (Bromley, 1990, 1996). The sinusoidal ichnogenus *Cochlichnus*, produced by both nematodes and insect larvae (e.g. ceratopogonids), is a typical example of a trace fossil produced by simple undulatory movement. The sinusoidal trail *Undichna* is another well-known biogenic structure generated by the undulatory movement of a fish with the fins touching the sediment–water interface (e.g. Anderson, 1976; de Gibert *et al.*, 1999).

Peristaltic movement characterizes worm-like animals that have an elongate body, circular cross-section, and double layer of muscles in the body wall. Locomotion is attained by the coordination of this double layer of muscles that work antagonistically (longitudinal in the inner layer and circular in the outer layer), involving contraction of one layer accompanied by relaxation of the other. In the simplest situation, the muscles of all segments contract at the same time, alternatively thickening or lengthening the body. Contraction of the circular muscles reduces the diameter and causes the extension of the worm, while recovery is attained by contraction of the longitudinal ones. In most complex cases, the animal stretches and telescopes section by section. This mechanism is employed by a wide variety of vermiform organisms displaying an internal cavity, including marine polychaetes and earthworms. Waves can move along the body to the head (direct waves in *Arenicola*) or vice versa (retrograde waves in earthworms). In contrast to undulatory movement, peristalsis requires the presence of an internal cavity essential for a hydrostatic mechanism of propulsion. In worms, peristalsis can be combined or alternated with other mechanisms, such as bolting, pacing, and undulatory movement. In the trace-fossil record, peristaltic movement has been inferred for a number of vermiform structures (e.g. *Planolites*), although diagnostic indicators of peristalsis are commonly absent. In other cases, the presence of constrictions in the burrow boundary suggests a deformable body and the use of peristalsis. Perhaps the best available evidence of peristalsis is found in ichnotaxa included in the ichnofamily Arthrophicidae (i.e. *Arthrophycus*, *Phycodes*, *Daedalus*) (Seilacher, 2000). These trace fossils exhibit a distinctive ornamentation ("fingerprints") that tell us about the locomotion mechanism involved: evenly spaced transverse rings visible to the bare eye (the "arthrophycid signature") and fine, submillimetric wrinkles only exceptionally preserved (Seilacher, 2007a). This fine ornamentation was imprinted by the animal cuticle on the burrow wall as a result of peristaltic movement.

Glide-crawling consists of the passage of a series of muscular waves along the body or the part of the body responsible for locomotion. A flat morphology or a flat foot that allows ample contact with the substrate is essential in glide-crawling. This is typically illustrated by gastropods, but also by other groups (e.g. turbelarians and nemertines). The gastropod foot is a hollow muscular organ consisting of numerous variable oriented fibers, which moves over the substrate through waves, locomotion being assisted by mucus secretion. In the trace-fossil record, a number of superficial and very shallow structures, such as *Archaeonassa*, have been assigned to gastropods employing a glide-crawling strategy (Knox and Miller, 1985; Buckman, 1994), although attribution to gastropods has been questioned by others (Yochelson and Fedonkin, 1997). Glide-crawling is commonly complemented by ciliary movement.

In push-and-pull-crawling (or the "double-anchor mechanism"), the penetration and the terminal anchors are applied alternately to produce a stepping motion. To work efficiently this mechanism requires organisms with an internal fluid cavity.

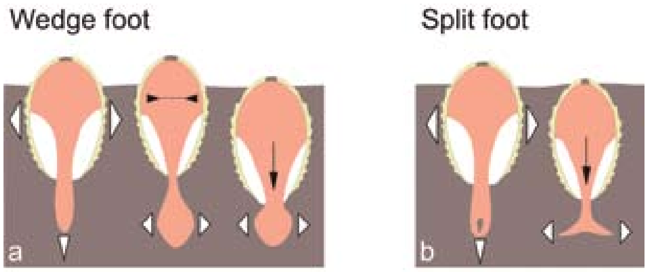


Figure 3.3 Bivalve push-and-pull-crawling ("double-anchor mechanism"). In this technique, the penetration and the terminal anchors are applied alternatively to produce a stepping motion. (a) Wedge foot bivalve burrowing cycle: extension of the food, shell opened against the sediment providing a penetration anchor (left), followed by contraction of adductor muscles and fluidization of the substrate (center), and final expansion of the foot (terminal anchor) and protraction of the shell. (b) Burrowing cycle in a protobranch bivalve: penetration anchor (left) and terminal anchor (right) displaying the open flaps of a split foot. Based on Seilacher and Seilacher (1994).

Bivalves represent the archetypal example, but other mollusks, such as gastropods and scaphopods, and many polychaetes push and pull, albeit in some cases in combination with other mechanisms. In the case of bivalves, the locomotion mechanism is based on rhythmic changes of shape performed by a single muscular foot (Trueman, 1966, 1975; Seilacher and Seilacher, 1994) (Fig. 3.3a–b). Trueman (1975) reconstructed the stages of the digging cycle based on the analysis of film and recordings of pressure measured by an electronic transducer. First, the foot makes a major probe downwards to penetrate into the sediment and be able to pull the shell into an erected position (initial penetration, see Trueman, 1975). Then, the animal moves into the substrate repeating regularly a digging cycle (Trueman, 1975) involving a sequence of steps: (1) adductors relaxed, siphons are closed (to avoid water from passing out during subsequent adduction), and the foot is extended into a slender blade-like structure; (2) valves are closed by contraction of adductor muscles and water is ejected from the mantle cavity through the pedal gape (fluidizing the sediment), at the same time a pulse of pressure causes dilation of the foot to form a terminal anchor; (3) contraction of foot retractor muscles results in the shell being dragged into the sand (siphon reopen at the end of retraction); (4) adductor muscles relax and the shell reopens (by the energy stored in the ligament), pressing into the sand to form a penetration anchor, and (5) the shell is static and the foot is protracted (plateau in cycle curve, Trueman, 1975). The cycle is repeated during the entire burrowing period. This digging cycle can be understood in terms of two phases: the penetration and the terminal anchor (Fig. 3.3a–b). During penetration, the foot is extended into a slender blade-like structure, the shell acts as a penetration anchor by opening the valves to avoid backslippage (Fig. 3.3a). Hydrostatic pressure generated by contraction of the adductor muscles and closure of the valves produces expansion of the foot generating a terminal anchor (Fig. 3.3b). Once a firm foot anchorage is obtained, pedal retractors (i.e. shell protractors) are contracted and the shell is pulled forward. Anchorage of the foot is generated by a pressure pulse which may produce a broad flat area of contact with the sand (e.g. *Donax*), a bulbous swelling (e.g. *Ensis*), or the outward spreading of the cleft foot of protobranchs. The locomotion trace *Protovirgularia* commonly associated with the resting structure *Lockeia* is interpreted as the product of a push-and-pull mechanism by protobranch bivalves (Seilacher and Seilacher, 1994; Mángano *et al.*, 1998; Carmona *et al.*, 2010) (see Section 1.2.7). Schäfer (1972) also regarded the locomotion of brittle stars as a variant of a push-and-pull mechanism, although it strongly differs from the archetypal double anchor mechanism of bivalves (Box 3.2).

Bolting consists of the forward ejection of a frontal organ. This is performed either rapidly as a bolt or slowly pressing into the sediment to form a cavity. Bolting is employed by various infaunal soft-bodied organisms, such as siphunculids, priapulids, and polychaetes, the latter usually in conjunction with peristaltic or undulatory movements. Although biogenic structures produced by bolting have been observed in modern environments, their recognition in the fossil record is not straightforward. However, recent neoichnological experiments suggested that the burrow system *Treptichnus pedum* may be the product of priapulids employing a bolting mechanism (Vannier *et al.*, 2010).

Schäfer (1972) defined multiple circular shoveling as a mechanism consisting of the coordinated use of locomotory appendages in a circular fashion and associated it with spatangoids and some polychaetes. Multiple circular shoveling is essentially performed by organisms with rigidly armored bodies and appendages equipped with their own musculature. Interestingly, Trueman (1975) also affiliated this mechanism to arthropods, including echinoids and arthropods within the same group: organisms with a hard internal or external skeleton. A classic example is illustrated by the burrowing activities of the spatangoids *Echinocardium cordatum* and *E. mediterraneum* (Bromley and Asgaard, 1975; Kanazawa, 1995). Heart urchins have a calcareous thin test covered by delicate and highly specialized spines, perfectly adapted for different tasks during burrowing, sediment transport and maintenance of the structure. Spatangoids use the spatulate spines on the plastron to propel themselves forwards and the spines on the ambitus and aboral part of the test are used for digging down and transporting the sediment (mixed with mucus) from the frontal part backwards around the body (Bromley and Asgaard, 1975). Metachronal waves seem to run over the armor from the front and below backward and upward. The burrowing activities and feeding habits of *E. cordatum* and *E. mediterraneum* have been thoroughly investigated by Bromley *et al.* (1995), who convincingly proposed that chemosynthesis is a common strategy in some deep-tier burrowing spatangoids. In the ichnological record, this mechanism is illustrated by the spatangoid echinoids ichnogenera *Scolicia* and *Bichordites* (Smith and Crimes, 1983; Uchman, 1995). Some of these structures are constructed in relatively deep, partially dewatered firm substrate, completely impregnated with mucus and can preserve scratch marks produced by the work of the spines.

Pacing or stepping results in walking or running. Pacing involves the use of mobile supports (i.e. locomotory appendages) to allow the body to be carried above and ideally not touching the

Box 3.2 The trace-fossil record of ophiuroid movement

Modern ophiuroid locomotion is quite versatile, the animal being able to move in many possible ways. Flexible arms are a key evolutionary innovation of brittle stars, providing freedom of movement exploited in diverse modes of life and feeding strategies (Fig. 3.4a–e). Contrary to asteroids (Fig. 3.5a), ophiuroid locomotion is mainly performed by horizontal and vertical undulatory movements of the long, flexible arms; the tube feet, protruding from the underside of the arms, playing a subordinate role. Four, strong longitudinal muscles press the calcareous vertebra-like segments together achieving joint-like mobile connections between them. Freedom of movement is illustrated in feeding strategies (e.g. coiling) and in the rowing action of the muscular arms during horizontal locomotion, swimming, and digging. One of the most common locomotion strategies, the so-called walking gait, involves four arms organized in two pairs, the two arms of a pair working symmetrically. The odd arm is located at the front or is trailed behind, and does not participate in locomotion, although may serve as a sensor. Whip-like movements of the arms performed in a rowing mode are generated by contraction of longitudinal muscles. When the anterior pair of arms swings forwards, the angle between them decreases, they are laid down and grip the substrate with their tips providing an anterior anchor. As the arms are arched, the body is slightly dragged forward. Then, the posterior pair performs a forward beat. These arms bend as soon as they touch the ground, lift the body, and push it forward. As the amplitude of the beat of the anterior arms is typically larger than the posterior ones, the front ones pull, and the posterior ones push and lift. In a faster gait, only the anterior pair of arms is used in propulsion producing a series of leaps. In *Arcichnus saltatus*, described from the Devonian Hunsrück Slate of Germany, horseshoe trace fossils of the anterior arms are arched forwards and those of the posterior arms are lacking, suggesting “ophiuroid jumping”. The distance between consecutive horseshoe imprints suggests that the action of the current most likely allowed the producer to be carried further than it could normally leap. Yet another curious biogenic structure, recording another variant of ophiuroid locomotion, is the hook-shaped or sinuous trace fossil *Ophioichnus aysenensis* from the Lower Cretaceous Apeleg Formation of Chile. These structures are associated with *Asteriacites lumbricalis*. These ophiuroid trackways were produced by the sculling action of the flexible, long arms while the body was held clear off the ground. Ophiuroids are also active burrowers in soft substrates; some of them resting shallowly within the sediment, whereas others can inhabit semipermanent structures up to 10 cm deep, extending their arm tips above the sediment–water interface (Fig. 3.5f). When digging, the animal is fully extended; arms perform lateral undulations while the tips remain mostly stationary, anchored to the surface. As a result, the central disc rotates penetrating into the sediment, aided by the sweeping action of the disc tube feet. Resting and burrowing activities of brittle stars, mostly in marginal- to shallow-marine deposits, are commonly preserved in the trace-fossil record (Fig. 3.4a–e). Specimens of the resting trace *Asteriacites lumbricalis* with a distinct central disc impression or slender vermiform arms, or both, clearly point to an ophiuroid producer. However, irrespective of the asteroid appearance, morphotypes displaying proximal expansion of the arms, arm branching, or opened or curling arm tips are most likely the work of brittle stars (Figs. 3.4a–e, 3.5b–e). According to this view, the different morphological variants of *Asteriacites lumbricalis* are regarded as “snapshots” of burrowing ophiuroids moving up, down, or laterally as they interacted with the sediment. Proximal expansion of the arms and lanceolate shape result from the back and forth rotation of the central disc generated by the undulatory movement of the arms, while the tips remained mostly stationary on the surface. Specimens with a deep central impression and shallower short arms record a life position in which the disc and proximal arms were completely hidden in the sand, with the arm tips extended upwards. Some shallowly impressed structures with transverse delicate ornamentation on the arms or chevron-like ornamentation in the central disc-like structure reveal the sweeping action of the tube feet. Evidence of brittle star burrowing behavior is also displayed by deep, plug-shaped structures showing pentameral symmetry, assigned to the ichnogenus *Pentichnus*. These structures, described from the Carboniferous of Kansas, are interpreted as ophiuroid dwelling burrows (Fig. 3.5f).

References: Seilacher (1953b); Fell (1966); Reese (1966); Maerz *et al.* (1976); Heddle (1967); Schäfer (1972); Sutcliffe (1997); Mángano *et al.* (1999, 2002a); Bell (2004).

substrate. Appendages capable of pacing are arranged in pairs. If substrate conditions are appropriate, appendages imprint tracks on the sediment, which are in turn, organized in trackways (e.g. Davis *et al.*, 2007). Pacing is mostly employed by terrestrial organisms rather than aquatic ones, although limulids and many marine crustaceans (e.g. benthic decapods, isopods, notostracans) may also use this mechanism if moving on the sediment–water interface. In arthropods, the basic limb movements employed in pacing consist of combining promotor–remotor swing and levator–depressor movements (Trueman, 1975; Manton, 1977). While the promotor–remotor swing is implemented by muscles from the proximal part of the leg, which pass into the trunk, the levator–depressor movements are mostly controlled by intrinsic muscles within the leg. In most arthropods, the swing movement takes place at the proximal end of the limb (i.e. at the coxa–body junction) around an axis lying in the transverse plane of the body (Manton, 1977). The levator–depressor movement takes place at right angles to the promotor–remotor swing and distal to the coxa, using one or two pivot articulations situated between leg segments. During the forward swing, the leg is outstretched with its tip on the substrate at the beginning of the backstroke, halfway through the backstroke the leg flexes (if the limb tip is not to slip on the ground), and finally it is extended again during the latter part of the backstroke (Manton, 1977, Fig. 2.3b). The

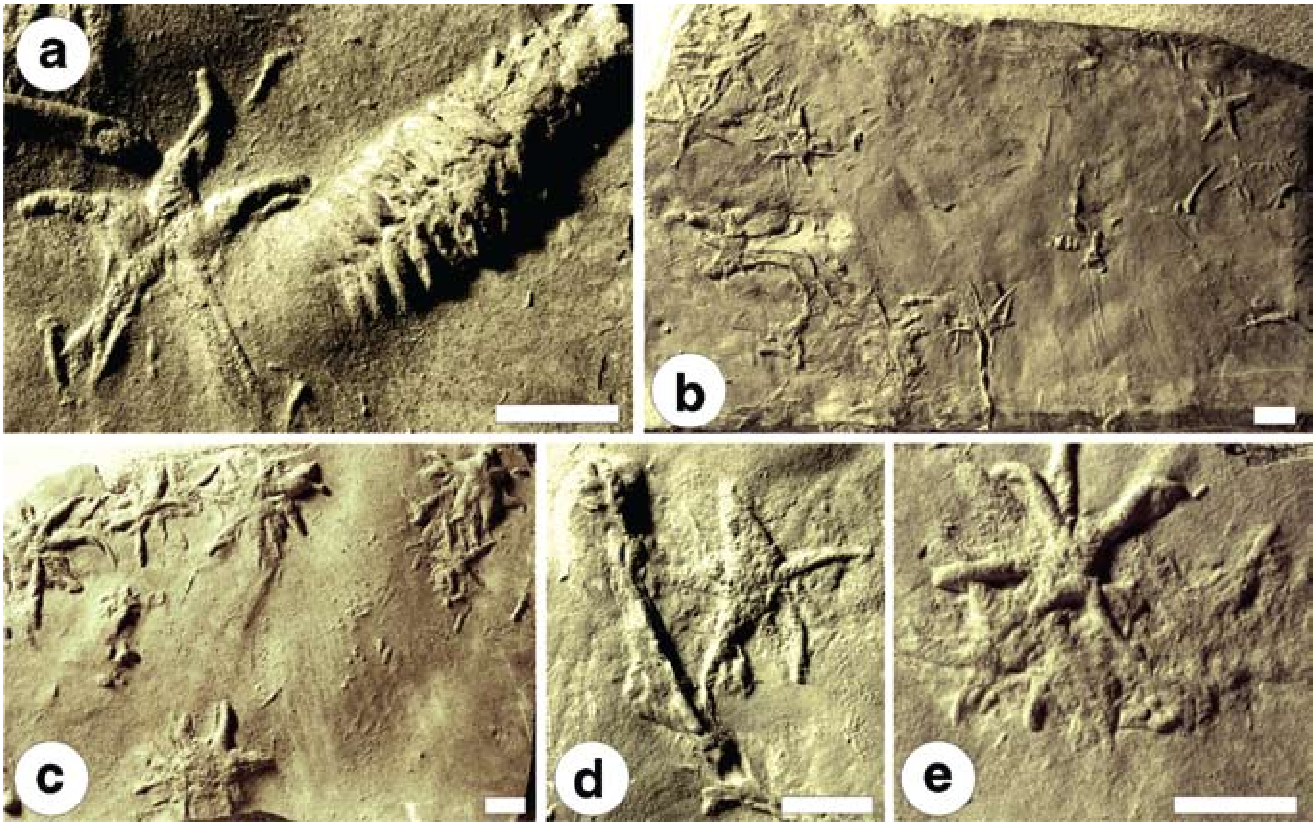


Figure 3.4 The ophiuroid resting trace *Asteriacites lumbricalis* from the Upper Carboniferous Rock Lake Shale Member, Stanton Formation, Lansing Group. Site south of the Kansas City International Airport, Missouri, central United States. All scale bars are 1 cm. (a) Arm proximal expansion recording the burrowing action of the tube feet in the disk area. (b) Assemblage consisting of multiple specimens displaying lateral and vertical repetition, resulting from animals trying to escape a sedimentation event. Note asteroid-like specimen (upper right) and structure reminiscent of an ophiuroid with well-defined polygonal disk (upper left). (c) Specimens displaying irregular morphology and multiple arms, produced by the superposition of successive impressions due to slight lateral shifting and repositioning. (d) Specimen displaying arms with variable morphology resulting from modification during burrowing: some arms are asteroid-like in appearance (upper and lower left arms), but others clearly reveal the ophiuroid origin (upper right). (e) Specimen exhibiting a double arm (upper) as result of passive rotation of the disk during arm rowing. The hook-like tip also reveals the flexible nature of the ophiuroid arm.

levator–depressor actions involve the flexure and extension of the limb, the limb being firmly pressed on the ground during the propulsive backstroke. This results in the forward movement of the body. In principle, large angles of swing and long legs can result in long strides and fast running. In Onychophora, the shortening and extension of the soft, non-articulated limbs during stepping is only performed by muscles without joints.

In a multi-legged organism steady locomotion is most commonly achieved by the existence of a phase difference between one leg and the next creating a metachronal rhythm. Successive limbs are coordinated so when some swing forward off the ground (forward recovery swing), others are pressing backward performing the propulsive backstroke. This results in cycles of limb movement or metachronal waves. The fields of movement of successive legs may overlap considerably, but legs themselves do not touch one another. The phase difference between one leg (n) and the next (n + 1) can range between 0 (both legs are moved synchronously) and 1 (phase difference is one complete cycle). The swing angle, limb length, and phase difference between successive legs (or groups of legs) together with the relative duration of the forward and backstroke are critical to gait pattern and speed of movement. Pacing or stepping represents a slow kind of walking. Increased speed turns into running, which involves a more rapid succession of paces. The slowest method of walking in arthropods and polychaetes involves stepping by the limbs or parapodia, respectively, while the trunk remains straight (Fig. 3.6a). In polychaetes, an increase in speed of pacing is accompanied by horizontal undulations of the trunk, which as they increase in amplitude lead to a swimming-like motion (Manton, 1977). However, in arthropods, trunk undulations tend to be inhibited. If undulatory movements are present, they do not contribute to locomotion or to an increase in speed of walking or running. The appearance of body undulations in centipedes and chilopods during their fastest gaits reduces the effective angles of swing of the propulsive legs, and, therefore, reduces the speed potential of the fastest gaits, wasting energy in lateral movements (Fig. 3.6b). Typically, as the relative duration of the backstroke decreases, the points of support of the body against the substrate also decrease (and are located further apart), and the distance between successive propulsive legs increases (compare Fig. 3.6c with Fig. 3.6d).

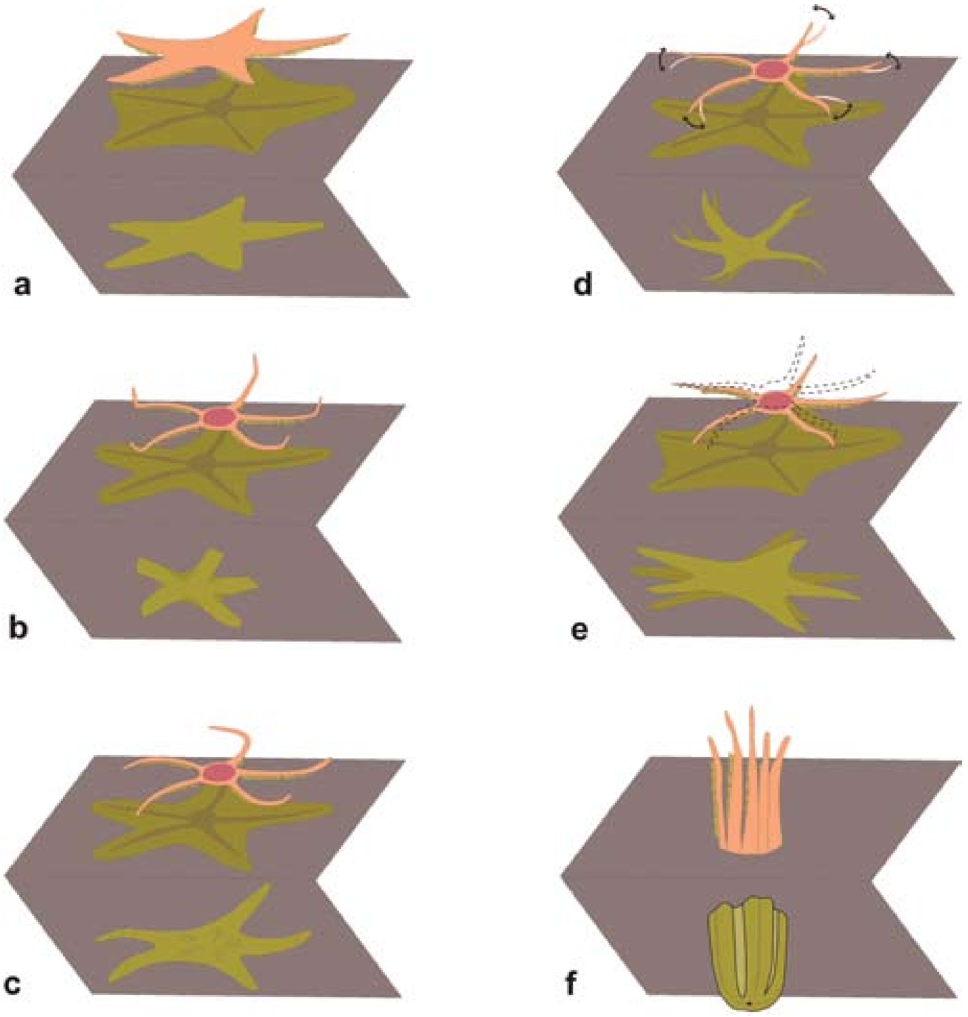


Figure 3.5 Asteroid and ophiuroid burrowing mechanisms and resulting biogenic sedimentary structures. (a) Asteroids stay still on the substrate with their arms extended and their tube feet projecting from the underside of the arms; arms perform a sweeping action that creates a shallow, inflated, five-rayed hypichnial structure (*Asteriacites quinquefolis*). (b–f) Wide range of behaviors recorded by extant burrowing ophiuroids. (b) Ophiuroid is resting with central disk deeper into the sediment and the tips projected upward. The resulting *A. lumbricalis* specimen displays a deeper central part and short truncated arms. (c) Ophiuroid is undulating its flexible arms in a horizontal plane at the same time as the tube feet of the disk area perform a sweeping action. The resulting *A. lumbricalis* specimen may display curved arm impressions and delicate chevron-like ornamentation in the disk area. (d) If the rowing action of the arms continues, the central part is buried into the sediment, the tips moving sideways on the sediment. The resulting *A. lumbricalis* specimen displays a deeper central area and arms with bifurcated tips. (e) Ophiuroid is migrating upwards escaping a rapid sedimentation event. The rowing action of the arms may result in rotation. The resulting *A. lumbricalis* specimen displays multiple superimposed impressions with slight lateral movement. (f) The disk of some burrowing ophiuroids can penetrate more than 10 cm into the sediment, generating a plug-shaped structure with pentameral symmetry (*Pentichnus gugelhupf*).

In high-speed variants, not only secondary undulations, but also abdominal marks indicating unsteady movement, may be present (Fig. 3.6b, d). Gait pattern is highly variable, and controlled by intrinsic (e.g. limb number and morphology) and extrinsic factors (e.g. substrate consistency, slope, temperature). Brady (1947) documented variations in arthropod gait patterns in trackways preserved in eolian-dune deposits, and related them to variations in slope, temperature of the environment, and sand moisture. The trace-fossil record hosts abundant evidence of structures produced by pacing, including a wide variety of arthropod and vertebrate trackways. The list of erected arthropod trackways documenting walking and running is impressive. Many of the available names, however, require further taxonomic revision, including some very common ichnotaxa such as *Diplichnites* (e.g. Buatois *et al.*, 1998b; Minter and Braddy, 2009). Many trackway names have been based on poorly preserved material or a poor evaluation of the locomotion mechanism and taphonomic controls (e.g. substrate consistency). Well-established, distinct ichnogenera include: *Paleohelcura* and *Octopodichnus*, attributed to the work of scorpions or spiders, respectively (Brady, 1947; Braddy, 1995; Minter and Braddy, 2009); *Palmichnium*, assigned to the walking of eurypterids (Braddy and Almond, 1999); *Dendroidichnites*, related to locomotion by myriapods on very soft surfaces (Demathieu *et al.*, 1992; Buatois *et al.*, 1998a;

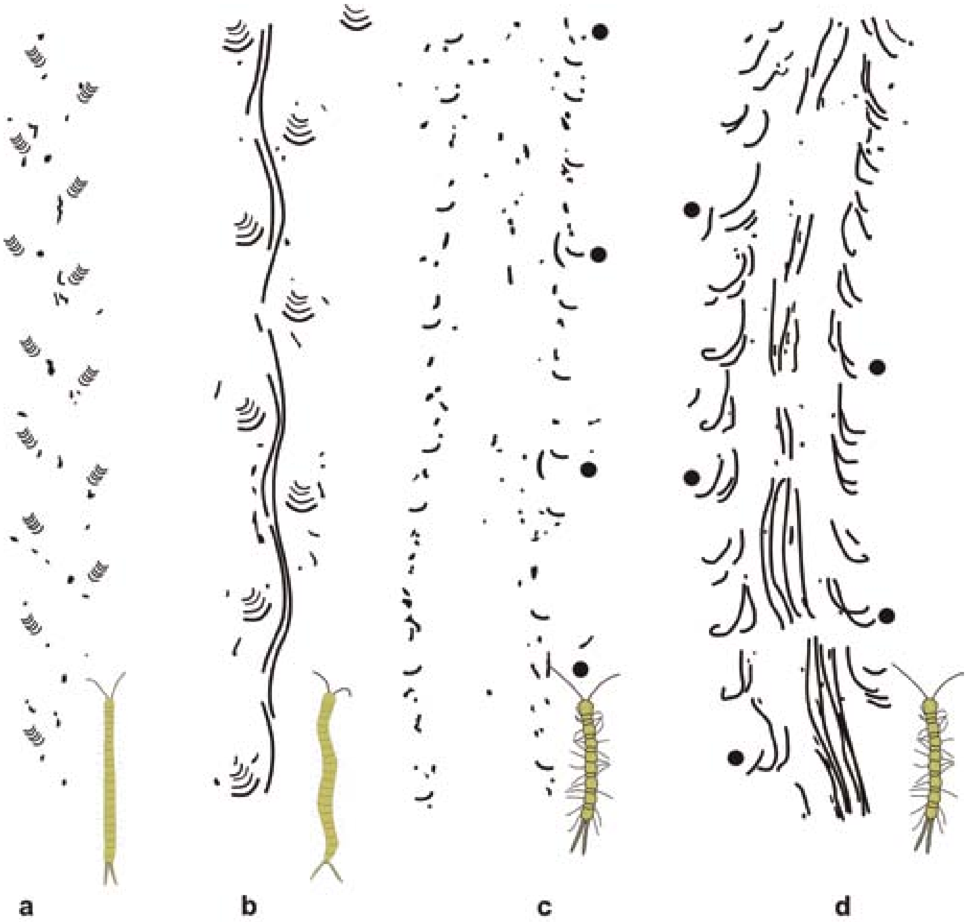


Figure 3.6 Extant centipede running trackways. Centipedes running over smoked paper (printed in reverse). All tracks 50 mm long. (a–b) Tracks of the centipede *Cormocephalus pseudopunctatus*. (a) Running at a slow gait. Tracks form oblique forwardly directed groups, no axial mark. (b) Running at a fast gait. Tracks fall on almost the same spot, and the stride is so long that the animal is unable to hold the body off the ground, resulting in an axial drag mark. (c–d) Tracks of the centipede *Lithobius forticatus*. Black spots are one stride length apart. (c) Running at a slow gait, stride length 14 mm, approximate speed 80 mm/s. Tracks look scattered, but in fact form a regular series. Legs of a pair are in phase. (d) Running at a fast gait, stride length 21 mm, approximate speed 280 mm/s. Tracks are grouped into four rows per stride length. Legs of a pair are in opposite phase (notice staggered black spots). Icons of the producers on lower right. Based on Manton (1977).

Minter and Braddy, 2009); *Lithographus*, attributed to trackways of pterygote insects (Minter and Braddy 2009); and *Stiallia*, interpreted as the feeding activities of an arthropod (Walker, 1985; Buatois *et al*., 1998a; Minter and Braddy, 2009). However, a cautious approach in interpreting the producers from trackways is needed as emphasized by recent experimental neoichnological studies. Davis *et al*. (2007) demonstrated that a wide range of morphologies can produce very similar trackways and, in contrast, one producer can generate trackways potentially attributable to different ichnotaxa.

Using what is essentially a modification of the mechanism for walking on the substrate, some arthropods are able to burrow within the sediment producing structures of variable complexity. An excellent example displaying ample representation in the trace-fossil record is the ichnogenus *Cruziana*, commonly, although not exclusively, attributable to the combined locomotion and feeding activities of trilobites in Lower Paleozoic rocks (Box 3.3).

Moving into hard substrates, drilling involves penetration in a cemented substrate (laterally persistent hardground or isolated wood logs or shells). This mechanism is typically associated with protection in the case of dwelling structures of boring bivalves such as *Petricola* and *Zirphaea*, or predation in the case of drill holes produced by carnivorous gastropods such as *Murex*, *Natica*, and *Thais*. The most general term "bioerosion" is preferred today because it includes every form of biological penetration into a hard substrate, such as etching, rasping, scraping, and drilling (Bromley, 1992). A wide variety of morphologies and ethological types are the product of bioerosion at all scales (see Section 1.1). Many groups of animals are able to interact with a hard substrate producing biogenic structures, including sponges, siphunculids, polychaetes, phoronids, acrothoracican cirripedians, patelled gastropods; holothurians, regular echinoids and cephalopods (Trueman, 1975; Bromley, 1992; Taylor and Wilson, 2003). Bioerosion can be performed by mechanical abrasion, chemical means, or a combination of both. In the first case, the animals use special tools to scrape off tiny particles. In the second case, a scar, tube, or cavity is generated by means of a corrosive secretion. As a generalization, mechanical bioerosion is mainly performed in calcareous substrates, and chemical bioerosion is performed in harder substrates. One of the best-known examples of mechanical drillers is that of pholadid bivalves. These borers employ cycles of successive contractions of the anterior and posterior adductor muscles, causing the movement of the valves in various directions, with consequent abrasion of the walls (Nair and Ansell, 1968; Trueman, 1975; Röder, 1977; Carmona *et al*., 2007). The valves of rock-boring bivalves have two axes around which they can pivot, in such a way that their marginal spines form a series of scratch ornaments arranged as if they were a row of chisels (Seilacher, 1985). In the ichnological record, structures of boring bivalves are represented by the ichnogenus *Gastrochaenolites*

Box 3.3 Trilobite burrowing: the trunk-limb feeding mechanism

Ichnological and functional-morphological evidence suggest that trilobites display a peculiar locomotion and burrowing strategy, which is herein referred to as the trunk-limb feeding mechanism. In fact, trilobites fed as they moved sweeping the sediment with their appendages in an inward direction (as opposed to most extant arthropods, such as insects). This mode involved moving sediment inward and backward towards the ventral midline. Scratch-mark ornamented bilobate trace fossils, typically preserved as hypichnial ridges on sandstone soles, provide excellent examples in Lower Paleozoic marine rocks. These ribbon-like bilobate structures ornamented by V-shaped striations are commonly assigned to the ichnogenus *Cruziana* and attributed, although not exclusively, to the combined locomotion and feeding activities of trilobites (Fig. 3.7a–e). *Rusophycus* is a short bilobate structure similar to, and in many cases forming compound structures with, *Cruziana* but recording stationary burrowing for resting, hiding, laying eggs, or feeding purposes. Functional analysis of the fine ornamentation of *Cruziana* and *Rusophycus* reveals details of the ventral morphology of trilobites and its peculiar feeding strategy. Contrary to the excavating strategy of many arthropods that move sediment away from under their body in a centrifugal fashion, the delicate scratch marks covering the lobes indicate that trilobites swept the sediment *towards* the ventral midline. Each walking (endopodal) leg describes a trajectory from the marginal-external area towards the mid-ventral surface where food is passed, close to the body towards the backwardly opening mouth. As multi-legged animals, trilobites use metachronal waves passing from the rear to the front of the organism to efficiently coordinate appendage movement. In trackways resulting from steady walking, series of imprints commonly overlap as each metachronal wave only advances the body a fraction of its length. In plunging structures or excavations, the coordinated action of the walking appendages (endopodites) on the substrate is responsible for the classic V-shaped ornamentation, the "V" opening being in the direction of movement. Trilobites lack specialized appendages able to manipulate large food items. In the absence of mandibles and chelipods, trilobites must have only been able to collect small food particles from the sediment (i.e. deposit feeders), using the inward sweeping action of their limbs. According to ichnological and anatomical evidence, a microphagous mode of feeding was most likely the primary habit, although the close association of some conspicuous *Rusophycus* with worm structures and the hypostome morphology suggest that a macrophagous feeding habit was attainable by some large trilobites. Filter feeding can also be inferred as a secondary feeding habit in trilobites based on ichnological evidence. Trilobites possessed biramous undifferentiated limbs only varying in size along the body, typically with the cephalic appendages being the most robust ones. The inner rami, the endopodite (also endite or telopodite), had the primary function of locomotion and assisted in feeding. The function of the outer rami, the exopodite (also exite), has been the subject of discussion. In principle, these feathered appendages primarily served for respiration purposes and swimming. Dolf Seilacher considered that the feathered exopodites were involved in straining the sediment while feeding and occasionally used in swimming. However, Jan Bergström proposed that exopodites could have played a dominant role in burrowing, with respiration being performed by other soft, non-preserved structures. In his interpretation, exopodites were provided with strong lamellar spines rather than soft gill filaments. According to this view, spines are the main tools recorded in some well-known *Cruziana* (e.g. the *rugosa* group) characterized by multiple (8 to 12) sets of parallel scratches. Behind the cephalon, a series of segments articulated with one another permitted dorso-ventral, but not lateral bending of the body. Posteriorly, the pygidium was formed by fused segments, each of which carried a pair of biramous legs. These posterior legs are typically the smallest in size. This basic body plan allowed trilobites to burrow in different positions, resulting in what has been called "segmental variation". The dorsally flexed attitude records the isoclinal burrowing position, the front and rear ends being slightly arched to promote the formation of a flushing current. Head down (prosocline) burrowing resulted in cruzianids characterized by conspicuous endopodal scratch marks performed by a few pairs of strong cephalic appendages. In this position, scratch marks are wide angled and are transverse to the midline; genal spines, being upwardly directed, are not recorded in biogenic structures. Some trilobites may have used the cephalon margin as a shovel in a way similar to modern xiphosurans. Deep prosocline rusophycid structures may show anterior crescentic ridges or exceptionally the impression of the anteriormost antennae (Fig. 3.8). In contrast, tail down (opisthocline) burrowing involved smaller pygidial endopodites and the brushing of the outer rami of the leg (exopodites). Exopodal scratch marks are commonly much more delicate than endopodal scratch marks, present at a more external position in relation to the axis (in many cases forming an external lobe, such as in *Cruziana semiplicata*), and tend to be more or less subparallel to the median line. In this position, the backward bend of genal and pleural spines may favor the formation of marginal ridges in the biogenic structure produced (Fig. 3.8).

References: Seilacher (1970, 1985); Eldredge (1970); Bergström (1973, 1976).

(Kelly and Bromley, 1984; Carmona *et al*., 2007). Carmona *et al.* (2007) demonstrated that boring bivalves perform the same patterned behavior to penetrate firm- and hardgrounds, putting a cautionary note on recognizing hardgrounds based on the presence of the boring *Gastrochaenolithes* and restricting the distribution of this ichnogenus to hard substrates (see Section 2.7). Other bivalves (e.g. *Teredo*) are adapted to bore exclusively in xylic substrates. They do so by using the valves as boring tools, rather than employing them to enclose the soft body. Each valve consists of a beak-like front section, a protruding middle section

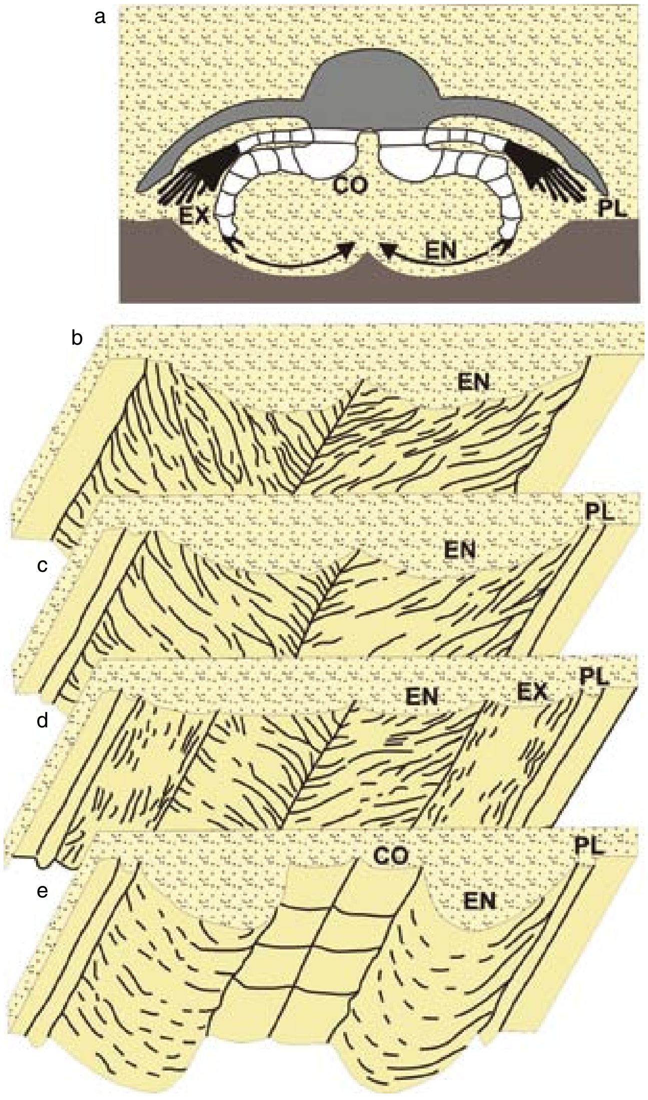


Figure 3.7 Trilobite burrowing and variability in the morphology of *Cruziana*. (a) Cross-sectional view of a trilobite showing first appendage segment (CO, coxae) and biramous appendages characterized by a strong inner branch (EN, endopodite) and feather-like outer branch (EX, exopodite). Some parts of the exoskeleton (gray), such as pleural/genal spines (PL), may also be recorded in some *Cruziana* and *Rusophycus*. (b) *Cruziana* displaying only endopodal lobes excavated by the endopodites (EN). (c) *Cruziana* exhibiting endopodal lobes (EN) and a marginal pleura/genal spine mark (PL). (d) *Cruziana* displaying a four-lobe geometry with two internal endopodal lobes (EN) adjacent to two external exopodal lobes (EX); pleural spine marginal mark may be present. (e) *Cruziana* displaying prominent axial coxal impression, two convex endopodal lobes and a marginal pleural/genal spine mark. Based on Seilacher (1970).

with rows of double pointed teeth, and a back section consisting of a smooth end. The activity of wood-boring bivalves is represented in the trace-fossil record by the ichnogenus *Teredolites* (Bromley *et al.*, 1984). The well-known ichnogenus *Oichnus* is recorded by circular to oval holes produced by the predatory activity of carnivorous gastropods, although small holes, also included in the same ichnogenus, can be generated by octopodes to inject poison into their prey (Bromley, 1981, 1993). In addition to these classic examples, a large number of borings displaying diverse morphologies are known in the ichnological record (Bromley, 1992, 1994, 2004; Taylor and Wilson, 2003).

Schäfer (1972) included chimney climbing as a distinctive mechanism involved in the ascending and descending movement within vertical burrows with mucus-lined or constructed walls, although the same behavior should be expected on unlined vertical structures in firmgrounds. However, in the case of crustaceans or some polychaetes (e.g. *Sabellaria*), the use of appendages or parapodia during climbing is analogous to pacing or "walking on the walls". Animals build their burrows with the right inner diameter (not too small, not too large) to allow for chimney climbing. The construction of sand tubes by the polychaete *Sabellaria* is one of the best-documented examples. *Sabellaria spinulosa* lives freely suspended in its tube, held only by three pairs of thoracic parapodia, which are used in locomotion up and down the tube. The worms settle in colonies forming large constructions referred to as sand-coral reefs (Ekdale and Lewis, 1993). If the internal diameter of the tube is too large, contact with the internal surface is insufficient to push effectively against the wall and move the body upward. On the other hand, if the body fits too tightly within the burrow, climbing is impossible and usually peristalsis, in the case of worms, is used to move up and down the tube (Schäfer, 1972). In other cases, organisms find an appropriate burrow built by another animal, and may occupy it either for protection or to hunt. In the trace-fossil record, *Skolithos* may illustrate strategies such as chimney climbing, as well as the crustacean burrow shafts of *Ophiomorpha* and *Spongeliomorpha*.

Jumping is a mechanism that requires large amounts of energy and is commonly used combined with swimming, walking, or running. It is exclusive of vertebrates and arthropods. The adaptations and dynamics involved in jumping are specific to different taxa. Most multi-legged animals cannot achieve steady locomotion by moving all of their legs or all legs of one side of the body in unison (Manton, 1977). Large flat thoracic legs of copepods are an exception; they move synchronously resulting in intermittent jumping through the water (Manton, 1977). However, the trace-fossil record suggests that several marine benthic arthropods were able to achieve jumping by multiple legs performing a backstroke in unison (Seilacher *et al.*, 2005; Seilacher, 2007a). The oldest record of this jumping mechanism is recorded in the Cambrian by *Tasmanadia cachii* in which subsequent series of imprints do not overlap. Instead, they form individualized patterns that probably correspond to the general outline of the tracemaker (Seilacher *et al.*, 2005). This means that the animal was not continuously supported; rather it must have moved in jumps, driven by the simultaneous action of all appendages (and most likely help by the current). The distinctive Carboniferous trackway *Orchesteropus atavus* also records a similar mechanism, most likely produced by "galloping" xiphosuran (Seilacher, 2007a). Based on functional morphology analysis, Manton (1977) concluded that some trilobites (e.g. *Olenoides*) were able to perform multiple-leg jumping. In marginal-marine and terrestrial settings, examples of jumping structures attributed to monuran apterygote insects have been included in the ichnogenus *Tonganoxichnus*

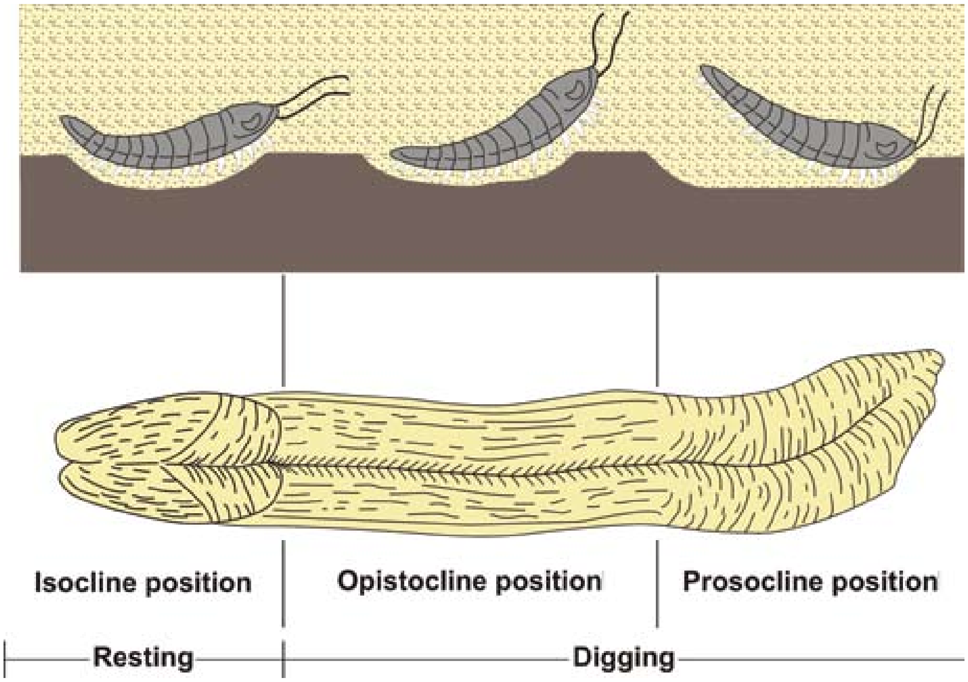


Figure 3.8 Trilobite burrowing position and the resulting biogenic structure. From left to right. Isocline resting position, *Rusophycus* displaying dorsoventral morphology; coxal and pleural/genal-spine marginal ridge may be present in some *Rusophycus* ichnospecies. Opisthocline (tail-down) burrowing position. Exopodal lobes get better representation; pleural or genal marginal ridge typically present. Prosocline burrowing position, endopodal lobes get full representation, exopodal markings uncommon, head-shield mark may be present in some rusophysid versions. Based on Seilacher (1970).

Box 3.4 The jumping of monuran insects

Superbly preserved trace fossils attributed to monuran insects (an extinct group of archaeognathan apterygote insects) occur in late Paleozoic paralic deposits in the United States. In particular, detailed study of specimens from Kansas and New Mexico allows the reconstruction of the functional morphology and behavior of their producers. These trace fossils, assigned to the ichnogenus *Tonganoxichnus*, provide evidence of monuran jumping behavior, favoring comparisons with modern machilid archaognathans, as illustrated by the genus *Petrobius*. The ichnospecies *T. ottawensis* (Fig. 3.9a) is characterized by a fan-like arrangement of mostly bifid scratch marks at the anterior area that records the head- and thoracic-appendage backstrokes against the sediment. The posterior area displays chevron-like markings or small subcircular impressions recording the abdominal appendages of the animal, ending in a thin straight terminal extension. Specimens display lateral repetition, and are commonly grouped into twos or threes with a fixed point at the posteriormost tail-like structure. *Tonganoxichnus ottawensis* is thought to record the ability of these apterygote insects to perform successive lateral jumps with a pivot point at the posterior tail-like extension. This ichnospecies most likely represents jumping in connection with a defensive strategy or feeding purposes (i.e. raking the microbial mat). The ichnospecies *Tonganoxichnus robledoensis* (Fig. 3.9b) has an anterior region characterized by the presence of a frontal pair of linear imprints, three pairs of lateral linear imprints, a middle medial oval imprint, and a posterior elongate axial imprint. Specimens are aligned, suggesting a forward progression via a linear succession of jumps. Jump distances were up to eight times body length. Monuran trackways, assigned to the ichnospecies *Stiaria intermedia*, are closely associated with the jumping structures. Ichnological evidence indicates that jumping was a common strategy in apterygote Paleozoic insects and developed very early in the evolutionary history of insects.

References: Mángano *et al*. (1997, 2001a); Braddy and Briggs, 2002; Minter and Braddy (2006a, 2009).

(Mángano *et al*., 1997; Braddy and Briggs, 2002; Minter and Braddy, 2006a, 2009) (Box 3.4). Interestingly, monuran jumping trace fossils display similarities with modern archaeognathan takeoff structures documented by Sturm (1955).

3.3.2 BURROWING PRE-ADAPTATIONS: THE MORPHO-STRUCTURAL APPROACH

Another approach to the problem of burrowing mechanisms is to look at particular morphological adaptations to burrowing displayed by the different organisms (Carney, 1981). This approach assumes that burrowing is primarily constrained by organism morphology. Based on this assumption, Carney (1981) recognized five main morphologies: (1) completely soft bodied-lacking significant lateral appendages (e.g. some annelids and most worm-like organisms, almost all coelenterates, some holothurians, shell-less mollusks); (2) completely soft bodied with significant lateral appendages (e.g. annelids with large parapodia, most holothurians); (3) soft bodied with partial rigid external covering (e.g. most benthic mollusks,

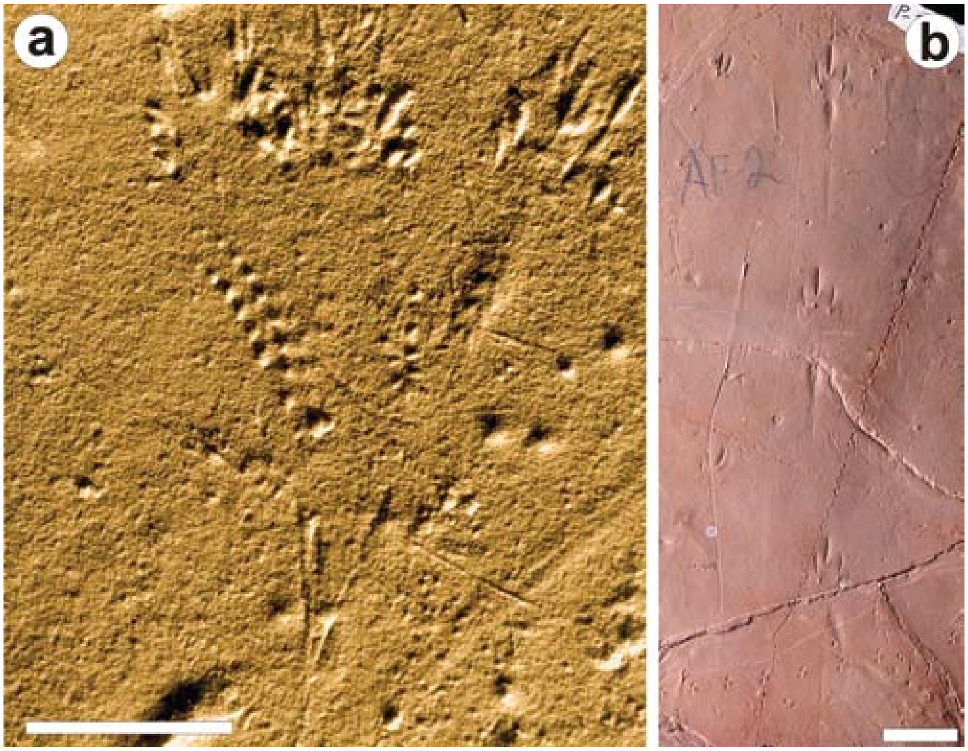


Figure 3.9 The ichnogenus *Tonganoxichnus* as evidence of jumping behavior in late Paleozoic monuran insects. (a) *Tonganoxichnus ottawensis*. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, central United States. See Mángano *et al.* (1997). Scale bar is 1 cm. (b) *Tonganoxichnus robledoensis*. Upper Permian, Robledo Mountains, Robledo Mountains Formation, southern New Mexico, southern United States. See Minter and Braddy (2006). Scale bar is 2 cm.

inarticulate brachiopods); (4) completely rigid external covering with numerous flexible appendages (e.g. most arthropods, echinoids), and (5) externally soft animals with some rigid internal structure (e.g. vertebrates, pennatulid coelenterates).

From an ichnological and functional standpoint, this morpho-structural classification is hard to adopt. For example, although large parapodia may be involved in locomotion, their presence or absence is not generally a determinant of the primary mechanism of locomotion involved. Also, the presence of a shell implies an additional cost of energy for locomotion, but does not itself determine the adopted burrowing mechanism. Regardless of the presence of the shell, the burrowing mechanism is controlled by the deformable body of the mollusk, resulting in the double anchor mechanism. In fact, this mechanism is employed by many animals lacking a shell (e.g. polychaetes). Finally, although both echinoids and arthropod exhibit multiple appendages coordinated in metachronal waves, the burrowing mechanisms are remarkably different, as clearly evidenced by the biogenic structures produced.

3.3.3 IN SEARCH OF A UNIVERSAL MECHANISM: THE RATIONALIST APPROACH

A different approach to the problem of locomotion is to search for a universal mechanism that essentially results from very basic mechanical principles. This has been the approach undertaken by Trueman (1975) and, although it may be termed a "rationalistic approach" (in the sense of being a major generalization based on inferential reasoning), it is firmly rooted in a well-founded experimental tradition (e.g. Ansell and Trueman, 1968; Trueman, 1966, 1967, 1968a, b, 1971; Trueman and Ansell, 1969). The underlying hypothesis to this approach is that despite the many morphological plans and particular locomotion techniques used by invertebrates, there are just a few basic principles involved in animal locomotion. These first principles are explained in terms of basic physical laws, such as the Newtonian laws of movement and the principles of hydraulics (Trueman, 1975; Barnes *et al*., 1993). For example, Newton's third law established that for any action there is a reaction of the same magnitude but in the opposite direction. In ichnological terms, this means that, for example, when an organism attempts to penetrate the substrate by a propeller force (action), this is balanced by the substrate frictional resistance (reaction). The organism will only be able to move if an efficient anchoring system is created (e.g. the penetration and terminal anchors) to overcome substrate resistance.

According to Trueman (1975), the animal locomotory system can be subdivided into three main components, engine, transmission, and propeller. In the engine, the chemical energy is converted into mechanical energy due to contraction of the muscles. This energy is transmitted to the propeller by means of a system of levers in the case of organisms with hard parts (mechanic transmission) or through the fluids of a hydrostatic system in soft-bodied organisms (hydraulic transmission). The propeller is the part of the organism that is in contact with the substrate and, therefore, becomes the visible element acting in animal–substrate interaction. In vertebrates and arthropods, the propeller is commonly a specialized structure (rigid propeller), while in soft-bodied invertebrates or invertebrates that use soft processes of the body in locomotion, the propeller is generally represented by part of the corporal mass, such as the proboscis of a polychaete or muscular foot of a bivalve (deformable propeller).

Based on these elements, Trueman (1975) identified one universal mechanism: the double-anchor or push-and-pull mechanism (see Section 3.3.1), involving all soft-bodied invertebrates with a hydrostatic or fluid skeleton; in other words, all invertebrates with a body cavity containing incompressible fluid that functions as a hydraulic system. In such a system, a force generated by muscle contraction is transmitted to another region of the body where it may be used in locomotion. This soft-bodied group includes animals that are completely soft, such as most worms and sea anemones, and animals that utilize soft processes of the body to burrow, such as bivalves. A circular cross-section is ideally suited to penetrate and move through the substrate using the double-anchor mechanisms as the body wall is in contact with the substrate in all directions and muscles may contribute in locomotion without loss of anchorage. The body cavity used differs according to the phylum: coelenteron in Cnidaria, coelom in Annelida, and haemacoel in Mollusca (e.g. bivalves). Organisms with some rigid skeletal support (e.g. sea urchins, arthropods, and vertebrates) constitute a second group or organisms. Members of this functional group require an exo- or endoskeleton to allow muscular antagonism (e.g. flexor–extensor). These invertebrates with rigid skeleton, are unable to attain deformation of any soft part of the body and the propeller force is applied directly by muscles incepted in the inner zone of the exoskeleton.

3.4 MOVEMENT ECOLOGY

In recent years, movement ecology has been introduced in an attempt to generate a unifying paradigm for studying movement of all types of organisms within a broader framework (Nathan *et al.*, 2008). The approach undertaken consists of the formulation of basic principles to link empirical and theoretical movement studies. The four principles proposed aim to address the internal state (why move?), motion (how to move?), and navigation (when and where to move?) capacities of the individual, as well as the influence of external factors (Nathan *et al.*, 2008; Holyoak *et al.*, 2008). The internal state accounts for physiological and/or psychological motivations that determine why to move. This implies proximate (i.e. ecological), such as searching for food, avoiding a predator, and finding a mate, and ultimate (i.e. evolutionary), such as minimizing energy cost and surviving payoffs. Motion capacities reflect the biomechanical abilities to move, embracing the multiple modes of locomotion (e.g. push-and-pull, pacing) that determine how to move (see Section 3.3). Navigation capacities are displayed by mobile animals using their sensory and cognitive traits to obtain and process information about the environment, and to determine when and where to move. In doing so, animal movement includes interaction with the external environment, encompassing biotic factors (e.g. presence of resources, competitors, mates, predators) and abiotic factors (e.g. flow of water or air, presence of obstacles, light, oxygen).

Many of the previous proposals analyzed (see Sections 3.3.1 and 3.3.3) focused on the biomechanics of movement. The movement ecology paradigm complements other approaches to movement, such as those of the biomechanical, cognitive, random, and optimality paradigms. Of these, the optimality paradigm has a relatively strong tradition in ichnology (e.g. Raup and Seilacher, 1969; Papentin, 1973; Hammer, 1998; Hayes, 2003; Plotnick and Koy, 2005; Koy and Plotnick, 2007, 2010), while a few studies have adopted the perspective of the random paradigm (Kitchell *et al.*, 1978a; Kitchell, 1979; Hofmann, 1990). Ichnological studies are commonly framed within optimal foraging theory, which assumes that organisms are driven by a tendency to maximize net energy gained per unit of time feeding (e.g. Schoener, 1987). While foraging, animals are guided by a set of basic reactions, namely strophotaxis, phobotaxis, and thigmotaxis (Richter, 1928; Raup and Seilacher, 1969). Strophotaxis is a proclivity to make U-turns so that the animal turns around 180° at intervals. The length of the animal determines the geometry of the turn. Phobotaxis keeps the organism from crossing its own and other trails. Thigmotaxis makes the animal stay in close contact with a former trail. Based on these principles, computer simulations have been developed to reproduce foraging patterns (e.g. Raup and Seilacher, 1969; Hammer, 1998). Meandering and spiral trails can be understood as paths resulting from an organism's response to the perceived spatial distribution of resources (Koy and Plotnick, 2010). Neoichnological experiments have been recently designed to evaluate animal movements as a response to the location, shape, and density gradient of food patches (Koy and Plotnick, 2010). Optimal foraging theory considers that foraging patterns are intrinsically controlled by a series of commands written in the genetic code of the organism. However, more recent studies have emphasized that patchiness in resource distribution is a strong control on foraging movement and path morphology. Organisms interact with the environment using their sensory and cognitive traits (navigation capabilities) to explore the landscape and detect spatial heterogeneity (see Section 6.8).

More recently, there have been attempts to apply ideas derived from movement ecology to the study of the fossil record by introducing so-called "movement paleoecology" (Dornbos *et al.*, 2009; Plotnick, 2009). This approach may help to place ichnological studies into a broader theoretical framework, including both internal and external determinants of movement. Although the extrapolation of ecological frameworks to the fossil record always represents a challenge, adapting conceptual tools from ecology (e.g. the guild) has historically expanded the explanatory potential of ichnology. As in the case of the notion of complex trace fossils and extended organisms, movement paleoecology represents an approach that is worth exploring. Further work is needed in order to realize its potential, and to demonstrate how it can illuminate our understanding of the trace-fossil record.

4 The ichnofacies model

Anyone can make the simple complicated. Creativity is making the complicated simple.

Charles Mingus
Unsourced quote

Ichnofacies stand today as one of the most elegant but widely misunderstood concepts in ichnology.

Robert Frey, George Pemberton, and Thomas Saunders
"Ichnofacies and bathymetry: a passive relationship" (1990)

The ichnofacies model was introduced in a series of papers originally published in German by Seilacher (1954, 1955b, 1958, 1963b), and later expanded into English (Seilacher, 1964a, 1967b). In doing so, he created from a series of apparently disparate worldwide observations an elegant and coherent conceptual model. This body of work resulted in the first paradigm in ichnology, and transformed this field of research from a parochial discipline practiced by a few into a mainstream paleontological and geological science with a rich conceptual framework and multiple fruitful applications. Subsequently, the model was refined and expanded in a series of papers (e.g. Frey and Seilacher, 1980; Bromley *et al.*, 1984; Frey and Pemberton, 1984, 1985, 1987; Bromley, 1990, 1996; Pemberton *et al.*, 1992b; Bromley and Asgaard, 1993a; Lockley *et al.*, 1994; Buatois and Mángano, 1995b, 2009; Gibert *et al.*, 1998, 2007; Genise *et al.*, 2000, 2010a; Ekdale *et al.*, 2007; Hunt and Lucas, 2007; Minter and Braddy, 2009), remaining at the core of ichnology, both as a theoretical framework and as a tool. The aim of this chapter is to provide an updated review of the ichnofacies model, addressing not only marine softground and substrate-controlled ichnofacies, but also invertebrate and vertebrate continental ichnofacies. Vertebrate ichnofacies are still in flux and what is presented herein should be understood as a preliminary "state-of-the-art" rather than a consensus view on the matter.

4.1 THE ICHNOFACIES CONCEPT

In our definition (Box 1.1), Seilacherian or archetypal ichnofacies are conceptual constructs based on the identification of key features shared by different ichnocoenoses of a wide range of ages formed under a similar set of environmental conditions. A key component of any ichnofacies is their archetypal nature, being both individual ichnofacies and, at a different scale, the ichnofacies model, conceptual constructs. Ichnofacies is not simply a concept. The notion of ichnofacies itself involves a group of concepts that are linked and interrelated providing a new meaning. The elaboration of an ichnofacies involves two steps: (1) the distillation process or selection of key features (e.g. dominant ethologies, ichnodiversity levels, feeding strategies) within a representative sample of ichnocoenoses of different ages, and (2) the articulation of these key features with ecologic factors and depositional processes. Any potential ichnofacies should be based on a series of examples carefully selected from the ichnological record, rather than a mere list of theoretical assemblages or documentation of local examples.

Seilacherian archetypal ichnofacies should not be confused with and should not be replaced by ichnocoenoses (see Box 1.1). An ichnocoenosis refers to a group of biogenic structures that results from the work of a single community and, therefore, is a very different concept than ichnofacies, and is applicable to different scale analysis (Bromley, 1990, 1996). Occasionally, the term "ichnofacies" has been used at a different scale. For example, Lockley *et al.* (1987) introduced the *Curvolithus* ichnofacies, but specified that this may be better understood as a subdivision of the *Cruziana* ichnofacies (see also Bromley, 1990, 1996). Another related concept is ichnosubfacies, which has been used mostly in the context of deep-marine ichnofaunas (e.g. Uchman, 2009).

As noted by Pemberton *et al.* (1992b), the ichnofacies model is analogous to facies models and, accordingly, archetypal ichnofacies are produced through a "distillation" process that concentrates the diagnostic features of various ichnofaunas and eliminates the local peculiarities or the "noise" of the particular examples (Walker, 1984). As in the case of facies models, an ichnofacies serves as a norm for purposes of comparison, framework, and guide for future observations, predictor in new situations, and basis for interpretation. Of course, at a local scale, discrete ichnofacies may be subdivided into different assemblages with paleoecological and paleoenvironmental implications, integrating sedimentological and ichnological datasets (MacEachern *et al.*, 1999a; McIlroy, 2004a). In

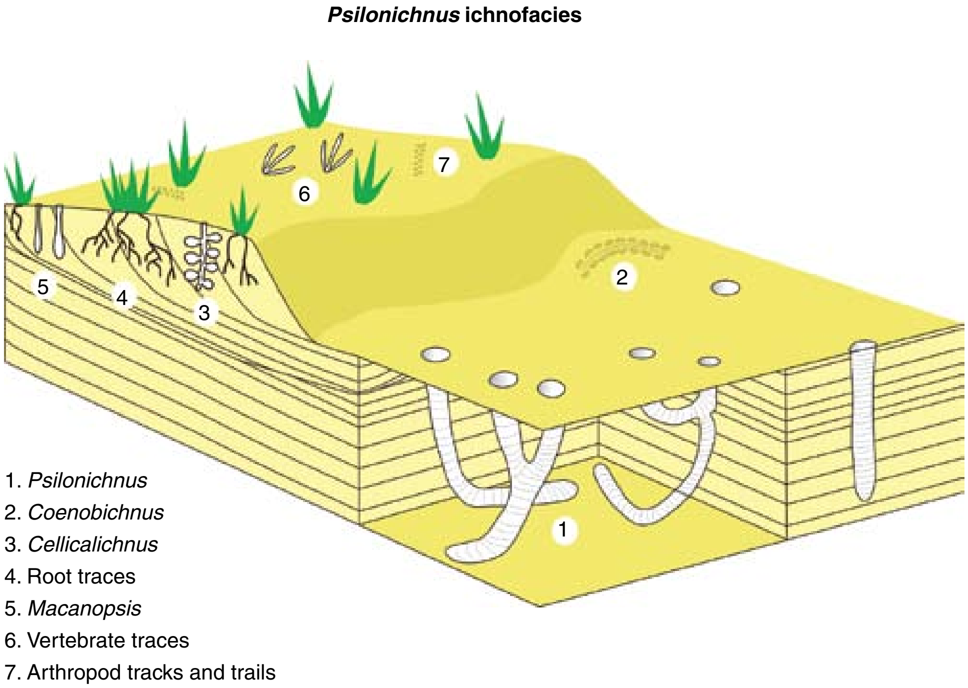


Figure 4.1 Schematic reconstruction of the *Psilonichnus* ichnofacies.

shallow-marine clastic successions, this approach has resulted in models of onshore–offshore ichnofacies gradients that have been extremely useful in refining environmental zonations (e.g. MacEachern *et al.*, 1999a). Similar subdivisions have been suggested for tide-dominated shorelines (Mángano and Buatois, 2004a). Additionally, the incorporation of concepts and methods derived from the ichnofabric approach, such as the recognition of the taphonomic factors involved in the shaping of particular ichnofacies (Bromley and Asgaard, 1991), should be taken into account to produce more robust models. Based on these ideas, Bromley and Asgaard (1991) noted that some ichnofacies are closely related to biofacies, while others are more akin to taphofacies.

Ichnofacies has been historically established based on invertebrate ichnotaxa. Exceptionally, vertebrate trace fossils, such as the fish trail *Undichna*, were noted as common in the freshwater *Mermia* ichnofacies (Buatois and Mángano, 1995b), and various vertebrate trackways are documented in the *Psilonichnus* and *Scoyenia* ichnofacies (e.g. Frey and Pemberton, 1986). More recently, attempts have been made to establish ichnofacies based on vertebrate trace fossils (Lockley *et al.*, 1994; Hunt and Lucas, 2007). Hunt and Lucas (2007) noted the existence of two traditions in ichnology, the ethological and the biotaxonomic. Invertebrate ichnologists mostly use an ethological approach characterized by naming structures based on the behavior represented. This is the most standard practice in ichnology. However, vertebrate ichnologists commonly apply a biotaxonomic approach, attempting to relate trackways to the taxonomy of the producer. Ichnologists working with insect trace fossils in paleosols represent a departure from this dichotomy because they commonly employ a taxonomic approach (e.g. Genise, 2004). Accordingly, Hunt and Lucas (2007) noted that invertebrate ichnofacies are ethoichnofacies, while vertebrate ichnofacies are biotaxonichnofacies. Ichnofacies fall broadly into four main categories: softground marine ichnofacies, substrate-controlled ichnofacies, continental invertebrate ichnofacies, and vertebrate ichnofacies. The rest of this chapter is mainly devoted to analyzing each of these ichnofacies.

4.2 SOFTGROUND MARINE ICHNOFACIES

Softground marine ichnofacies are probably the most traditional ichnofacies, and have been the focus of the majority of ichnological research until the recognition of the sequence-stratigraphic significance of substrate-controlled ichnofacies (Pemberton *et al.*, 1992b). Five archetypal softground marine ichnofacies are recognized at present: *Psilonichnus*, *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites*.

4.2.1 *PSILONICHNUS* ICHNOFACIES

The *Psilonichnus* ichnofacies is a subsequent addition to the set of Seilacherian ichnofacies, and was introduced by Frey and Pemberton (1987). This ichnofacies has been further explored in more recent papers (e.g. Nesbitt and Campbell, 2006; Netto and Grangeiro, 2009). It characterized by: (1) dominance of vertical J-, Y-, or U-shaped dwelling burrows produced by ghost crabs; (2) presence of small, unlined vertical dwelling burrows with bulbous basal cells produced by arachnids and insects; (3) local presence of vertebrate trackways and invertebrate trails and trackways; (4) root traces; (5) coprolites; (6) low ichnodiversity; and (7) low abundance (Fig. 4.1).

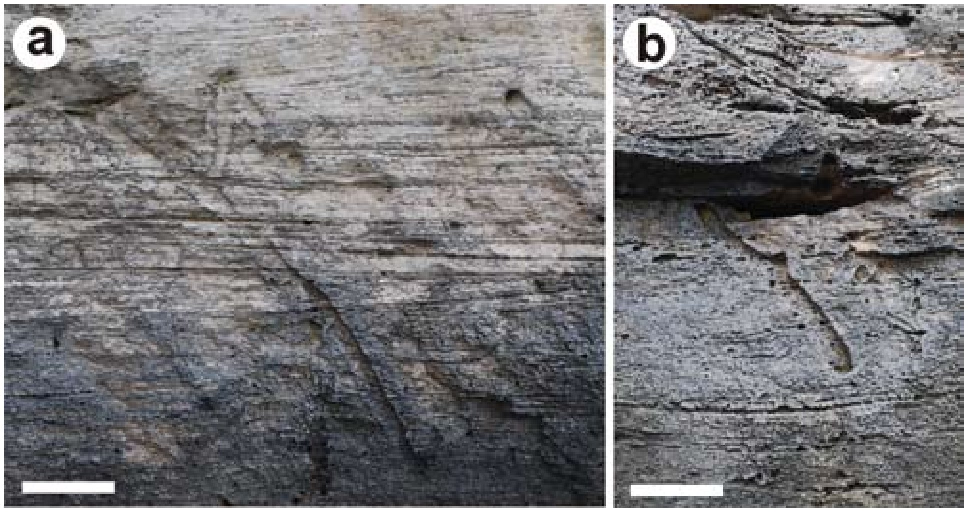


Figure 4.2 *Psilonichnus upsilon* in eolian calcarenites. Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay, San Salvador Island, Bahamas. (a) Holotype preserved. (b) Inclined shaft with partially preserved branching. All scale bars are 20 cm. See Curran (2007).

The most common component of this ichnofacies is, by far, the ichnogenus *Psilonichnus* (Fig. 4.2a–b), which is produced by ghost crabs of the family Ocypodidae and includes several ichnospecies (Frey *et al*., 1984a; Frey and Pemberton, 1987; Mynt, 2001, 2007; Nesbitt and Campbell, 2002; Netto and Grangeiro, 2009). Arachnid and insect burrows are currently assigned to *Cylindricum* or *Skolithos*. Stellate nests of halictid bees (*Cellicalichnus*) may also occur (Curran and White, 2001; Curran, 2007). More rarely, trackways of land hermit crabs (*Coenobichnus*) are present (Walker *et al*., 2003). There is a remarkable disparity between the relatively rich assemblages observed in modern environments, and the poorly diverse ichnofaunas preserved in the fossil record. Modern examples of the *Psilonichnus* ichnofacies contain incipient *Archaeonassa*, *Protovirgularia*, *Lockeia*, *Gordia*, and various trackways. Invertebrate tracemakers include gastropods, bivalves, worms and arthropods. Vertebrate structures include rodent and reptile burrows, and reptile, mammal, and avian trackways. All these invertebrate and vertebrate traces are rarely preserved in the fossil examples, clearly revealing very low preservation potential (MacEachern *et al*., 2007a). Trophic types mostly include scavengers, deposit feeders, predators, and herbivores (Frey and Pemberton, 1987). Halophyte plants may occur in these coastal settings and are represented in the ichnological record by abundant root traces (Curran, 2007).

The *Psilonichnus* ichnofacies is linked to remarkable variations in energy, grain size, and salinity. In addition, it is associated with subaerial exposure, periodic influx of freshwater due to precipitation, and storm surges (Frey and Pemberton 1987). This ichnofacies indicates transitional conditions between marine and continental settings. According to MacEachern *et al.* (2007a), marine conditions usually prevail during spring tides and storms, while continental processes (mostly eolian) are dominant during neap tides and non-storm periods. In terms of specific depositional environments, the *Psilonichnus* ichnofacies is typical of coastal environments, both carbonate and clastic, including barrier islands, strand plains, delta plains, estuaries, lagoons, and bays. Within these settings it may be present in backshore areas, washover fans, coastal dunes and supratidal flats (Frey and Pemberton, 1987) (see Sections 7.1.1 and 11.1.1). Low diversity and abundance of trace fossils is related to the stressful conditions dominant in these environments, and to a taphonomic overprint resulting from low fossilization potential. Stressful conditions also promote the presence of opportunistic organisms, rather than climax faunas.

The *Psilonichnus* ichnofacies can be subdivided in landward and seaward associations. The landward association tends to be dominated by insect and arachnid burrows and nests, while the marine association is commonly monospecific and composed of *Psilonichnus* (Curran, 2007). The landward association grades towards the continent into freshwater and terrestrial ichnofacies, namely the *Scoyenia* ichnofacies and the *Coprinisphaera* or *Termitichnus* ichnofacies, depending on the nature of the plant formations in the coastal plain. In carbonate shorelines, the *Psilonichnus* ichnofacies grades into the *Celliforma* ichnofacies. The seaward association is replaced by the *Skolithos* ichnofacies in a seaward direction, this transition being relatively abrupt, at least as encountered in modern environments (Frey and Pemberton, 1987).

Due to its low diversity, recognition of the *Psilonichnus* ichnofacies is in practice, unfortunately, closely linked to the identification of the eponymous ichnogenus. This is complicated by the fact that ghost crabs and their burrows are unknown in pre-Cretaceous rocks. Therefore, recurrence of the *Psilonichnus* ichnofacies is much lower than that of the other marine softground ichnofacies and even of that of the freshwater ichnofacies.

4.2.2 *SKOLITHOS* ICHNOFACIES

The *Skolithos* ichnofacies is one of the original ichnofacies introduced by Seilacher (1963b, 1967b) as the *Skolithos* facies, and subsequently systematized in a series of papers (e.g. Frey and Seilacher, 1980; Frey and Pemberton, 1984, 1985). It is characterized by: (1) dominance of vertical, cylindrical, simple

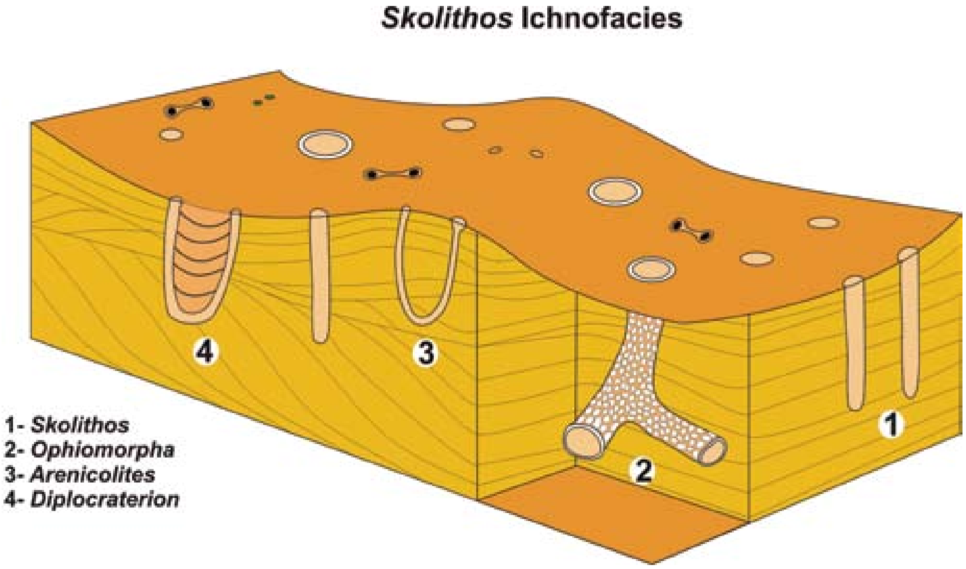


Figure 4.3 Schematic reconstruction of the *Skolithos* ichnofacies.

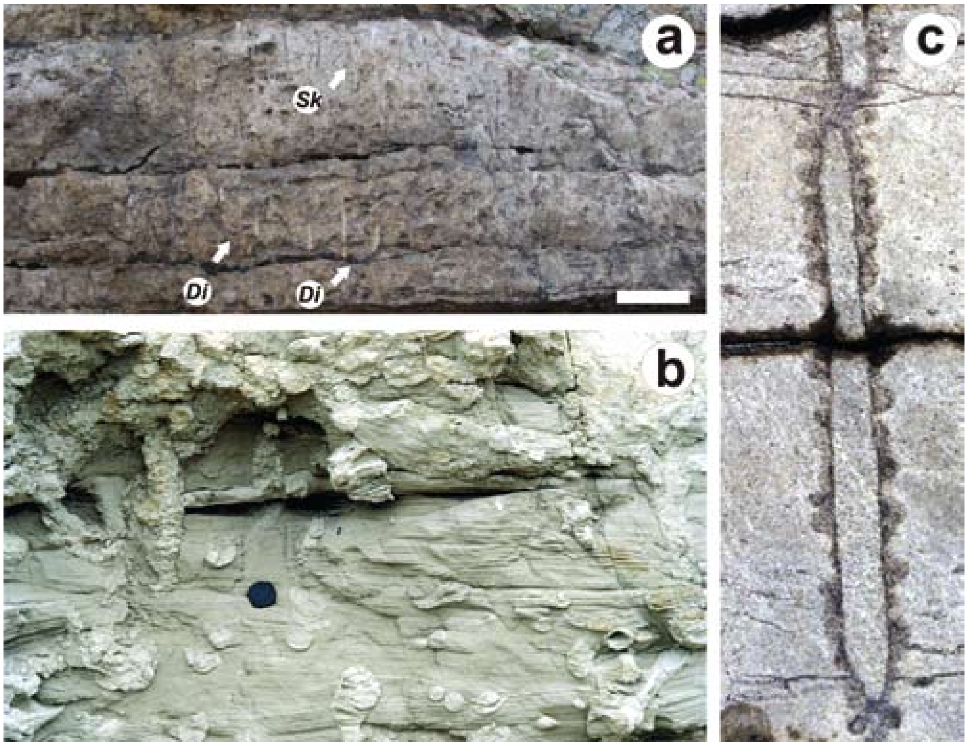


Figure 4.4 Examples of typical components of the *Skolithos* ichnofacies. Note dominance of vertical burrows and very low ichnodiversity. (a) Outcrop expression. *Skolithos linearis* (*Sk*) and *Diplocraterion parallelum* (*Di*). Lower Cambrian, Lake O'Hara Member, St. Piran Formation, Gog Group, Fairview Mountain, southern Canadian Rocky Mountains. Scale bar is 10 cm. See Desjardins *et al*. (2010a). (b) Outcrop expression. *Ophiomorpha borneensis*. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Scasso and Bellosi (2004). (c) Core expression. *Ophiomorpha nodosa*. Middle Eocene, Pauji Formation, Motatán Field, Maracaibo Basin, western Venezuela. Core width is 6 cm. See Delgado *et al*. (2001).

or U-shaped dwelling burrows of suspension feeders and passive predators; (2) presence of spreiten U-shaped equilibrium burrows and escape traces; (3) abundance of three-dimensional burrow systems dominated by vertical components; (4) scarcity of horizontal traces produced by a mobile fauna; (5) low ichnodiversity; and (6) variable abundance (Figs. 4.3 and 4.4a–c).

The most common ichnogenera of the *Skolithos* ichnofacies are *Skolithos*, *Ophiomorpha*, *Arenicolites*, and *Diplocraterion*. *Conichnus* and *Bergaueria* may occur locally. Typical producers are polychaetes, siphunculids, crustaceans, and sea anemones. Horizontal traces, although common in modern occurrences, are not preserved in fossil examples of the *Skolithos* ichnofacies, due to intense erosion that only allows preservation of deeper vertical burrows. Preservational bias reveals the importance of taphonomic factors in the final shaping of the ichnofacies (Bromley and Asgaard, 1991).

Dominance of vertical burrows of suspension feeders reveals high abundance of organic particles that are kept in suspension in the well-oxygenated water column by waves and currents. However, some U-shaped burrows commonly lacking spreite may be produced by a deposit-feeding infauna (Bromley, 1990, 1996). Other animals clearly display passive predation strategies seeking refuge within the burrow and preying on other organisms that are caught by the tentacles and carried to the mouth (Ruppert *et al.*, 2004). Deep emplacement of most of these burrows suggests relatively high energy and intense erosion. Erosion is also revealed by the common presence of truncated burrows. Spreite in U-shaped burrows may be either protrusive or retrusive, and develop in response to substrate aggradation or degradation, representing equilibrium structures. Under conditions of episodic sedimentation, escape traces develop. The predominance of vertical components over horizontal components indicates relatively high energy (Howard and Frey, 1984; Anderson and Droser, 1998). Burrows are permanent domiciles, which are lined to preclude collapse in shifting and soft sandy substrates that serve mainly as anchoring media (MacEachern *et al.*, 2007a). Low ichnodiversity, typically monospecific occurrences, reflects stressful conditions related to relatively high energy. Trace-fossil abundance is highly variable. Some deposits containing the *Skolithos* ichnofacies are sparsely bioturbated revealing short-term colonization windows. In contrast, other deposits are pervasively bioturbated forming *Skolithos* pipe rock (Droser, 1991; Desjardins *et al.*, 2010a).

In terms of depositional settings, the *Skolithos* ichnofacies is typical of foreshore to upper- and middle-shoreface environments of wave-dominated shorelines. In these wave-dominated systems, the *Skolithos* ichnofacies grades seawards into the *Cruziana* ichnofacies (see Section 7.1). However, similar conditions to that of nearshore settings also occur in a wide variety of sedimentary environments. Also in wave-dominated clastic environments, the *Skolithos* ichnofacies may be present displaying post-depositional suites in tempestites emplaced in deeper positions, typically lower shoreface to lower offshore, where they record opportunistic colonization of sandy substrates (e.g. Vossler and Pemberton, 1988). In the case of tide-dominated shorelines, the *Skolithos* ichnofacies typically occur in subtidal sandbars to lower-intertidal sand flats depending of the tidal regime and, therefore, grade landwards into the *Cruziana* ichnofacies (Mángano and Buatois, 1999b, 2004a) (see Section 7.2). The *Skolithos* ichnofacies may also occur in numerous marginal-marine environments, commonly in areas of moderately high energy, such as delta fronts, sandy bars and spits, tidal inlets, flood and ebb tidal deltas, sandy bay margins, estuary-mouth complexes, and bay-head deltas (MacEachern *et al.*, 2007a). However, these settings are usually associated with additional stress conditions due to salinity fluctuations and water turbidity and, therefore, the *Skolithos* ichnofacies displays even lower diversity than in their fully marine counterparts (see Chapter 8). The *Skolithos* ichnofacies is also present in deep-marine turbidite systems, commonly in channels and lobes of proximal to middle areas which are characterized by high energy, shifting sandy substrates, rapid deposition, high erosion, and good oxygenation, therefore mimicking conditions in shallow-marine zones (Crimes, 1977) (see Section 9.2). However, typical shallow-water forms (e.g. *Ophiomorpha, Skolithos*) are not restricted to the most proximal zones of deep-sea systems, but also occur in distal zones, if these are affected by turbidity currents (Uchman, 1991a). The presence of simple and U-shaped burrows in high-energy sites of continental systems, such as fluvial channels and lacustrine deltaic mouth bars, may indicate that the *Skolithos* ichnofacies also occurs in freshwater settings (Buatois and Mángano, 1998, 2004a) (see Sections 10.2 and 10.3). The broad spectrum of depositional environments in which the *Skolithos* ichnofacies may occur reflects the opportunistic nature of this ichnofacies.

The *Skolithos* ichnofacies may be subdivided in order to refine paleoenvironmental zonations. Bromley and Asgaard (1991) have even suggested the possibility of distinguishing two different ichnofacies. In this scheme, the *Skolithos* ichnofacies characterizes fair-weather conditions in nearshore, continuously agitated waters, while the *Arenicolites* ichnofacies is typical of opportunistic colonization of episodic sandstone beds (tempestites and turbidites). However, it has been noted that the archetypal *Skolithos* ichnofacies can accommodate this variability (Pemberton *et al.*, 1992d; 2001; Goldring, 1993). MacEachern *et al.* (2007a) suggested subdivisions of the *Skolithos* ichnofacies according to proximal–distal trends. These authors indicated that while the archetypal *Skolithos* ichnofacies characterizes proximal environments, a distal expression can also be recognized. Although still dominated by suspension burrows, the distal *Skolithos* ichnofacies includes some structures produced by detritus and deposit feeders (e.g. *Cylindrichnus*, *Rosselia*). Within this framework, the distal *Skolithos* ichnofacies is considered intergradational with proximal expressions of the *Cruziana* ichnofacies in wave-dominated settings. Under conditions of very high energy, such as those typical of the foreshore and upper shoreface in wave-agitated beaches, the archetypal *Skolithos* ichnofacies is replaced by an assemblage dominated by the ichnogenus *Macaronichnus* (Pemberton *et al.*, 2001) (see Section 7.1.2). Furthermore, distinction between shallow and deep occurrences of the *Skolithos* ichnofacies may be possible. Ongoing studies suggest that taxonomic assignments at ichnospecific level may help to distinguish the composition of the *Skolithos* ichnofacies in shallow- and deep-marine environments.

The *Skolithos* ichnofacies is known since the Cambrian, although it is not present in earliest Cambrian rocks (Mángano and Buatois, 2007). This ichnofacies has experienced variations in taxonomic composition through the Phanerozoic. The most notable one is the common replacement of *Skolithos* by *Ophiomorpha* as the dominant form in post-Paleozoic occurrences, probably reflecting the Mesozoic radiation of decapod crustaceans (Carmona *et al.*, 2004).

4.2.3 *CRUZIANA* ICHNOFACIES

The *Cruziana* ichnofacies originated from recurrent trace-fossil assemblages observed by Seilacher (1954, 1955b, 1958) in what were called molasse deposits, and was subsequently referred to as the *Cruziana* facies of the original ichnofacies model (e.g. Seilacher, 1963b, 1964a, 1967b). More formal definitions were provided by Frey and Seilacher (1980), and Frey and Pemberton (1984, 1985). It is characterized by: (1) dominance of horizontal

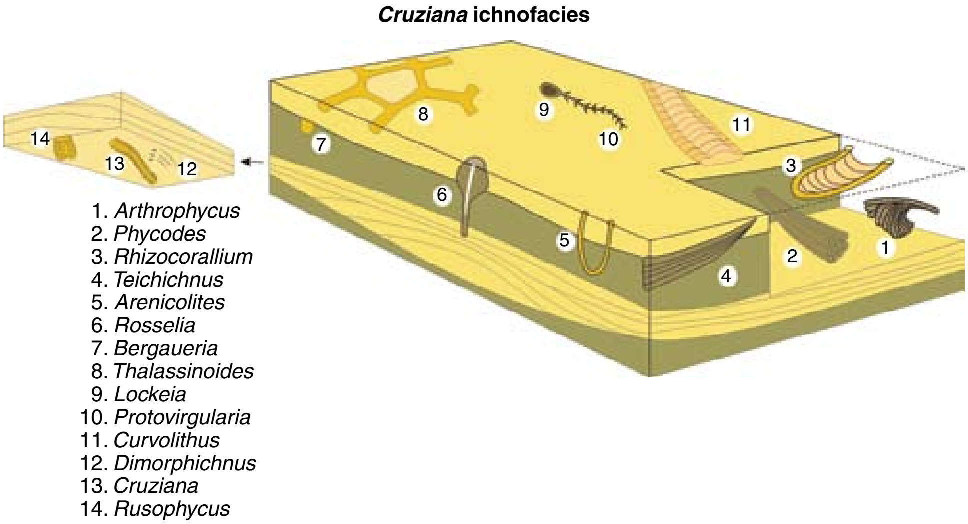


Figure 4.5 Schematic reconstruction of the *Cruziana* ichnofacies.

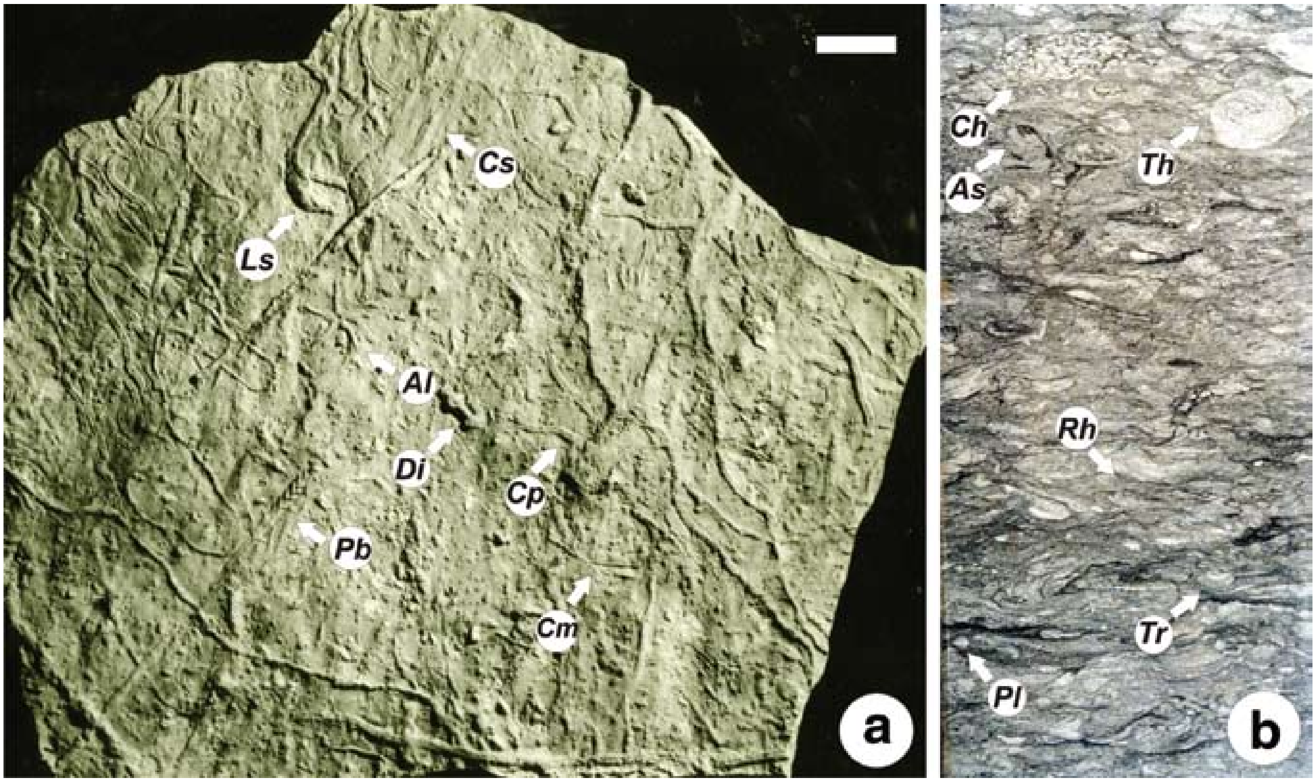


Figure 4.6 Examples of the *Cruziana* ichnofacies. Note dominance of horizontal structures and high ichnodiversity. (a) Outcrop expression. Base of sandstone slab containing *Curvolithus simplex* (*Cs*), *Curvolithus multiplex* (*Cm*), *Lockeia siliquaria* (*Ls*), *Diplocraterion* isp. (*Di*), *Asteriacites lumbricalis* (*Al*), *Cruziana problematica* (*Cp*), *Protovirgularia bidirectionalis* (*Pb*). Upper Pennsylvanian, Stull Shale Member, Kanwaka Shale Formation, Shawnee Group, Waverly, eastern Kansas, United States. Scale bar is 5 cm. See Mángano and Buatois (2004b). (b) Core expression. *Chondrites* isp. (*Ch*), *Thalassinoides* isp. (*Th*), *Teichichnus rectus* (*Tr*), *Planolites* isp. (*Pl*), *Asterosoma* isp. (*As*) and *Rhizocorallium* isp. (*Rh*). *Chondrites* is locally reworking *Thalassinoides* burrow fills. Upper Cretaceous, Napo Formation, Auca Field, Oriente Basin, northeast Ecuador. Core width is 8 cm.

traces and subordinate presence of vertical and inclined structures; (2) a wide variety of ethological categories, including locomotion, feeding, resting, dwelling, and grazing traces; (3) dominance of deposit and detritus feeding traces, although suspension feeding and predation are also involved; (4) dominance of traces produced by a mobile fauna and subordinate presence of permanent domiciles; (5) high ichnodiversity; and (6) high abundance (Figs. 4.5 and 4.6a–b).

The most common elements of the *Cruziana* ichnofacies are various types of locomotion, resting, feeding, dwelling, and grazing traces. Locomotion trails include *Cruziana*, *Didymaulichnus*, *Protovirgularia*, *Archaeonassa*, *Gyrochorte*, and *Curvolithus*, while *Diplichnites*, *Dimorphichnus*, and *Monomorphichnus* represent examples of trackways. Resting traces are illustrated by *Rusophycus*, *Asteriacites*, and *Lockeia*. Feeding structures may include inclined to horizontal U-shaped traces, such as *Rhizocorallium*, and other structures of variable complexity, such as *Phycodes*, *Heimdallia*, *Arthrophycus*, *Teichichnus*, *Phoebichnus, Phycosiphon*, and *Asterosoma*. Dwelling-burrow systems are mostly represented by the facies-crossing ichnogenus *Palaeophycus* and by *Ophiomorpha* and *Thalassinoides* displaying dominance of horizontal to inclined components. Vertical cylindrical burrows, such as *Rosselia*, *Cylindrichnus*, and *Schaubcylindrichnus*, may be present but are rarely dominant. Nonspecialized simple grazing trails (e.g. *Helminthoidichnites*, *Gordia*, *Helminthopsis*) may occur also.

Producers are extremely variable, reflecting the abundance and diversity of benthic fauna, and include arthropods, mollusks (mostly bivalves and gastropods), echinoderms (ophiuroids and echinoids), and many different types of worm-like animals (e.g. polychaetes). The *Cruziana* ichnofacies not only includes deep-tier structures but traces emplaced close to the sediment–water interface. The overall aspect of the assemblage varies according to the degree of maturity reached by the community that controls the degree of bioturbation and burrowing depth (Bromley and Asgaard, 1991; Bromley, 1990, 1996).

Dominance of horizontal structures produced by a mobile fauna reflects accumulation of organic detritus in the sediment under moderate- to low-energy conditions. Associated substrates vary from silty to sandy, and are represented by interbedded layers of sandstone and siltstone forming heterolithic successions. Preservation of horizontal trace fossils is favored by the presence of these sandstone–mudstone interfaces. Lack of lithological contrast usually inhibits preservation and visibility of biogenic structures. The variable ethologies and trophic types represented, and the high diversity and abundance of biogenic structures commonly reflect overall environmental stability and low to moderate sedimentation rates. However, episodic sedimentation (i.e. storms) may punctuate fair-weather conditions, leading to ichnofaunal turnovers.

Environmentally, this ichnofacies occurs from slightly above the fair-weather wave base to the storm wave base, in a zone ranging from the lower shoreface to the lower offshore in wave-dominated seas (MacEachern and Pemberton, 1992; MacEachern *et al*., 1999a) (see Section 7.1). Conversely, in tide-dominated shorelines the *Cruziana* ichnofacies occurs landward of the *Skolithos* ichnofacies, broadly between high and low tide, albeit depending on tidal regime (Mángano and Buatois, 2004a) (see Section 7.2). The *Cruziana* ichnofacies also occurs in protected areas of marginal-marine, brackish-water environments, such as estuarine basins, bays, and lagoons. However, stressful conditions in these restricted settings dramatically reduced overall diversity, resulting in impoverished assemblages (MacEachern and Pemberton, 1994) (see Chapter 8).

Subdivisions of the *Cruziana* ichnofacies have been proposed in a series of studies by MacEachern *et al*. (1999a, 2007a). While the archetypal *Cruziana* ichnofacies characterizes the upper offshore to offshore transition, proximal and distal expressions are typical of the lower shoreface and the lower offshore, respectively. The proximal *Cruziana* ichnofacies is transitional with the *Skolithos* ichnofacies. Accordingly, although assemblages are dominated by deposit-feeding structures, they contain large numbers of dwelling traces of suspension feeders and passive predators. Distal expressions of the *Cruziana* ichnofacies are transitional with the *Zoophycos* ichnofacies. Assemblages of the distal *Cruziana* ichnofacies contain significant numbers of grazing trails and specialized feeding traces. *Phycosiphon*, *Helminthopsis*, *Chondrites*, *Zoophycos*, and *Planolites* tend to dominate.

The *Cruziana* ichnofacies is known since the Cambrian. However, an incipient *Cruziana* ichnofacies occurs in Ediacaran rocks, but is poorly diverse and dominated by grazing trails. The *Cruziana* ichnofacies has experienced remarkable evolutionary changes through the Phanerozoic, mostly reflecting faunal replacements and an increase in burrowing depth and extent of bioturbation (see Section 14.2.1).

4.2.4 *ZOOPHYCOS* ICHNOFACIES

The *Zoophycos* ichnofacies, one of the original ichnofacies proposed in the Seilacherian model, was formerly referred to as the *Zoophycos* facies. It has subsequently been systematized in different studies (e.g. Frey and Seilacher, 1980; Frey and Pemberton, 1984, 1985; Bromley, 1990, 1996). It is characterized by: (1) dominance of relatively simple to complex feeding structures with spreite; (2) subordinate occurrence of grazing traces; (3) dominance of deep-tier structures of deposit feeders or farmers; (4) low ichnodiversity; and (5) high abundance (Fig. 4.7).

Zoophycos is the typical ichnogenus, but *Phycosiphon*, *Chondrites*, and certain ichnospecies of *Nereites* (notably *N. missouriensis*, previously referred to as *Scalarituba*) are present also. In fact, Frey and Pemberton (1984) noted that replacement of *Zoophycos* by *Phycosiphon* as the dominant ichnogenus is common. In many instances, the presence of the *Zoophycos* ichnofacies is recorded by monospecific occurrences of the ichnogenus itself. The inferred producers of *Zoophycos* are echiuran worms (Kotake, 1992). Other tracemakers in this ichnofacies include different types of worm-like animals, such as enteropneusts and polychaetes. Ethologically, *Zoophycos* was originally considered the feeding trace of a deposit-feeding organism (Seilacher, 1967a). However, more recently it has been regarded as reflecting bacterial farming (Bromley, 1991; Fu and Werner, 1995).

The *Zoophycos* ichnofacies is in all probability the most problematic of all archetypal ichnofacies, and has been dubbed "the black sheep of the family of marine softground ichnofacies" by Bromley (1990, 1996). Most of the complications result from the fact that recognition of this ichnofacies is, in practice, too dependent on the identification of *Zoophycos* itself. Therefore, uncertainties in the ethological interpretation of *Zoophycos* complicate evaluation of the paleoecological significance of the ichnofacies. The classical interpretation is that the *Zoophycos*

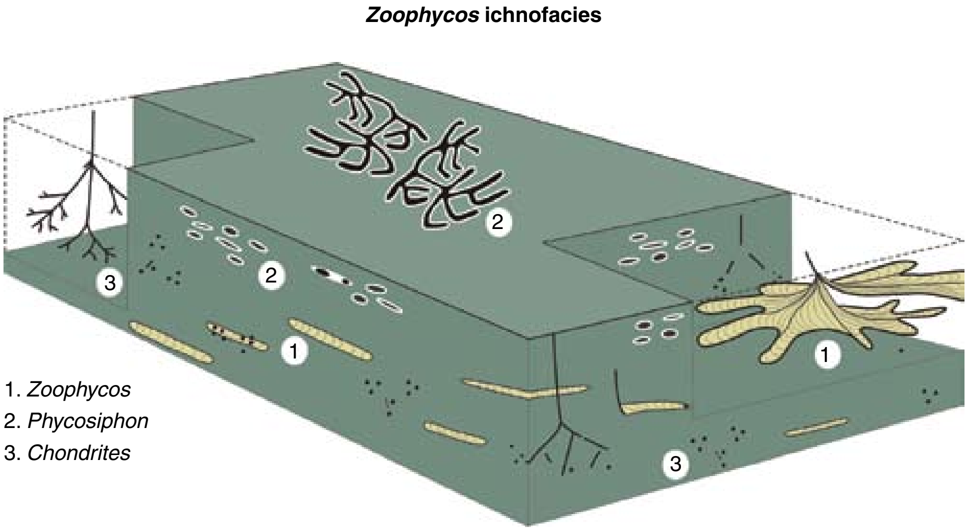


Figure 4.7 Schematic reconstruction of the *Zoophycos* ichnofacies.

ichnofacies is linked to poor oxygenation (e.g. Frey and Seilacher, 1980; Frey and Pemberton, 1984, 1985). According to this view, the ichnogenus *Zoophycos* and other members of the ichnofacies are seen as the product of opportunistic organisms (Ekdale, 1985; M. Miller, 1991). Subsequently, other authors noted that the *Zoophycos* ichnofacies is dominated by deep-tier structures in intensely bioturbated substrates that result from the activity of climax communities (Bromley and Asgaard, 1991; Bromley, 1990, 1996). Furthermore, complexity and downward increase in size of some specimens of *Zoophycos* seem to be inconsistent with its interpretation as the product of opportunistic organisms and, in contrast, indicate "once in a lifetime" construction (Bromley, 1990, 1996). *Zoophycos* and *Chondrites* penetrate deeply into the substrate in oxygen-depleted sediment, but this does not necessarily indicate poor oxygenation in bottom waters. Intense bioturbation also argues against oxygen depletion. Also, it was originally thought that the *Zoophycos* ichnofacies occurs in areas free of turbidity currents (Seilacher, 1967b). This is supported by the fact that typically the *Zoophycos* ichnofacies occurs in silt and clay substrates that slowly and continuously accumulate due to suspension fallout, allowing intense levels of bioturbation (MacEachern *et al.*, 2007a). However, it has been also recognized in sandy substrates deposited by turbidity currents and debris flows in slope environments, albeit with traces emplaced during times of background sedimentation (Buatois and Mángano, 1992). It has also been proposed that the *Zoophycos* ichnofacies is present in organic-rich substrates under conditions of abundant food supply that may have inhibited development of the *Nereites* ichnofacies (D'Alessandro *et al.*, 1986; Buatois and López Angriman, 1992b). However, this interpretation only seems to work if *Zoophycos* and the associated components of the ichnofacies represent the work of deposit feeders rather than microbial farmers.

Another problem derives from the fact that *Zoophycos* has a broad paleobathymetric range. MacEachern *et al.* (2007a) concluded that such a widespread environmental range suggests that the *Zoophycos* animal tolerates a considerable range of water depths, substrate types, food resources, energy levels, and oxygen content. To complicate matters further, *Zoophycos* experienced an onshore–offshore migration throughout the Phanerozoic (Bottjer *et al.*, 1988). Because *Zoophycos* is very common in Paleozoic shallow-marine rocks, recognition of the ichnofacies in deposits of this age may become problematic, and some authors have even suggested that the utility of this ichnofacies is very limited in Paleozoic strata (M. Miller, 1991).

In the original model proposed by Seilacher (1964a, 1967b), the *Zoophycos* ichnofacies occurs between the *Cruziana* and *Nereites* ichnofacies. Environmentally, it characterizes quiet-water settings below the storm wave base, particularly in shelfal to slope areas (see Sections 7.1.9 and 9.1). However, it may occur at shallower and deeper water. Shallow-water occurrences are common in Paleozoic epeiric seas (Marintsch and Finks 1982; Frey and Pemberton, 1984), while deep-marine examples are more typical of post-Paleozoic mudstone that characterizes interturbidite times (Wetzel, 1984). According to MacEachern *et al.* (2007a), the *Zoophycos* animal was able to compete successfully with the diverse benthic fauna associated with the *Cruziana* and *Nereites* ichnofacies, but few other organisms were able to compete with *Zoophycos* in oxygen-depleted environments. Therefore, *Zoophycos* tends to be dominant in shelf and slope environments. The *Zoophycos* ichnofacies is known since the Ordovician, although it is well established in shelf and slope areas by the Silurian (Bottjer *et al.*, 1988).

4.2.5 *NEREITES* ICHNOFACIES

The *Nereites* ichnofacies originated from recurrent trace-fossil assemblages that Seilacher (1954, 1958) documented from what were referred to as flysch deposits. These examples form the basis of what was subsequently named the *Nereites* facies (e.g. Seilacher, 1963b, 1964a, 1967b) of his original ichnofacies model. A more systematic treatment and formal definitions were subsequently provided by Frey and Seilacher (1980) and Frey and Pemberton (1984, 1985). It is characterized by: (1) dominance of complex graphoglyptids produced by animals that farm bacteria and trap microorganisms; (2) presence of sophisticated grazing trails and

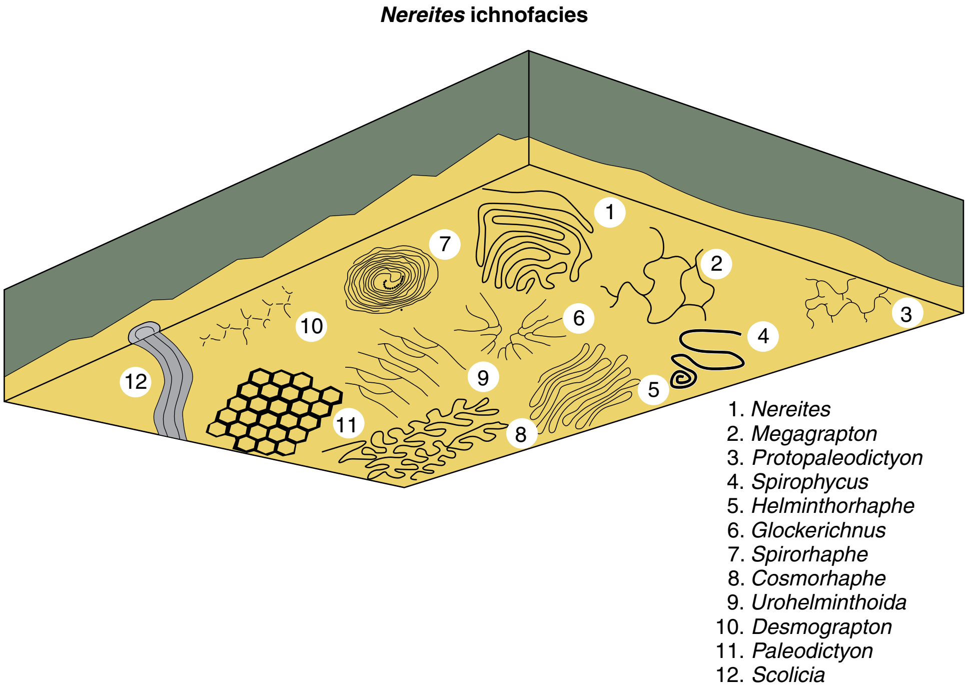


Figure 4.8 Schematic reconstruction of the *Nereites* ichnofacies.

feeding traces of detritus and deposit feeders; (3) dominance of shallow-tier trace fossils; (4) very high ichnodiversity; and (5) high abundance, but low density, of individual ichnotaxa (Fig. 4.8).

Graphoglyptids are arguably the diagnostic components of the ichnofacies. Typical graphoglyptid ichnogenera are *Paleodictyon*, *Protopaleodictyon*, *Spirorhaphe*, *Urohelminthoida*, *Desmograpton*, *Megagrapton, Acanthorhaphe, Helicolithus*, *Belorhaphe*, *Spirocosmorhaphe*, and *Paleomeandron*. Grazing trails are represented by guided meandering traces, such as highly specialized ichnospecies of *Nereites* and *Scolicia*. *Helminthorhaphe* and *Cosmorhaphe* may either represent grazing trails or graphoglyptids. Feeding traces include radial structures (*Glockerichnus*, *Lorenzinia*, *Capodistria*), branched systems (*Polykampton*, some ichnospecies of *Treptichnus*) and simpler forms (*Halopoa*, *Fustiglyphus*, *Circulichnis*). Resting traces are relatively rare and mostly represented by the ichnogenus *Cardioichnus*, which commonly intergrades with *Scolicia*.

Although the *Nereites* ichnofacies is clearly dominated by shallow-tier traces, the presence of complex structures and the high ichnodiversity indicate the activity of climax communities with enough time to develop specialized and varied behavioral patterns (Seilacher, 1977a; W. Miller, 1991a). This is only possible under very stable environmental conditions in an overall low-energy, well-oxygenated setting. In addition, the presence of sophisticated feeding strategies suggests scarce food resources. In the case of delta-fed turbidity systems, the *Nereites* ichnofacies has been reported to occur in organic-rich deposits (Fürsich *et al*., 2007; Olivero *et al*., 2010). These occurrences either reflect that oligotrophy is not a limited factor in graphoglyptid distribution (Fürsich *et al*., 2007) or that trophic resources fluctuate, with graphoglyptids colonizing the sea bottom during times of oligotrophy (Olivero *et al*., 2010).

The benthic community associated with the *Nereites* ichnofacies typically flourishes in environments characterized by slow, continuous suspension fallout deposition of silt and clay. However, distinctive elements of the *Nereites* ichnofacies are typically preserved as positive hyporeliefs on the base of sandstone turbidites. While graphoglyptids of the *Nereites* ichnofacies reflect the activity of a benthic fauna developed in muddy, low-energy substrates, their preservation is linked to turbidity currents that punctuate fallout of fine-grained sediment (Seilacher, 1962, 1977a). The standard explanation is that turbidity currents erode the uppermost millimeters of the substrate and cast with sand the shallowly emplaced biogenic structures. More recently, Seilacher (2007a) proposed that the excellent preservation of these delicate traces is due to a shock wave immediately prior to deposition that sucks the unconsolidated mud into suspension without significant erosion. In either case, preservation of graphoglyptids can only take place in zones affected by turbidity currents. In the absence of event sedimentation, the activity of the deep-tier bioturbators would have destroyed all the shallowly emplaced traces (Bromley and Asgaard, 1991). In fact, biogenic structures similar to those in the *Nereites* ichnofacies have been observed in modern abyssal plains in areas beyond the reach of turbidity currents (Hollister *et al*., 1975; Ekdale and Berger, 1978; Kitchell *et al*., 1978b; Ekdale, 1980; Gaillard, 1991). However, pelagic deposits are characterized in the fossil record by intensely mottled textures and a few discrete traces, such as *Zoophycos*, *Planolites*, and *Teichichnus* (Ekdale, 1977; Ekdale and Berger, 1978). Ekdale and Berger (1978) suggested the existence of an abyssal or deep-sea ichnofacies that occupies deeper settings than the *Nereites* ichnofacies, although the absence of discrete trace fossils in these sediments complicates further characterization of this potential ichnofacies (see Section 9.4).

The *Nereites* ichnofacies is arguably the one that displays the closest links with a certain bathymetry. It occurs in base-of-slope turbidity systems and is particularly common in thin-bedded turbidites that accumulate in the fringe of terminal splays, crevasse splays and levees (see Section 9.2.1). Potential occurrences in shallower settings await further documentation (Gierlowski-Kordesch and Ernst, 1987; Ernst and Gierlowski-Kordesch, 1989; Ting *et al.*, 1991). However, the ichnogenus *Paleodictyon*, a typical component of the *Nereites* ichnofacies, has been documented in shallow-water prodelta turbidites (Fürsich *et al.*, 2007). In addition, it has been demonstrated that the *Nereites* ichnofacies may extend into sub-neritic environments during rapid shallowing (Uchman *et al.*, 2004a) and relatively shallow-water delta-fed turbidite systems (Olivero *et al.*, 2010).

The *Nereites* ichnofacies was subdivided by Seilacher (1974) into the *Nereites* and *Paleodictyon* ichnosubfacies. The *Nereites* ichnosubfacies typifies the most distal parts of the turbidite systems characterized by very thin intercalations of turbidite sandstone and background mudstone. This ichnosubfacies is dominated by backfilled trace fossils of deposit feeders, such as *Nereites*, *Phycosiphon*, *Dictyodora*, and *Zoophycos*. According to Seilacher (1974), the *Paleodictyon* ichnosubfacies tends to occur in slightly more proximal settings where turbidite sandstones weather out as resistant beds with graphoglyptids (e.g. *Paleodictyon*, *Helicolithus*, *Urohelminthoida*, *Desmograpton*) preserved at the base. Although proximality trends may be established, local factors play a key role in controlling distribution of these two ichnosubfacies, with food supply probably being a limiting factor (Wetzel and Uchman, 1998). More recent research has suggested the existence of a third ichnosubfacies, the *Ophiomorpha rudis* ichnosubfacies, which consists of a few ichnotaxa, typically *Ophiomorpha rudis*, *O. annulata*, and *Scolicia*, and less commonly, *Nereites irregularis*, *Chondrites*, and a few graphoglyptids (Uchman, 2009). This ichnosubfacies occurs in channel and proximal-lobe deposits (see Section 9.2).

The *Nereites* ichnofacies is known since the Ordovician. Cambrian deep-marine ichnofaunas are remarkably different from their younger counterparts, and deviate from the basic features of the *Nereites* ichnofacies (Orr, 2001, Buatois and Mángano, 2003a). Furthermore, the *Nereites* ichnofacies has experienced numerous changes through the Phanerozoic, including progressive size decrease of its components, increase in diversity and increase in the degree of complexity of some of the trace fossils (Seilacher, 1974, 1977a; Uchman, 2003, 2004a) (see Section 14.2.2).

4.3 SUBSTRATE-CONTROLLED ICHNOFACIES

Substrate-controlled ichnofacies have received a lot of attention during the last two decades after the realization that they are very useful to delineate surfaces with sequence-stratigraphic implications (MacEachern *et al.*, 1992; Pemberton *et al.*, 1992b, 2004) (see Chapter 12). Four substrate-controlled ichnofacies are regarded here as valid: *Glossifungites*, *Trypanites*, *Gnathichnus*, and *Teredolites*.

4.3.1 *GLOSSIFUNGITES* ICHNOFACIES

The *Glossifungites* ichnofacies was originally proposed by Seilacher (1967b), subsequently redefined by Frey and Seilacher (1980) and, more recently, reviewed in a number of papers, mostly in the context of its sequence-stratigraphic implications (Pemberton and Frey, 1985; MacEachern *et al.*, 1992, 2007a; Pemberton *et al.*, 1992b, 2001, 2004). It is characterized by: (1) sharp-walled, unlined, passively filled, dwelling burrows of suspension feeders or passive predators; (2) dominance of robust, vertical to subvertical, simple and spreite U-shaped burrows; (3) presence of branched burrow systems; (4) presence of burrows with ornamented walls; (5) low ichnodiversity; and (6) high abundance (Figs. 4.9 and 4.10a–c).

The most common ichnotaxa in this ichnofacies correspond to the ichnogenera *Diplocraterion*, *Skolithos*, *Arenicolites*, *Gastrochaenolites*, *Thalassinoides*, *Spongeliomorpha*, and *Rhizocorallium*. More rarely, the ichnogenera *Fuersichnus* and *Zoophycos* have been recognized to occur in the *Glossifungites* ichnofacies (Buatois, 1995; MacEachern and Burton 2000). Ironically, the eponymous ichnogenus is a junior synonym of *Rhizocorallium* (Uchman *et al.*, 2000). Firmground burrowers include various bivalves, crustaceans, nemerteans, and polychaetes (Pemberton and Frey, 1985; Gingras *et al.*, 2001) (Box 4.1).

The *Glossifungites* ichnofacies develops in stable and cohesive substrates (firmgrounds), commonly dewatered muds, and, more rarely, highly compacted sands (MacEachern *et al.*, 1992, 2007a; Pemberton *et al.*, 1992b, 2004). The presence of vertical, unlined shafts penetrating into fine-grained intervals reflects the cohesiveness of the substrate. Additional evidence of substrate stability at the time of excavation is provided by the passive burrow fill and the presence of walls ornamented with striations, as commonly revealed by *Spongeliomorpha*, *Rhizocorallium*, *Fuersichnus*, *Diplocraterion*, and *Gastrochaenolites*. Passive burrow fills reflect colonization by suspension feeders or passive predators that construct open domiciles, which are subsequently filled by sedimentation. Other animals, such as crabs, may leave their burrows in search for food (Pemberton *et al.*, 1992b). Trace fossils of deposit feeders are typically absent in this ichnofacies because nutritious particles are scarce in compacted muds. However, corkscrew burrows similar to *Gyrolithes* have been recorded (Netto *et al.*, 2007). Although ichnodiversity is commonly relatively low, the abundance of trace fossils is high in the *Glossifungites* ichnofacies. In modern examples, densities of approximately 150 specimens/m^2 have been documented (Gingras *et al.*, 2001). Even higher densities have been estimated in cores and outcrops (Pemberton *et al.*, 2004; Buatois and Encinas, 2006).

In siliciclastic deposits, the *Glossifungites* ichnofacies is typically associated with erosional exhumation of previously buried sediments, more commonly linked to relative sea-level changes, although autogenic erosional processes may be also responsible (see Section 12.8; MacEachern *et al.*, 1992, 2007a; Pemberton *et al.*, 2004). Colonization of these firmground substrates occurs during a depositional hiatus that takes place between the erosional event and sedimentation of the overlying

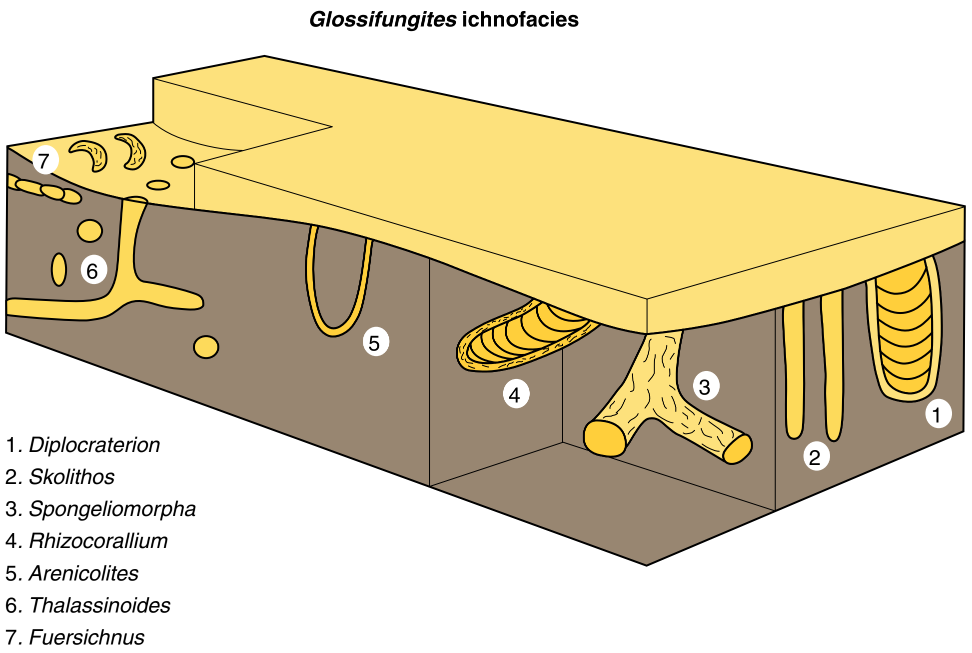


Figure 4.9 Schematic reconstruction of the *Glossifungites* ichnofacies.

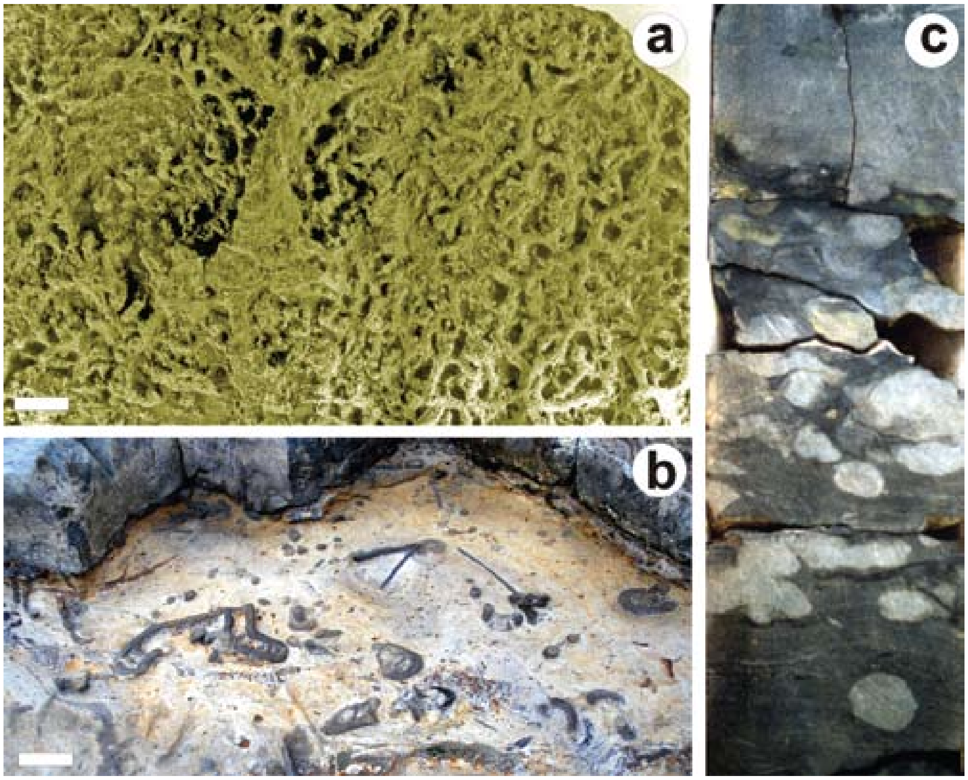


Figure 4.10 Examples of the *Glossifungites* ichnofacies. (a) Outcrop expression. High-density association of small *Thalassinoides suevicus* and large specimen of the same ichnotaxa. Upper Cretaceous, Hidden Lake Formation, Brandy Bay, James Ross Island, Antarctica. Scale bar is 1cm. (b) Outcrop expression. *Rhizocorallium* isp. penetrating from the overlying bed into a firmground. Upper Jurassic, Rodiles Formation, El Puntal Cliffs, San Martín del Mar, Villaviciosa, Asturias, northern Spain. Scale bar is 5 cm. (c) Core expression. *Thalassinoides* penetrating into mudstone and passively filled with sand from an overlying sandstone. Note circular to subcircular cross-sections and absence of lining. Upper Oligocene-Lower Miocene, Naricual Formation, Pirital Field, Eastern Venezuela Basin. Core width is 9 cm.

unit. The typical examples of the *Glossifungites* ichnofacies have been recorded in shallow- to marginal-marine environments. In these settings, it is associated with alostratigraphic surfaces, such as regressive surfaces of erosion formed during forced regressions (see Section 12.2.1), lowstand erosion surfaces due to relative sea level fall (see Section 12.2.2), ravinement surfaces formed during transgressions (see Section 12.2.3), and co-planar surfaces or amalgamated surfaces of lowstand and transgressive erosion (e.g. estuarine valley incision surfaces) (see Section 12.2.4; MacEachern *et al.*, 1992, 2007a; Pemberton *et al.*, 1992b, 2004). More rarely, the *Glossifungites* ichnofacies has been recorded in deep-marine environments associated to incised submarine canyons (see Section 12.2.1; Hayward, 1976). Firmground surfaces demarcated by the *Glossifungites* ichnofacies may be also formed

Box 4.1 A modern example of the *Glossifungites* ichnofacies along the Georgia coast of the United States

Information from modern environments, although commonly overlooked, may provide valuable information to characterize and understand ichnofacies. The Georgia coast of the eastern United States is a fascinating natural laboratory to elucidate the producers and mechanisms of formation of the *Glossifungites* ichnofacies. Here, the *Glossifungites* ichnofacies occurs in previously buried and dewatered muds of Holocene salt marshes that have been subsequently exhumed by beach or tidal-channel erosion. Three main intergradational ichnocoenoses have been recognized: (1) a petricolid ichnocoenose; (2) a petricolid–pholad–crustacean ichnocoenose; and (3) a petricolid-crustacean-polydoran ichnocoenose. Petricolid and pholad bivalves produce incipient *Gastrochaenolites*, the polychaete *Polydora* excavate small *Diplocraterion*-like burrows, various polychaetes produce incipient *Palaeophycus*, shrimps construct *Thalassinoides* galleries, and crabs produce *Psilonichnus*. Crustaceans tend to be dominant in more protected back-barrier settings influenced by low-energy tidal currents, while petricolid and pholad bivalves are more characteristic of high-energy foreshore areas affected by wave-induced currents. Other factors influencing the distribution of trace-making organisms are density of the relict *Spartina* root mats, substrate cohesiveness, sediment texture, duration of subaerial exposure, and sandblasting from nearshore areas. Neoichnological observations have been essential in furthering our understanding of the nature and significance of the *Glossifungites* ichnofacies.

Reference: Pemberton and Frey (1985).

due to autogenic sedimentary processes (see Section 12.8). In this case, erosion due to migrating tidal channels and tidal creeks represent a common environmental scenario conducive to the production and colonization of firmground substrates (Gingras *et al*., 2000; MacEachern *et al*., 2007a). MacEachern *et al*. (2007a) also noted that long periods of quiescence may be conducive to the formation of relatively firm mudstones, allowing the establishment of the *Glossifungites* ichnofacies. According to these authors, examples of the *Glossifungites* ichnofacies related to autogenic processes tend to show some evidence of burrow compaction, contain more deeply penetrating burrows due to minimal substrate stiffness, and include ichnogenera less typical of firmground settings.

Stratigraphic and environmental implications of the *Glossifungites* ichnofacies in carbonate rocks are rather different (see Section 12.6). Because carbonates commonly undergo rapid consolidation and cementation due to early diagenetic processes, firmgrounds are not necessarily related to erosional exhumation of the substrate as in siliciclastic rocks. On the contrary, endurated substrates in carbonate rocks are commonly related with omission surfaces representing reduced rates of sedimentation (Bromley, 1975). However, spectacular examples of the *Glossifungites* ichnofacies in ravinement surfaces, analogous to those formed in siliciclastic substrates may occur in carbonates (Rodríguez-Tovar *et al*., 2007).

This ichnofacies can be very heterogeneous displaying remarkable spatial variations. Gingras *et al*. (2001) found that degree of substrate firmness, position within the intertidal zone, sediment texture, and presence of a sediment veneer rank were among the most important controlling factors of the nature and composition of modern examples the *Glossifungites* ichnofacies. Spatial heterogeneity revealed by changes in the proportion of their components has been documented also in ancient examples of this ichnofacies (Carmona *et al*., 2006). MacEachern and Burton (2000) documented an unusual occurrence of the *Glossifungites* ichnofacies dominated by *Zoophycos*, and also having *Thalassinoides*, *Spongeliomorpha*, and *Rhizocorallium* in lower offshore deposits. Therefore, these authors suggested potential subdivisions of the *Glossifungites* ichnofacies corresponding to proximal–distal trends. According to this scheme, the archetypal *Glossifungites* ichnofacies occurs most commonly in high-energy shallow water, while the association with *Zoophycos* represents a distal expression of the *Glossifungites* ichnofacies. Although in its original definition the *Glossifungites* ichnofacies was not restricted to marine environments (Seilacher, 1967b), continental firmground ichnofaunas are dominated by the ichnogenus *Scoyenia* and related trace fossils, and seem to be remarkably different from their marine counterparts (e.g. Buatois *et al*., 1996a) (see Section 12.7). However, an occurrence of firmground *Rhizocorallium* in Miocene fluvial deposits has been noted (Fürsich and Mayr, 1981). The *Glossifungites* ichnofacies is known since the Early Cambrian (Bromley and Hanken, 1991).

4.3.2 *TRYPANITES* ICHNOFACIES

The *Trypanites* ichnofacies was originally introduced by Frey and Seilacher (1980), and subsequently revised in a number of papers (e.g. Frey and Pemberton, 1984; Pemberton *et al*., 1992b, 2001, 2004; Bromley and Asgaard, 1993a; Gibert *et al*., 1998, 2007). Bromley and Asgaard (1993a) noted that the *Trypanites* ichnofacies includes two different associations: *Entobia* (dominated by deep-tier borings) and *Gnathichnus* (dominated by shallow- to very shallow-tier raspings and etchings). These two associations were regarded either as subdivisions of the *Trypanites* ichnofacies or as archetypal ichnofacies that replace the more general *Trypanites* ichnofacies. Subsequent work demonstrated the archetypal nature and recurrence of the *Entobia* association in cliffs and sediment-starved hardgrounds during most of the Mesozoic and Cenozoic (Gibert *et al*., 1998, 2007). MacEachern *et al*. (2007a) stated that the *Entobia* and *Gnathichnus* associations are closely associated with tiers and, therefore, serve as expressions of the suites that characterize the

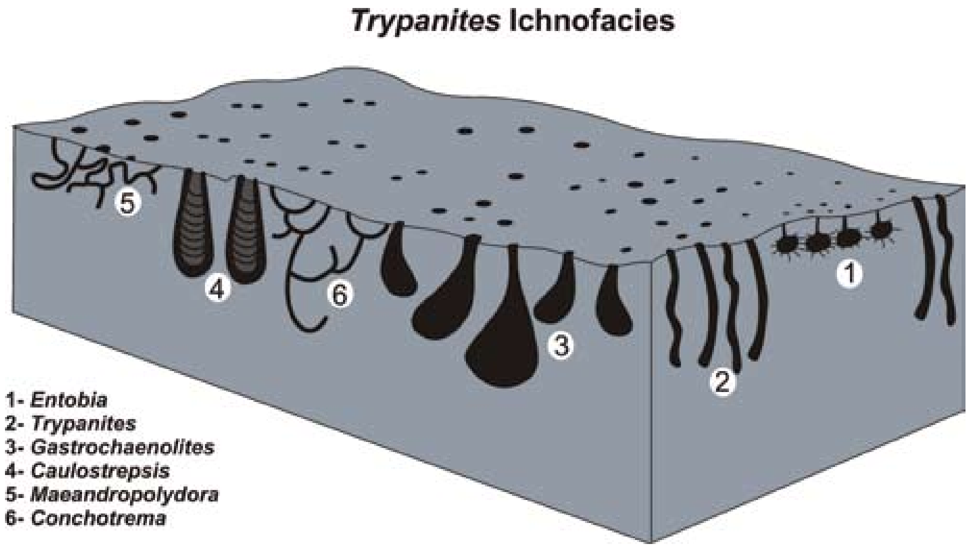


Figure 4.11 Schematic reconstruction of the *Trypanites* ichnofacies.

Trypanites ichnofacies as a whole. Interestingly, this is not really different from the distinction between the *Nereites* (shallow-tier structures preserved at the base of turbidites) and *Zoophycos* (deep-tier structures preserved in the fine-grained background mudstone) ichnofacies (Wetzel, 1984; Bromley, 1990, 1996). Also, it has been noted that the *Entobia* association is identical to the *Trypanites* ichnofacies on morpho-ethological grounds (MacEachern *et al*., 2007a). Accordingly, the *Entobia* association is regarded here as an equivalent of the *Trypanites* ichnofacies (see Section 14.2.3).

The *Trypanites* ichnofacies is characterized by: (1) dominance of deep-tier borings; (2) dominance of sharp-walled, unlined, passively filled, vertical to subvertical, cylindrical, simple, tear-, vase- or U-shaped dwelling borings of suspension feeders or passive predators; (3) presence of branched and multi-chambered borings produced by suspension feeders; (4) low to moderate ichnodiversity; and (5) high abundance (Fig. 4.11).

The most common components of the *Trypanites* ichnofacies are *Trypanites* (simple vertical borings), *Gastrochaenolites* (tear-shaped borings), and *Entobia* (branched systems). Other elements are *Caulostrepsis* (U-shaped pouches), *Maeandropolydora* (multi-entrance networks), *Conchotrema* (branched, multi-apertured cylindrical borings) and *Ubiglobites* (vase-shaped borings). Typical producers include polychaetes (*Trypanites*), bivalves (*Gastrochaenolites*), and sponges (*Entobia*). Microborings are also elements of this ichnofacies (Glaub *et al*., 2002; Glaub and Vogel, 2004).

The *Trypanites* ichnofacies is typical of cemented, fully lithified substrates, such as sediment-starved hardgrounds, cliffs, beachrock, and reefs (Frey and Pemberton, 1984; Pemberton *et al*., 1992b, 2001, 2004). More rarely, this ichnofacies can occur in bone beds or coquinas. The *Trypanites* ichnofacies indicates long periods of bioerosion without any interruption by frequent depositional events. Continuous activity by deep bioeroders leads to destruction of shallow tiers (Bromley and Asgaard, 1993a). The *Trypanites* ichnofacies is directly associated with different types of unconformities forming either omission or erosive surfaces and, as such, is significant in sequence stratigraphy (see Sections 12.2, 12.3, and 12.6). Only bioerosion in laterally persistent substrates should be included in the *Trypanites* ichnofacies (Pemberton *et al*., 1992b). Bored, isolated shells or clasts, although significant in terms of information potential (Gibert *et al*., 1996; Siggerud and Steel, 1999), do not represent the *Trypanites* ichnofacies. Evidence of emplacement in lithified substrate is revealed by the fact that borings cut through shells or grains instead of avoiding them (Bromley, 1975). A high density of borings indicates major breaks in sedimentation and sediment starvation. In ancient examples, bioerosion densities of up to 1500 borings per m^2 have been measured (Gibert *et al*., 1996; Domènech *et al*., 2001). However, as noted by Bromley and Asgaard (1993b), overall boring density is highly dependent of boring size. As in the case of the *Glossifungites* ichnofacies, deposit-feeding trace fossils are typically absent in the *Trypanites* ichnofacies due to the absence of nutritious particles in lithified substrates.

The *Trypanites* ichnofacies may be intergradational with the *Glossifungites* ichnofacies. In this case, the *Trypanites* suite cross-cuts the *Glossifungites* suite, reflecting progressive cementation of the original substrate (Bromley, 1975). Hardground formation may occur in both siliciclastic and carbonate substrates, although it tends to be more common in the latter (MacEachern *et al*., 2007a). In siliciclastic substrates most hardgrounds are associated with erosionally exhumed surfaces, which are typically formed during relative sea-level changes (Pemberton *et al*., 1992b, 2004). MacEachern *et al*. (2007a) cautioned against assignment of sequence-stratigraphic significance of the *Trypanites* ichnofacies in carbonate sediments. Because carbonates commonly undergo rapid lithification due to early diagenesis, hardground formation is not necessarily related to erosional exhumation in this type of substrates (see Section 12.6). Occurrences of the *Trypanites* ichnofacies in connection to sediment-starved omission surfaces are probably the rule rather than the exception (e.g. Bromley, 1975; Mángano and Buatois, 1991). In

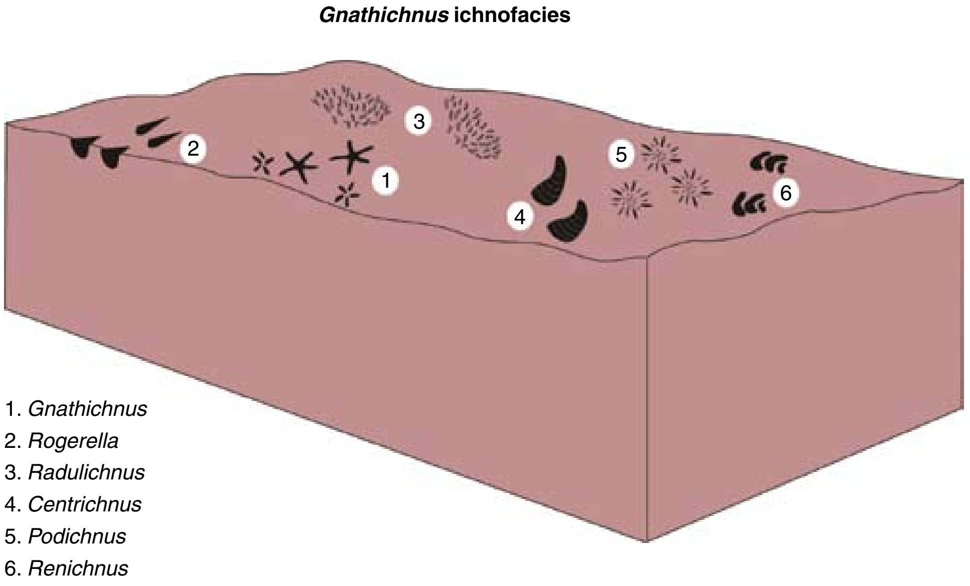


Figure 4.12 Schematic reconstruction of the *Gnathichnus* ichnofacies.

any case, the *Trypanites* ichnofacies has been recognized in erosionally exhumed carbonates associated with a regional unconformity (Pemberton *et al.*, 1980). A depauperate *Trypanites* ichnofacies has been introduced recently for non-carbonate substrates (Buatois and Encinas, 2011). Comparable bioeroded surfaces in continental environments are poorly known. Borings in modern lacustrine stromatolites from Lake Turkana (Kenya) have been documented by Ekdale *et al.* (1989). Embedment cavities have been recorded in Cenozoic lacustrine carbonates of Kenya and Wyoming by Lamond and Tapanila (2003). Artificial lakes in Kansas contain Recent U-shaped structures produced by chironomids penetrating into Carboniferous shale. The *Trypanites* ichnofacies is known since the Early Cambrian (James *et al.*, 1977).

4.3.3 *GNATHICHNUS* ICHNOFACIES

The *Gnathichnus* ichnofacies or association was introduced by Bromley and Asgaard (1993a) for bored shells and boulders. MacEachern *et al.* (2007a) noted that this example of the *Gnathichnus* association does not form continuous mappable surfaces, and therefore does not qualify as an ichnofacies. However, Bromley and Asgaard (1993a) suggested that the same suite may be present in rapidly buried laterally continuous substrates. In fact, the assemblage was subsequently recognized in the Miocene of Spain (Mayoral and Muñiz, 1996), and its archetypal nature and temporal recurrence during most of the Mesozoic and Cenozoic have been now demonstrated (Gibert *et al.*, 2007).

The *Gnathichnus* ichnofacies is characterized by: (1) dominance of shallow to very shallow-tier grazing structures; (2) presence of other ethological categories, such as domichnia, fixichnia, and praedichnia; (3) subordinate occurrence of deeper structures; (4) dominance of radulation and gnawing traces produced by algal grazers; (5) presence of etched attachment scars; (6) occurrence of sock-shaped borings; (7) low to moderate ichnodiversity; and (8) high abundance (Fig. 4.12).

The most common components of the *Gnathichnus* ichnofacies are *Gnathichnus* (stellate gnawing traces), *Radulichnus* (radulation traces), *Renichnus* (spiral- to arcuate-shaped etched attachment scars), *Podichnus* (radiating arcs of attachment pits), and *Centrichnus* (drop-shaped attachment pits). The deeper-tier *Maeandropolydora* (multi-entrance networks) may be present. Gastropods, chitons, regular echinoids, brachiopods, acrothoracican barnacles, and bryozoans are among the most common producers.

This association suggests short-term bioerosion interrupted by rapid sedimentation, allowing preservation of shallow-tier bioerosion in the absence of a mature deep-tier endolithic community (Bromley and Asgaard, 1993a). In contrast to the long-term colonization windows that typify the *Trypanites* ichnofacies, the *Gnathichnus* ichnofacies reflects short-term colonization windows. It commonly occurs in spatially restricted, mobile shell-grounds formed under moderate energy conditions (Gibert *et al.*, 2007). The *Gnathichnus* ichnofacies is known since the Jurassic (Gibert *et al.*, 2007).

4.3.4 *TEREDOLITES* ICHNOFACIES

The *Teredolites* ichnofacies was introduced by Bromley *et al.* (1984), and has been recently revised by Gingras *et al.* (2004). Additional work on the *Teredolites* ichnofacies focused on the implications of bored log-grounds in sequence stratigraphy (e.g. Savrda, 1991a; Savrda *et al.*, 1993, 2005). This ichnofacies is characterized by: (1) dominance of clavate borings; (2) boring walls ornamented with the texture of the host substrate; (3) very low ichnodiversity, most commonly monospecific suites; and (4) high density of borings, albeit with rare interpenetration (Fig. 4.13).

The ichnogenus *Teredolites* (Fig. 4.14a–b), a clavate boring produced by pholadid bivalves (e.g. *Teredo*, *Martesia*, *Lyrodus*, *Bankia*), is the typical component of this ichnofacies (Bromley *et al.*, 1984). However, analysis of a modern example reveals

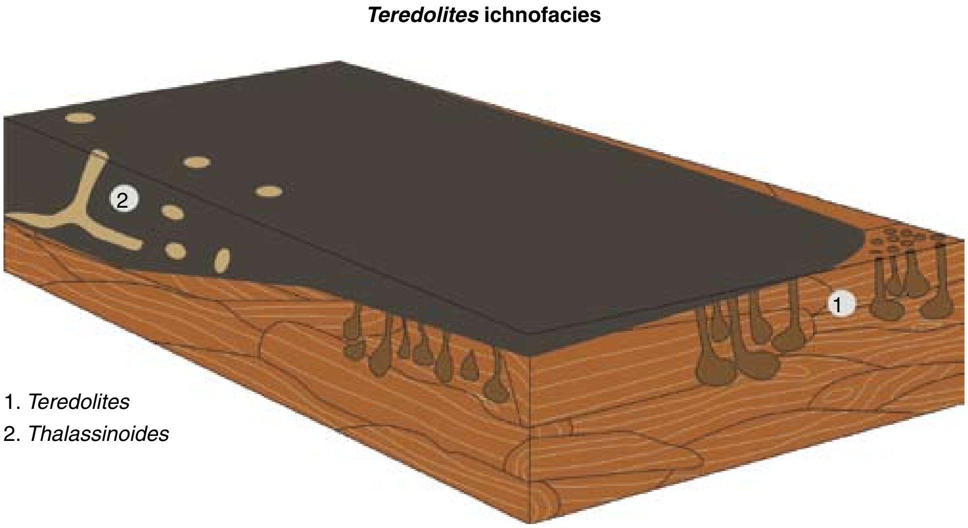


Figure 4.13 Schematic reconstruction of the *Teredolites* ichnofacies.

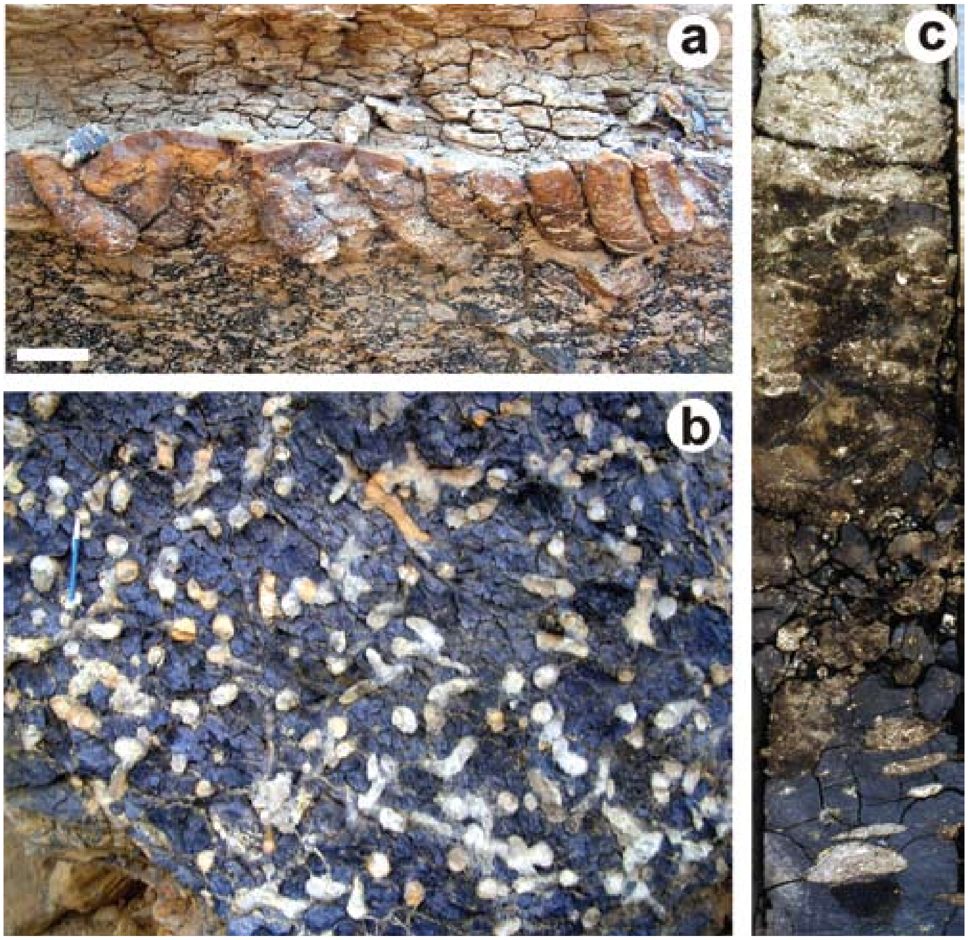


Figure 4.14 Examples of the *Teredolites* ichnofacies. (a) Type locality of the *Teredolites* ichnofacies showing high density of *Teredolites clavatus* in a coal layer. Upper Cretaceous, Horseshoe Canyon Formation, East Coule, Drumheller, Alberta, western Canada. Scale bar is 5 cm. See Bromley *et al.* (1984). (b) Bedding-plane view showing high density of *Thalassinoides suevicus* in coal layer. Middle to Upper Miocene, Urumaco Formation, Urumaco River, northwestern Venezuela. Pen is 15 cm. (c) *Thalassinoides* isp. in coal layer. Lower Miocene, Oficina Formation, Oritupano Field, Eastern Venezuela Basin. Core width is 8 cm.

the presence of borings similar to *Caulostrepsis*, *Entobia*, *Maeandropolydora*, *Psilonichnus*, *Rogerella*, *Thalassinoides*, and *Trypanites* emplaced in log-grounds (Gingras *et al.*, 2004). According to this study, other potential tracemakers for the *Teredolites* ichnofacies are spionid polychaetes (*Polydora proboscidea*) and isopods (*Limnoria lignorum*). While a variety of woodground borings are known from modern environments, fossil examples are almost invariably monospecific, containing only the ichnogenus *Teredolites*. Although the ichnospecies *Teredolites longissimus* is the most common ichnotaxa, *T. clavatus* may occur also (Bromley *et al.*, 1984). Occasionally, the ichnogenus *Thalassinoides* has been recognized in fossil woodgrounds both in outcrops (Gingras *et al.*, 2004) (Fig. 4.14b) and cores (Buatois *et al.*, 2002a) (Fig. 4.14c). Differences between modern and ancient examples of the *Teredolites* ichnofacies reveal taphonomic filters of the fossilization barrier. Deep-penetrating borings, such as *Teredolites*, have a higher preservation potential that shallowly emplaced structures, such as *Rogerella* or *Maeandropolydora* (Gingras *et al.*, 2002).

The *Teredolites* ichnofacies characterizes resistant xylic (woody and coaly) substrates, such as drifted log pavements and peat deposits that may be preserved as coal or lignite in the rock record (Pemberton *et al.*, 2001). In contrast to lithic substrates, xylic substrates are flexible, consist of organic matter, and are rapidly biodegradable (Bromley *et al.*, 1984). Ecologically, while hardground borings are commonly produced for protection, woodground borings are related with the quest for food (Bromley *et al.*, 1984). Boring walls are commonly ornamented with the host substrate texture, and xenoglyphs of tree growth rings may be present. Size-class variations are commonly present in *Teredolites* suites, suggesting animals at different stages of maturity (Bromley *et al.*, 1984; Savrda *et al.*, 1993; Gingras *et al.*, 2004). Bimodal size distributions probably reveal successive colonization events (Gingras *et al.*, 2004). Only occurrences associated with a laterally persistent substrate should be included in the *Teredolites* ichnofacies; bored, isolated log fragments do not represent the ichnofacies (Pemberton *et al.* 1992b). The term "log-ground" may be used for high concentrations of allochthonous wood (Savrda *et al.*, 1993). As noted by MacEachern *et al.* (2007a), these concentrations may form useful mapping surfaces, particularly where associated with stratigraphic discontinuities (e.g. Savrda, 1991a; Savrda *et al.*, 1993, 2005) (see Box 12.1).

Typically, the *Teredolites* ichnofacies is associated with omission surfaces formed in shallow-marine and marginal-marine environments, commonly bays, estuaries, lagoons, and deltas (Bromley *et al.*, 1984; Pemberton *et al.*, 1992b; MacEachern *et al.*, 2007a). The ichnogenus *Teredolites* is confined to environments with salinities ranging from brackish to fully marine, and apparently cannot tolerate freshwater. This is consistent with almost all the examples documented in the stratigraphic record (e.g. Bromley *et al.*, 1984; Savrda, 1991a; Savrda *et al.*, 1993, 2005). Two occurrences in Cretaceous and Eocene supposed fluvial environments (Plint and Pickerill, 1985) are in rocks now regarded as formed in marginal-marine, brackish-water settings (Plint, 2000; MacEachern *et al.*, 2007a). However, a freshwater example was documented by Bertling and Hermanns (1996) in Neogene fluvial deposits. Wood borings are also present in continental settings, and are mostly produced by isopods (Genise, 1995; Genise and Hazeldine, 1995; Mikuláš and Cílek, 1998; Mikuláš, 2008). Further research is still necessary in order to erect a continental equivalent of the *Teredolites* ichnofacies; recognition of laterally extensive substrates will be critical. The *Teredolites* ichnofacies is known since the Cretaceous (Bromley *et al.*, 1984).

4.4 INVERTEBRATE CONTINENTAL ICHNOFACIES

The ichnofacies model has been expanded into the continental realm in recent years, and efforts have been made to recognize archetypal invertebrate ichnofacies (Buatois and Mángano, 1995b, 2007; Genise *et al.*, 2000, 2010a; Hunt and Lucas, 2007; Ekdale *et al.*, 2007; Minter and Braddy, 2009). In his original model, Seilacher (1967b) recognized only one ichnofacies for continental environments, the *Scoyenia* ichnofacies. The fact that the *Scoyenia* ichnofacies was only one of the many potential recurrent trace-fossil assemblages of continental environments, and that these settings are as diverse as marine environments was acknowledged by ichnologists long ago and illustrated by Bromley and Asgaard (1979) in a seminal paper. However, it is only in the last 15 years that studies addressing the problem of recognizing additional continental ichnofacies have been published (Smith *et al.*, 1993; Buatois and Mángano, 1995b; Bromley, 1996; Genise *et al.*, 2000, 2010a; Ekdale *et al.*, 2007; Hunt and Lucas, 2007). At present, six continental archetypal ichnofacies have been proposed: the *Scoyenia*, *Mermia*, *Coprinisphaera*, *Termitichnus*, *Celliforma*, and *Octopodichnus–Entradichnus* ichnofacies. Part of this scheme has received quantitative support by recently performed cluster analysis (Minter and Braddy, 2009). The continental invertebrate ichnofacies model has reached a level of resolution similar to that of marine environments. While the *Scoyenia* and *Mermia* ichnofacies are mostly controlled by the position of the water table (Buatois and Mángano, 1995b, 2002, 2009a), terrestrial ichnofacies show a close correspondence with the plant formations identified by Mueller-Dombois and Ellenberg (1980). In fact, Genise *et al.* (2010a) noted that of the seven global plant formations recognized by these authors, four display correlation with terrestrial ichnofacies.

4.4.1 *SCOYENIA* ICHNOFACIES

Seilacher (1967b) proposed the *Scoyenia* ichnofacies for "nonmarine sands and shales, often red beds, with a distinctive association of trace fossils", and referred to a previous schematic illustration (Seilacher 1963b, Fig. 7), which included meniscate traces, arthropod trackways, and bilobed traces, as well as several physical sedimentary structures (e.g. desiccation cracks). Frey *et al.* (1984b) noted that the *Scoyenia* ichnofacies subsequently was used as a catchall for all occurrences of continental trace fossils, and proposed a refined definition in order to retain its ecological and environmental significance. Further refinements were suggested by Buatois and Mángano (1995b), who noted the abundance of arthropod trackways in the *Scoyenia* ichnofacies. The *Scoyenia* ichnofacies is characterized by: (1) abundance of horizontal meniscate backfilled traces produced by mobile deposit feeders; (2) abundance of locomotion traces, including both trackways and bilobate trails; (3) presence of vertical domiciles; (4) a mixture of invertebrate (mostly arthropod), vertebrate and plant traces; (5) low to moderate ichnodiversity; and (6) localized high abundance (Fig. 4.15).

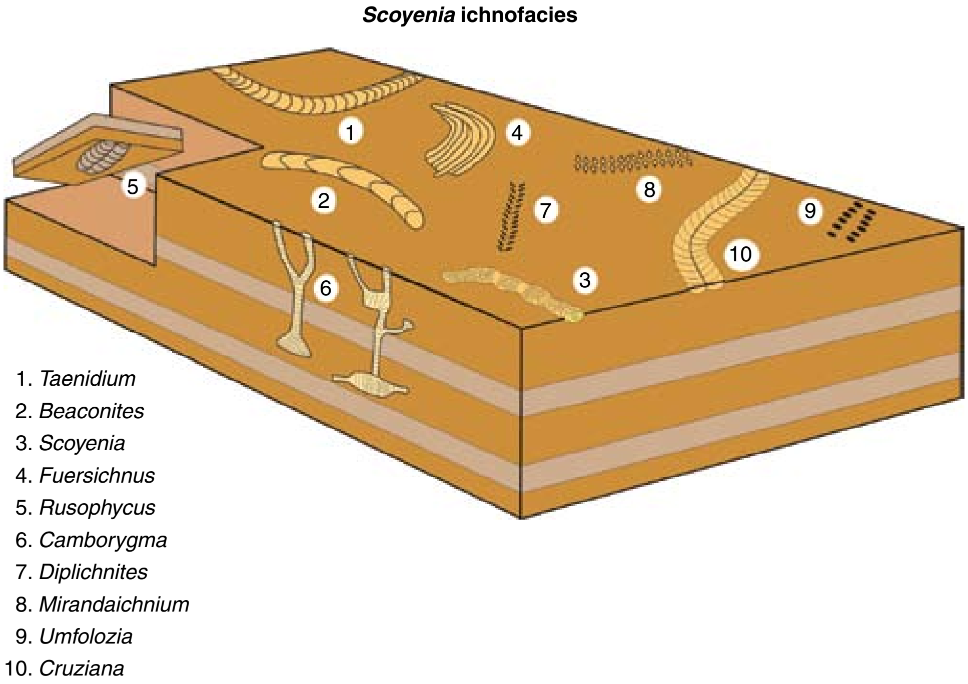


Figure 4.15 Schematic reconstruction of the *Scoyenia* ichnofacies.

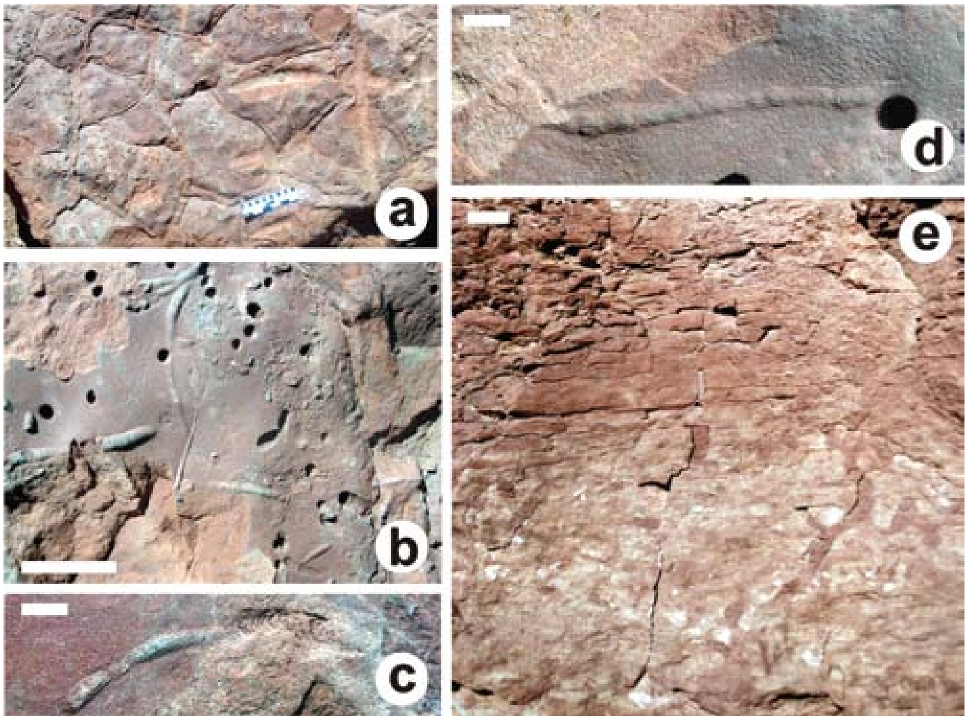


Figure 4.16 Examples of the *Scoyenia* ichnofacies, illustrating the typical dominance by meniscate trace fossils. (a) General view of a bedding plane with several specimens of *Scoyenia gracilis* associated with desiccation cracks. Lower Jurassic, Kayenta Formation, Grandview Point, Canyonland National Park, Utah, United States. Scale bar is 10 cm. (b) Close-up showing burrow sculpture and presence of raindrop imprints. Scale bar is 5 cm. (c) Close-up showing meniscate fill and wall with parallel striations. Scale bar is 1 cm. (d) Close-up of wall striations. Scale bar is 1 cm. (e) Vertical cross-section showing intense bioturbation by *Taenidium* isp. Middle Triassic, Youfangzhuang Formation, Nanshan Forest Park, Jiyuan City, Henan Province, central China. Scale bar is 1 cm. See M. Wang *et al*. (2009).

Meniscate trace fossils include *Scoyenia* (Fig. 4.16a–d), *Beaconites*, and *Taenidium* (Fig. 4.15e). Adhesive meniscate burrows of Hasiotis (2004), recently referred to the new ichnogenus *Naktodemasis* by Smith *et al*. (2008a), actually belong in *Taenidium* (Krapovickas *et al*., 2009). Arthropod trackways are represented by a wide variety of ichnotaxa, including *Umfolozia*, *Merostomichnites*, *Diplichnites*, *Hexapodichnus*, *Permichnium*, and *Acripes*. Bilobate traces include locomotion (*Cruziana*) and associated resting structures (*Rusophycus*). Simple facies-crossing ichnotaxa, such as *Planolites*, *Palaeophycus*, and *Cochlichnus*, are common. Vertical burrows are currently assigned to *Skolithos* and *Cylindricum*. Some examples of the ichnofacies may include crayfish burrows (*Camborygma*) and banana-shaped feeding traces (*Fuersichnus*). Vertebrate tracks may be abundant and varied (Hunt and Lucas, 2007).

The *Scoyenia* ichnofacies is characterized by very low-diversity assemblages, mostly monospecific occurrences of meniscate trace fossils (Frey *et al.*, 1984b). However, moderately diverse assemblages of arthropod trackways may occur (Buatois and Mángano, 1995b). The dominance of horizontal traces of deposit feeders suggests low-energy settings. Furthermore, the abundance of meniscate traces and arthropod trackways is typical of sediments periodically exposed to air or periodically inundated, and intermediate between aquatic and terrestrial environments (Frey *et al.*, 1984b; Frey and Pemberton, 1984, 1987). This environmental scenario is consistent with the associated physical structures, which are indicative of periodic subaerial exposure (e.g. desiccation cracks, raindrop imprints) (Fig. 4.16a).

The *Scoyenia* ichnofacies is typical of fluvial and lacustrine systems, although it may also occur in certain eolian subenvironments. In fluvial settings, it is present in floodplain deposits, covering a wide variety of subenvironments, such as ponds, levees, and crevasse splays (Frey *et al.*, 1984b; Frey and Pemberton, 1984, 1987; Buatois and Mángano, 1995b, 2002, 2004a) (see Section 10.2). In lacustrine environments, the *Scoyenia* ichnofacies typically characterizes lake-margin areas, being present in both open and closed lacustrine basins, and in both ephemeral and perennial lakes (Buatois and Mángano, 1998, 2004a) (see Section 10.3). It is not restricted to siliciclastic systems, but is also present along the margins of carbonate lakes (Genise *et al.*, 2010a). In eolian systems, it may occur in wet interdunes (Buatois and Mángano, 2004a) (see Section 10.4).

Bromley (1996) proposed a more restricted definition of the *Scoyenia* ichnofacies as a continental equivalent of the firmground *Glossifungites* ichnofacies of the marine realm. In fact, the *Scoyenia* ichnofacies may be subdivided into two distinct suites: one characterized by meniscate structures without ornamentation (*Taenidium*, *Beaconites*) developed in a soft substrate, and the second typified by striated traces (*Scoyenia*, *Spongeliomorpha*), cross-cutting the former and developed in a firm substrate (Buatois *et al.*, 1996a; Savrda *et al.*, 2000; Buatois and Mángano, 2002, 2004a). The resulting palimpsest surfaces reflect progressive desiccation of sediment.

Bromley (1996) also tentatively proposed the *Rusophycus* ichnofacies for fluvial to shallow-lacustrine environments, and the *Fuersichnus* ichnofacies for lake settings below the fair-weather wave base. The *Rusophycus* ichnofacies is dominated by arthropod locomotion and resting trace fossils, and cannot be distinguished at present from the *Scoyenia* ichnofacies (Buatois and Mángano, 2004a). The *Fuersichnus* ichnofacies is based on examples in which the eponymous ichnogenus occurs in continental environments. However, the "type" examples suggested are from fluvial (MacNaughton and Pickerill, 1995) and ephemeral alluvial plain and sand-flat deposits (Gierlowski-Kordesch, 1991) rather than relatively deep lakes. As presently defined, the *Fuersichnus* ichnofacies cannot be distinguished from the *Scoyenia* ichnofacies (Buatois and Mángano, 2004a). However, further research in these two types of ichnofaunas may hold the potential to distinguish trace-fossil associations with a lower degree of recurrence than archetypal ichnofacies, but of paleoenvironmental utility in basin-by-basin studies.

The *Scoyenia* ichnofacies is known since the Ordovician (Johnson *et al.*, 1994). Paleozoic occurrences of this ichnofacies tend to be dominated by arthropod trackways, while meniscate trace fossils seem to be more common since the Permian and particularly the Triassic (Buatois *et al.*, 1998c) (see Section 14.2.6). The crayfish burrow *Camborygma* is a common addition to the ichnofacies since the Triassic (Hasiotis and Dubiel, 1993).

4.4.2 *MERMIA* ICHNOFACIES

The *Mermia* ichnofacies was introduced by Buatois and Mángano (1995b) to fill some of the gaps in continental ichnofacies. It is characterized by: (1) dominance of horizontal to subhorizontal grazing and feeding traces produced by mobile deposit feeders; (2) subordinate occurrence of locomotion traces; (3) relatively high to moderate ichnodiversity; (4) high abundance; and (5) low degree of specialization of grazing and feeding patterns (Fig. 4.17).

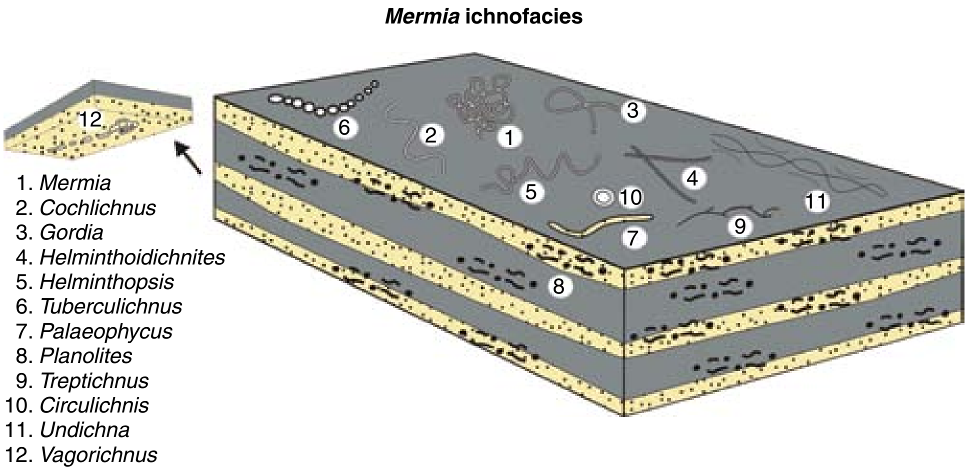


Figure 4.17 Schematic reconstruction of the *Mermia* ichnofacies.

The most typical components of the *Mermia* ichnofacies are a variety of unspecialized grazing traces, such as *Mermia*, *Gordia*, *Helminthopsis*, and *Helminthoidichnites*. The sinusoidal trail *Cochlichnus*, that may represent either locomotion or grazing, is also common. Simple feeding structures include very shallow-tier trace fossils, such as *Treptichnus* and *Circulichnis*. Locomotion traces are typically represented by the fish trail *Undichna* or by the invertebrate trail *Diplopodichnus*. However, arthropod trackways (e.g. *Maculichna*, *Diplichnites*) may occur also, although they are rarely the dominant elements.

Although some examples of the *Mermia* ichnofacies may attain relatively high ichnodiversity, the diversity of trace fossils does not necessarily equate with species richness (Buatois and Mángano, 1998). The various ichnogenera recorded in the *Mermia* ichnofacies may result from minor behavioral variations of a very simple, unspecialized grazing pattern developed by a single tracemaker (e.g. *Helminthopsis*, *Helminthoidichnites*, *Gordia*, *Mermia*). The simple patterns revealed by grazing and feeding traces mark a clear difference with respect to assemblages preserved in deep-marine turbidites. The dominance of horizontal grazing traces of deposit and detritus feeders suggests low-energy environments. Substrates are fine-grained, mostly unconsolidated silts and very fine- to fine-grained sands. Absence of scratch marks and common poor preservation of trace-fossil morphology suggest very soft, submerged substrates. Moderate ichnodiversity indicates relatively stable and well-oxygenated settings. Under anoxic conditions the *Mermia* ichnofacies is suppressed.

The *Mermia* ichnofacies typifies permanently subaqueous zones of lacustrine systems, extending from shallow to deep bathymetric zones (Buatois and Mángano, 1995b) (see Section 10.3). This ichnofacies is commonly present in open perennial siliciclastic lacustrine systems, but may occur in carbonate lakes also (Gibert *et al.*, 2000; Buatois *et al.*, 2000; Genise *et al.*, 2010a). However, the ichnofacies may be present in floodplain water bodies under subaqueous conditions (Buatois and Mángano, 2002; Mikuláš, 2003) (see Section 10.2.2). The lower ichnodiversity of these floodplain assemblages in comparison with their lacustrine counterparts probably reflects less stable conditions and the temporary nature of floodplain ponds. Also, the *Mermia* ichnofacies may occur in fjord settings under freshwater conditions due to glacial melting (Buatois and Mángano, 1995b, 2003b; Buatois *et al.*, 2006a, 2010a).

There are no archetypal trace-fossil associations that clearly distinguish shallow- and deep-lacustrine environments, probably because of the wide variability of lakes. Accordingly, Buatois and Mángano (1998) considered the *Mermia* ichnofacies as a continental equivalent of the *Cruziana*, *Zoophycos*, and *Nereites* ichnofacies in the classical Seilacherian scheme. Trace-fossil assemblages typically recorded from relatively deep-lacustrine areas may also occur in shallower zones (e.g. Pickerill, 1992).

The *Mermia* ichnofacies is known since the Carboniferous. In contrast to Paleozoic permanent subaqueous assemblages typified by surface trails, Mesozoic and Cenozoic assemblages tend to contain a higher proportion of infaunal burrows (Buatois *et al.*, 1996b).

4.4.3 *COPRINISPHAERA* ICHNOFACIES

The *Coprinisphaera* ichnofacies was introduced by Genise *et al.* (2000) in an attempt to detect recurrent trace-fossil assemblages in paleosols. This ichnofacies is characterized by: (1) dominance of trace fossils of bees, wasps, ants, and beetles; (2) subordinate presence of termite ichnofossils; (3) dominance of nesting traces or calichnia; (4) tiering structures that result from variable depths of emplacement of hymenopterous, termite, and dung-beetle nests; (5) moderate to relatively high ichnodiversity; and (6) high abundance (Fig. 4.18).

The typical component of this ichnofacies is the dung beetle nest *Coprinisphaera*, which is present in most recorded occurrences of the ichnofacies. Other beetle traces include *Pallichnus*,

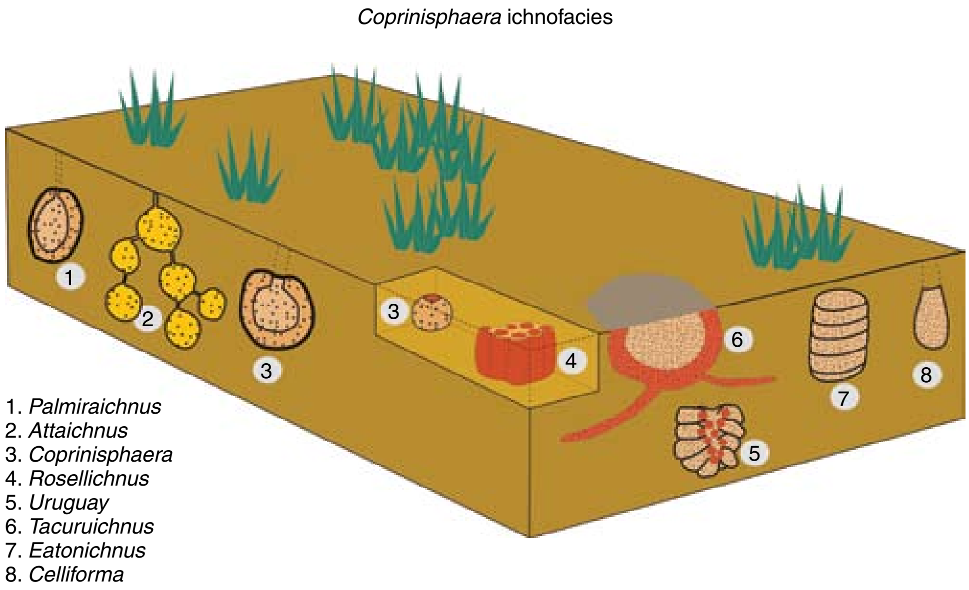


Figure 4.18 Schematic reconstruction of the *Coprinisphaera* ichnofacies.

Eatonichnus, Monesichnus, *Fontanai*, and *Teisseirei*. Common elements also include several bee trace fossils, such as *Celliforma*, *Uruguay*, *Ellipsoideichnus*, *Palmiraichnus*, and *Rosellichnus*. Other hymenopterous trace fossils belong to wasps (*Chubutolithes*, wasp cocoons), and ants (e.g. *Attaichnus, Parowanichnus*). Termite nests, mostly *Syntermesichnus*, *Coatonichnus*, *Tacuruichnus*, or even some ichnospecies of *Termitichnus* (*T. schneideri*) and *Vondrichnus* (*V. planoglobus*) may be locally present (Duringer *et al*., 2007). In addition, Genise *et al*. (2000) noted that other components still await formal taxonomic documentation. Root trace fossils are also present.

The *Coprinisphaera* ichnofacies strongly correlates with occurrences of herbaceous plant communities, mostly savannas, grasslands, prairies, and steppes (Genise *et al*., 2000). This correlation reflects the fact that dung beetles provision their nests with excrement of vertebrate herbivores. Hymenopterous insects seek bare, dry soil exposed to sun and, therefore, display similar environmental preferences to dung-beetles. On the other hand, termites display different environmental tolerances, and are strongly dependent on atmospheric and soil moisture, mostly inhabiting tropical rain forests (Grassé, 1986). Accordingly, termite nests are only occasionally present in the *Coprinisphaera* ichnofacies (Genise *et al*., 2000; Duringer *et al*., 2007).

The *Coprinisphaera* ichnofacies is typical of paleosols developed in paleoecosystems of herbaceous communities (*sensu* Mueller-Dombois and Ellenberg, 1980), climatically ranging from dry and cold to humid and warm conditions (Genise *et al*., 2000) (see Section 10.5). Evaluation of the relative abundance of the different trace fossils within the assemblage allows more refined paleoclimatological inferences. Hymenopterous traces tend to be dominant under drier conditions, whereas termite nests are linked to more humid environments (Genise *et al*., 2000; Duringer *et al*., 2007). The *Coprinisphaera* ichnofacies occurs in paleosols that have developed in various depositional systems subject to subaerial exposure, including alluvial plains, overbank, and eolian settings. Undoubtedly, this reflects the capacity of insects to nest in many different sedimentary environments. The emerging pattern suggests that paleosol ichnofaunas, and the *Coprinisphaera* ichnofacies, in particular, are controlled by ecological parameters, such as vegetation, climate, and soil, rather than by depositional processes (Genise *et al*., 2000).

The presence of the *Coprinisphaera* ichnofacies is well documented since the Paleocene (Genise *et al*., 2000). Although some Late Cretaceous assemblages contain fossil bee cells, coleopteran pupal chambers, wasp nests, and undetermined insect nests (e.g. Johnston *et al*., 1996; Elliott and Nations, 1998), assignation to the *Coprinisphaera* ichnofacies is doubtful. Further research in Mesozoic terrestrial ichnofaunas may yield valuable insights into the evolution of paleosol ichnofacies.

4.4.4 *TERMITICHNUS* ICHNOFACIES

The *Termitichnus* ichnofacies has a convoluted history. It was originally proposed by Smith *et al*. (1993) as a subset of the *Scoyenia* ichnofacies to include all paleosol trace-fossil assemblages. Subsequently, it was regarded as an ichnofacies for all paleosol assemblages, but at the same hierarchical level of the *Scoyenia* ichnofacies (Buatois and Mángano, 1995b). However, Genise *et al*. (2000) suggested that the *Termitichnus* ichnofacies as originally defined be abandoned, because it does not reflect the diversity of paleosol settings and, therefore, fails to reveal significant paleoecological information. A definition of a *Termitichnus* ichnofacies *sensu strictu* that includes assemblages dominated by termite nests in paleosols of closed forest ecosystems was suggested pending recognition of its temporal and spatial recurrence (Genise *et al*., 2000, 2004a, 2010a).

This ichnofacies is characterized by: (1) dominance of trace fossils of termites; (2) low ichnodiversity; and (3) high abundance (Fig. 4.19). Typical components are *Termitichnus*, *Vondrichnus*, *Fleaglellius*, and *Krausichnus* (Genise and Bown, 1994b). Root trace fossils are abundant, including ichnofossils of flank-buttressed trees (Wing *et al*., 1995). Other associated trace fossils, such as *Masrichnus* (Bown, 1982), are of uncertain affinities (Genise and Cladera, 2004).

The *Termitichnus* ichnofacies characterizes paleosols formed in closed forests (*sensu* Mueller-Dombois and Ellenberg, 1980) with plant growth under warm and humid conditions (Genise *et al*., 2000, 2004a, 2010a) (see Section 10.5). A high water table is indicated by the presence of trace fossils of flank-buttressed tress (Wing *et al*., 1995). The best-documented example of this ichnofacies was recorded in the Eocene-Oligocene Jebel Qatrani Formation of Egypt, which includes *Termitichnus* and other ichnotaxa attributable to fossil termite nests (Genise and Bown, 1994b). Additional examples are necessary to further document the stratigraphic recurrence of this ichnofacies, as well as its significance.

4.4.5 *CELLIFORMA* ICHNOFACIES

In a study dealing with the definition of paleosol ichnofacies, Genise *et al*. (2000) noticed the presence of a potentially recurrent association in carbonate-rich paleosols (see also Genise *et al*., 2004a). More recently, Genise *et al*. (2010a) introduced the *Celliforma* ichnofacies to account for this specific type of ichnofauna. This ichnofacies is characterized by: (1) dominance of halictid bee nests; (2) association with hackberry endocarps and freshwater and terrestrial snail shells; (3) dominance of callichnia; (4) presence of pupichnia; (5) moderate ichnodiversity; and (6) high abundance (Fig. 4.20). Typical components are *Celliforma*, *Rosselichnus*, *Pallichnus*, *Rebuffoichnus*, *Palmiraichnus*, and *Teisseirei*. Meniscate trace fossils (*Taenidium*) and root structures are also common.

The *Celliforma* ichnofacies characterizes carbonate-rich paleosols (Genise *et al*., 2010a). Most examples correspond to palustrine conditions, but occurrences in calcretes have been also documented (see Section 10.5). In the former case, the time of subaerial exposure was enough to allow the formation of well-aerated and bare soils required for hymenopteran nesting (Genise *et al*., 2010a). In the case of shorter subaerial exposure,

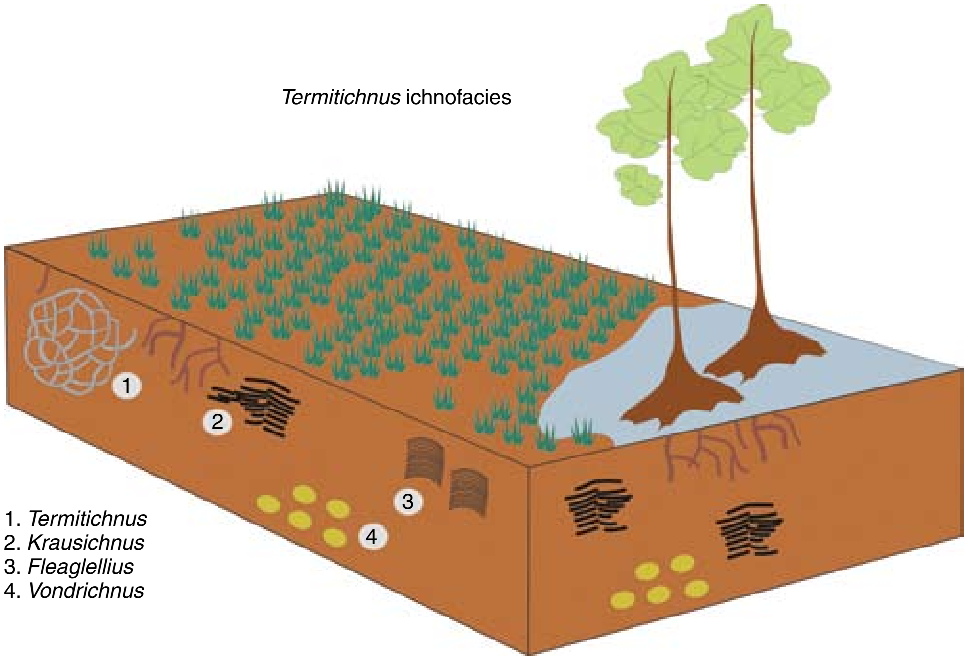


Figure 4.19 Schematic reconstruction of the *Termitichnus* ichnofacies.

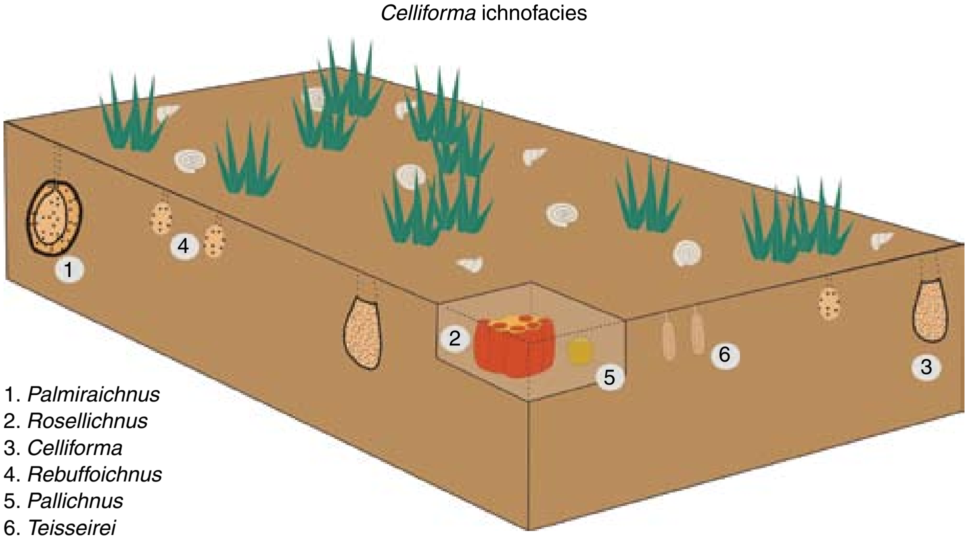


Figure 4.20 Schematic reconstruction of the *Celliforma* ichnofacies.

the *Scoyenia* ichnofacies develops. Under continuous and progressive desiccation of the substrate, the *Scoyenia* ichnofacies may be replaced by the *Celliforma* ichnofacies. Under terrestrial conditions, the *Celliforma* ichnofacies characterizes a drier climate than the *Coprinisphaera* ichnofacies (Genise *et al.*, 2010a). In terms of the global plant formations of Mueller-Dombois and Ellenberg (1980), the *Celliforma* ichnofacies characterizes scrubs and woodlands. In the case of palustrine environments, it ranges from subhumid to subarid settings (Alonso-Zarza, 2003).

The *Celliforma* ichnofacies is known since the Eocene (e.g. Melchor *et al.*, 2002). A potential older occurrence may be represented by the Calizas de Queguay, Uruguay, which may range into the Cretaceous, although more conclusive data on the age of this unit are necessary (Alonso-Zarza *et al.*, 2010; Genise *et al.*, 2010a).

4.4.6 *OCTOPODICHNUS–ENTRADICHNUS* ICHNOFACIES

Eolian ichnofaunas have received increasing attention in recent years, resulting in the proposal of archetypal ichnofacies in two independent studies (Fig. 4.21). Hunt and Lucas (2007) introduced the *Octopodichnus* ichnofacies, and Ekdale *et al.* (2007) the *Entradichnus* ichnofacies, both for eolian dune environments (see Section 10.4). The *Octopodichnus* ichnofacies of Hunt and Lucas (2007) consists of low diversity assemblages of arthropod trackways, mostly spiders and scorpions. The *Entradichnus* ichnofacies of Ekdale *et al.* (2007) consists of shallow traces of desert-dwelling arthropods, including vertical domiciles and meniscate traces. Diverging characterization of both eolian

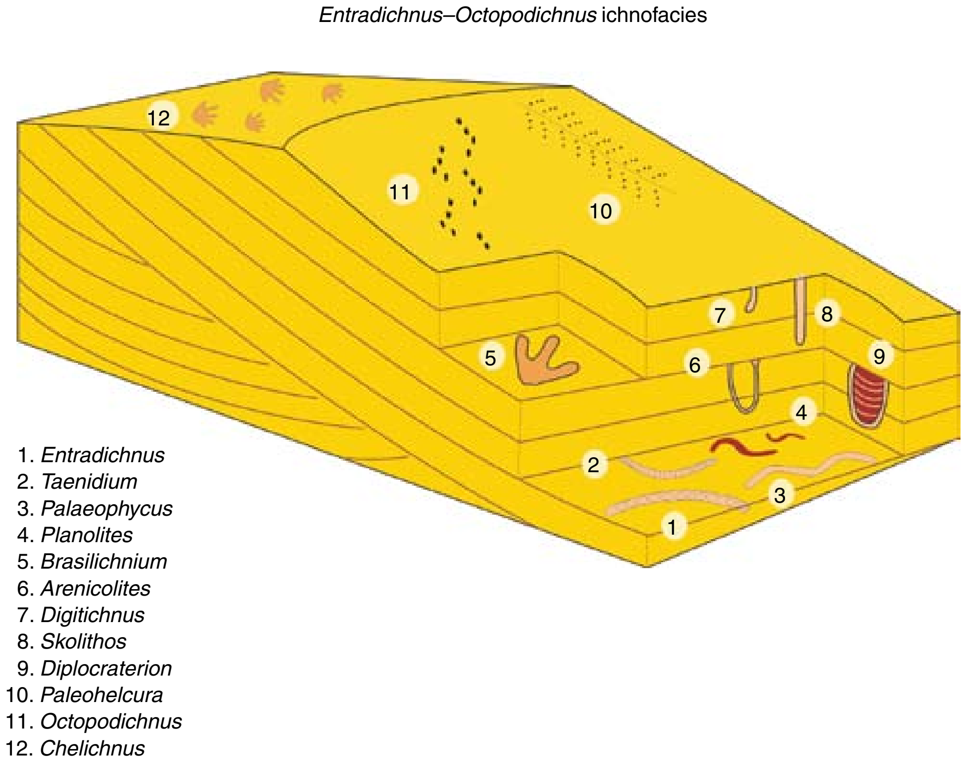


Figure 4.21 Schematic reconstruction of the *Octopodichnus–Entradichnus* ichnofacies.

ichnofacies undoubtedly results from disparate databases. Hunt and Lucas (2007) based the *Octopodichnus* ichnofacies essentially on Permian eolian dunes, the Coconino Sandstone of Arizona being the classic example. In contrast, the *Entradichnus* ichnofacies of Ekdale *et al*. (2007) is mostly based on the study of Jurassic examples, more specifically the Navajo Sandstone of Utah. Differences may result from the fact that a change in eolian ichnofaunas seems to have occurred by the Permian–Triassic transition with the appearance of more varied behavioral patterns, and an increase in infaunal bioturbators (Gradzinski and Uchman, 1994; Buatois *et al*., 1998c) (see Section 14.2.6). Both datasets are integrated and combined here in a single ichnofacies, referred to as the *Octopodichnus–Entradichnus* ichnofacies (Buatois and Mángano, 2008b). Further studies in eolian ichnofaunas should be undertaken in order to refine the characterization of this ichnofacies.

4.5 VERTEBRATE ICHNOFACIES

Lockley *et al*. (1994) first proposed a series of vertebrate ichnofacies. However, subsequent work by Hunt and Lucas (2007) demonstrated that those tetrapod ichnofacies should be considered ichnocoenoses because they represent the traces of specific communities that lack the recurrence that would warrant their consideration as archetypal ichnofacies. Accordingly, these authors re-evaluated vertebrate ichnofacies and defined five archetypal tetrapod ichnofacies for continental and coastal-plain environments: *Chelichnus, Grallator, Brontopodus, Batrachichnus*, and *Characichichnos* ichnofacies. In turn, they subdivided these ichnofacies into stratigraphically restricted, age-controlled ichnocoenoses. Vertebrate ichnofacies commonly have less temporal recurrence than their invertebrate counterparts. Hunt and Lucas (2007) suggested that vertebrate ichnofacies may provide greater resolution in terrestrial environments and that invertebrate ichnofacies may be of greater precision in subaqueous freshwater environments. However, recent developments in terrestrial invertebrate ichnology suggest increasing refinement of the paleosol ichnofacies model (Genise *et al*., 2010a). Some of the vertebrate ichnofacies directly correlate with invertebrate ichnofacies (e.g. *Chelichnus* and *Octopodichnus–Entradichnus* ichnofacies), while others may encompass more than one invertebrate ichnofacies (e.g. *Characichichnos* ichnofacies covering both the *Mermia* and *Skolithos* ichnofacies), or may represent a subdivision of an invertebrate ichnofacies (*Grallator*, *Brontopodus*, and *Batrachichnus* ichnofacies as subdivisions of the *Scoyenia* ichnofacies) (see Hunt and Lucas, 2007, Fig. 1). Freshwater invertebrate ichnofacies are controlled by the position of the water table and terrestrial invertebrate ichnofacies essentially by climate and plant formation. However, elucidation of the controlling factors in delineation and distribution of vertebrate ichnofacies requires further research. Recent work seems to indicate that the distribution of tetrapod trace fossils is more related to regional factors, such as climate and resource availability, than to local environmental factors at the scale of subenvironments (Krapovickas, 2010).

4.5.1 *CHELICHNUS* ICHNOFACIES

The *Chelichnus* ichnofacies was defined by Hunt and Lucas (2007) to replace the *Laoporus* ichnofacies formerly introduced by Lockley *et al*. (1994). It is characterized by: (1) dominance of tetrapod trackways whose manual and pedal tracks are equant in shape, subequal in size, and have short digit impressions; and (2) low ichnodiversity. *Chelichnus* and *Brasilichnium* are common elements. This ichnofacies occurs in dune faces of eolian environments (see Section 10.4). The *Chelichnus* ichnofacies encompasses two ichnocoenoses: the *Chelichnus* and the *Brasilichnium* ichnocoenoses (Hunt and Lucas, 2007). The former is common in the Permian, while the latter occurs in the Triassic and Jurassic. Overall the *Chelichnus* ichnofacies ranges in age from the Permian to the Jurassic. It correlates with the *Octopodichnus*–*Entradichnus* ichnofacies in the invertebrate realm.

4.5.2 *GRALLATOR* ICHNOFACIES

The *Grallator* ichnofacies was defined by Hunt and Lucas (2007) and represents a refinement of several ichnofacies formerly introduced by Lockley *et al*. (1994) and Lockley (2007) that are now regarded as ichnocoenoses. It is characterized by: (1) dominance of trackways of trydactil avian and non-avian theropods or other bipeds; and (2) moderate ichnodiversity. Typical components are *Grallator*, *Jindongornipes*, *Koreanoformis*, *Avipeda*, *Brachychirotherium*, *Rhychosauroides*, and *Eubrontes*. Environmentally, this ichnofacies typifies lacustrine shorelines (see Section 10.3). The *Grallator* ichnofacies includes four ichnocoenoses: the *Grallator*, *Eubrontes*, *Jindongornipes*, and *Avipeda* ichnocoenoses (Hunt and Lucas, 2007). The *Grallator* ichnocoenosis is typical of Late Triassic, the *Eubrontes* ichnocoenosis occurs in the Early Jurassic, the *Jindongornipes* ichnocoenosis is present in Early Cretaceous rocks, and the *Avipeda* ichnocoenosis (shorebird ichnofacies of Lockley *et al*., 1994) characterizes Cenozoic assemblages. Overall the *Grallator* ichnofacies ranges in age from the Triassic to the Recent.

4.5.3 *BRONTOPODUS* ICHNOFACIES

The *Brontopodus* ichnofacies was introduced by Hunt and Lucas (2007). As in the case of the *Grallator* ichnofacies, the *Brontopodus* ichnofacies encompasses several ichnofacies formerly introduced by Lockley *et al*. (1994) that are considered to be ichnocoenoses by Hunt and Lucas (2007). The *Brontopodus* ichnofacies is characterized by: (1) dominance of trackways of terrestrial herbivores; (2) subordinate presence of trackways of terrestrial carnivores; and (3) moderate ichnodiversity. Typical components of this ichnofacies are *Caririchnium*, *Ceratopsipes*, *Amblydactylus*, and *Brontopodus*. The *Brontopodus* ichnofacies tends to occur in coastal-plain to shoreline environments, including lacustrine margins (see Section 10.3). Therefore, there is some environmental overlap between the *Grallator* and *Brontopodus* ichnofacies, the latter encompassing, in addition, marine shorelines. Additional work is required to evaluate which specific controlling factors are involved in both ichnofacies (Krapovickas, 2010). The *Brontopodus* ichnofacies encompasses five ichnocoenoses: the *Parabrontopus*, *Caririchnium*, *Ceratopsipes*, *Amblydactylus*, and *Brontopodus* ichnocoenoses (Hunt and Lucas, 2007). The *Parabrontopus* ichnocoenosis occurs in Late Jurassic lacustrine shorelines, the *Caririchnium* ichnocoenosis is typical of Early Cretaceous clastic marine shorelines, the *Ceratopsipes* ichnocoenosis is present in Late Cretaceous coastal plains, the *Amblydactylus* ichnocoenosis characterizes Early to Late Cretaceous clastic marine shorelines, and the *Brontopodus* ichnocoenosis typifies Early Cretaceous carbonate marine shorelines. The *Brontopodus* ichnofacies ranges in age from the Jurassic to the Cretaceous.

4.5.4 *BATRACHICHNUS* ICHNOFACIES

The *Batrachichnus* ichnofacies was introduced by Hunt and Lucas (2007). This ichnofacies is characterized by: (1) dominance of trackways of quadrupedal carnivores; and (2) moderate ichnodiversity. Typical components are *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Dromopus, Dimetropus*, *Gilmoreichnus*, and *Chirotherium*. This ichnofacies represents a wide variety of environments ranging from distal alluvial fans, and fluvial plains to tidal flats (see Sections 10.2 and 7.2). Two ichnocoenoses are recognized within the *Batrachichnus* ichnofacies: the *Batrachichnus* and *Chirotherium* ichnocoenoses (Hunt and Lucas, 2007). The former is typically Early Carboniferous–Early Permian while the latter is Triassic. Overall the ichnofacies ranges from the Devonian to the Triassic.

4.5.5 *CHARACICHICHNOS* ICHNOFACIES

Hunt and Lucas (2007) proposed the *Characichichnos* ichnofacies. This ichnofacies is characterized by (1) dominance of swimming tracks and trails; and (2) moderate ichnodiversity. Typical components are *Characichichnos*, *Undichna*, *Lunichnium*, *Puertollanopus*, *Serpentichnus, Batrachichnus*, and *Hatcherichnus*. This ichnofacies represents lacustrine settings and inner zones of tide-dominated estuaries (see Sections 10.3 and 8.1.2). Three named ichnocoenoses have been recognized: *Serpentichnus*, *Characichichnos*, and *Hatcherichnus* (Hunt and Lucas, 2007). The *Serpentichnus* ichnocoenosis occurs in the late Paleozoic, the *Characichichnos* ichnocoenosis is of Middle Jurassic age, and the *Hatcherichnus* is present in Upper Jurassic strata. In terms of correlation with invertebrate ichnofacies, the *Characichichnos* ichnofacies commonly overlap with the *Mermia* ichnofacies in lacustrine settings. In the case of late Paleozoic inner-estuarine deposits (*Serpentichnus* ichnocoenosis), it is typically associated with a mixed *Scoyenia*–*Mermia* ichnofacies.

4.6 PITFALLS AND CONFUSIONS IN ICHNOFACIES ANALYSIS

Despite the efforts of many workers in addressing the ichnofacies model (e.g. Frey and Pemberton, 1984; Pemberton *et al*.,

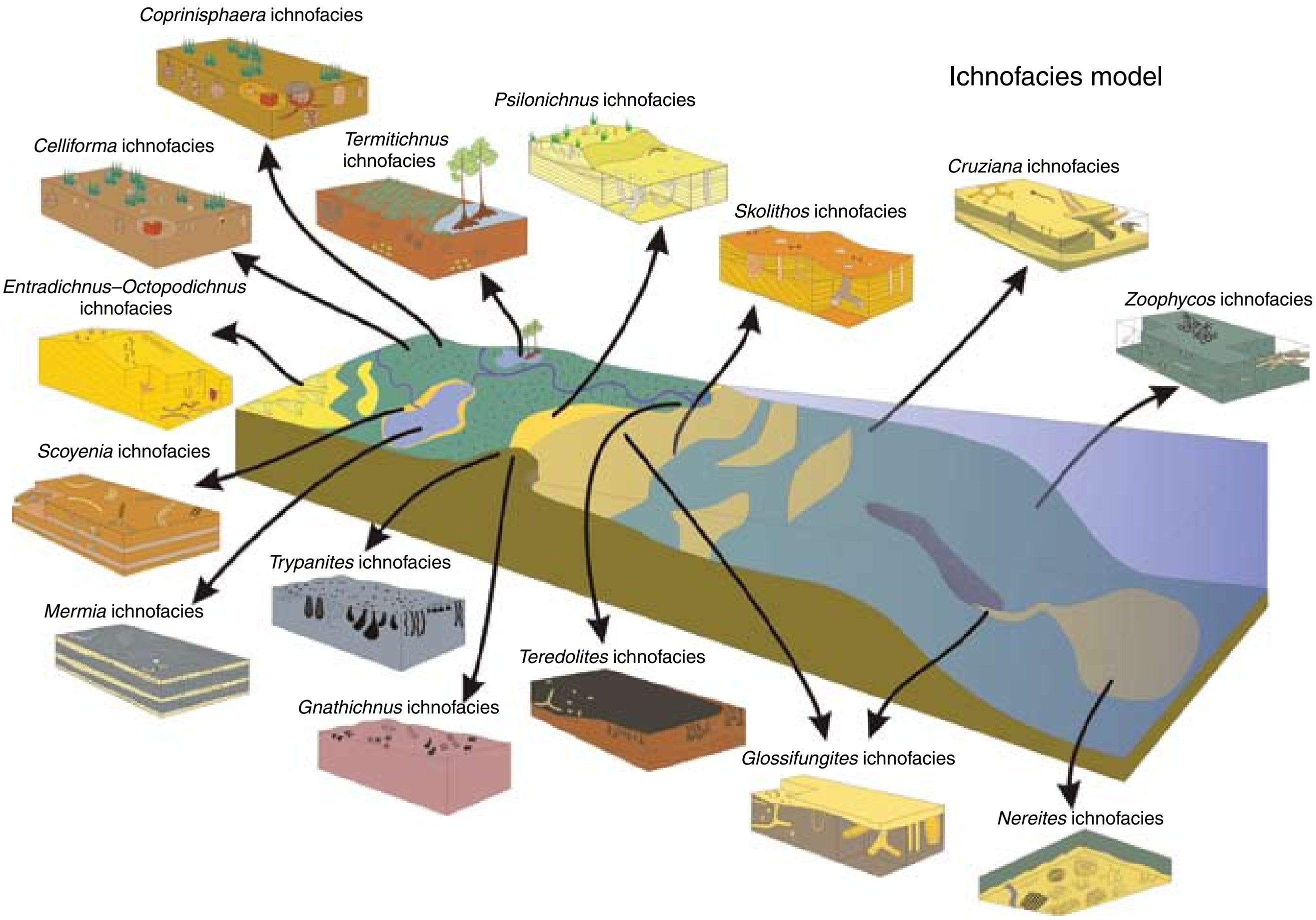


Figure 4.22 Schematic illustration of the ichnofacies model for invertebrate trace fossils. Individual ichnofacies indicate a precise set of environmental conditions rather than a depositional environment.

2001; MacEachern *et al*., 2007a), it is impossible to avoid the feeling that this model is still poorly understood. Because the ichnofacies model has been historically seen by some authors (e.g. Goldring, 1993, 1995) as competing against the ichnofabric approach, it will be discussed and evaluated in more detail at the end of the next chapter, which deals with ichnofabrics. However, some comments seem pertinent here.

A common misconception is to assume a direct correlation between ichnofacies and depositional environments. Ichnofacies are not indicators of sedimentary environments, but reflect the complex interplay of a set of environmental factors (Fig. 4.22). As expressed by Frey *et al*. (1990), ichnofacies are not intended to be paleobathymeters either. A well-known and repeated example is the occurrence of the *Skolithos* ichnofacies, typical of nearshore settings, in offshore tempestites and deep-marine turbidites (e.g. Crimes, 1977; Pemberton and Frey, 1984a; Pemberton and MacEachern, 1997). The *Cruziana* ichnofacies, though typical of lower-shoreface to offshore deposits, may be present in shallower settings, commonly intertidal flats of tide-influenced shorelines (e.g. Mángano *et al*., 2002a; Mángano and Buatois, 2004a, b). Regardless of the depositional environment, it is the animal response to a set of particular environmental conditions that defines an ichnofacies.

This is also true for continental ichnofacies and, therefore, the search for exact equivalences between continental ichnofacies and depositional environments is futile. Individual invertebrate ichnofacies occur in a wide variety of environmental settings. In these cases, water availability is a fundamental control in trace-fossil distribution (Gierlowski-Kordesch, 1991) and sediment water content strongly influences substrate consistency. The role of substrate consolidation as controlling trace-fossil preservation is remarkable (e.g. Buatois *et al*., 1997a; Buatois and Mángano, 2002, 2004a, 2007) and the *Scoyenia* and *Mermia* ichnofacies can be seen, at least in some sense, as taphofacies *sensu* Bromley and Asgaard (1991). As is the case of substrate-controlled ichnofacies in marine carbonates (e.g. Bromley, 1975), a single continental bed may represent the activity of more than one substrate-controlled suite, revealing the presence of composite ichnofacies (Buatois and Mángano, 2002, 2004a; Scott *et al*., 2009).

Further confusion derives from the idea that ichnofacies characterization is equivalent to the mere listing of presence or absence of morphological patterns, as in the approach undertaken by Keighley and Pickerill (2003) to analyze continental ichnofacies. There are two main flaws in this approach (see also Melchor *et al.*, 2006 for a critical re-evaluation). First, an ichnofacies is more than a collection of morphologies. Just to name a few additional aspects, ichnodiversity, relative abundance of their different components, preservational styles, and trophic types represented are equally important. Second, mere documentation of the presence of certain morphologies, albeit "objective", may not be informative because without a proper analysis in terms of functional morphology and behavior involved, the actual significance of the trace fossil cannot be evaluated (see Section 2.1). For example, group I of Keighley and Pickerill (2003) is labeled "Systematic-coverage branching burrow networks", and is exemplified by *Paleodictyon* and *Vagorichnus*. However, both ichnotaxa have little in common with respect to behavior, feeding strategies, and preservational style and, therefore, the presence of group I in a particular trace-fossil assemblage does not provide any precise information. Obviously, ichnofacies characterization and recognition imply to a certain degree interpretation, but this is intrinsic to any scientific enterprise: there is no algorithm that allows us to recognize an ichnofacies or to interpret a depositional environment.

Another misunderstanding is the idea that ichnofacies can be replaced by ichnocoenosis (e.g. Hasiotis, 2004). Both are very different notions and are applicable to different scales of analysis, so replacing ichnofacies by ichnocoenosis is not advisable, in fact, it is not possible without damaging the hierarchical conceptual framework of ichnology (Bromley *et al.*, 2007) (see Box 1.1). Ichnofacies are not real entities of the biological world, but constructs. One ichnofacies embraces a number of recorded ichnocoenoses in the fossil record and an unknown number of potential ichnocoenoses awaiting to be identified; here is rooted the predictive strength of the ichnofacies model. The ichnofacies extracts the biological signal to a complex interplay of physical parameters. In short, attempts to replace ichnofacies by ichnocoenosis represent a step backward in our search for common themes that allow us to use trace fossils as a predictive tool in facies modeling.

Finally, a common pitfall is the assertion that if a particular trace-fossil assemblage or ichnocoenosis cannot readily be ascribed to one ichnofacies, then the ichnofacies model is not valid (e.g. Hasiotis, 2004). On the contrary, the ichnofacies model serves as a norm and departures may serve to recognize anomalous situations. For example, the absence of the *Cruziana* ichnofacies in offshore deposits may be linked to the presence of some stress factor (e.g. limited oxygen). In the absence of a norm that helps in establishing predictions, it would be impossible to detect an anomaly, and any attempt to link a certain set of biogenic structures with environmental factors would be doomed.

5 The ichnofabric approach

> I confess frankly, it was the warning voice of David Hume that first, years ago, roused me from dogmatic slumbers, and gave a new direction to my investigations in the field of speculative philosophy.
>
> Immanuel Kant
> *Critique of Pure Reason* (1781)

> We now come to the more immediate subject of this volume, namely the amount of earth which is brought up by worms from beneath the surface.
>
> Charles Darwin
> *The Formation of Vegetable Mould Through the Action of Worms with Observations on their Habits* (1881)

The ichnofabric approach represents a relatively new trend in ichnology that started in the second half of the eighties, becoming much more popular since the nineties. As is the case of the ichnofacies model, the ichnofabric approach has been frequently misunderstood. Earlier studies involving ichnofabrics put too much emphasis on assessing bioturbation and other more significant aspects, such as tiering or evaluation of successive bioturbation events, were commonly overlooked. Even worse, the idea that measuring the intensity of bioturbation could replace trace-fossil identification as ground data for paleoenvironmental interpretations persisted for some years. At present, the idea that ichnofabric analysis is simply measuring the degree of bioturbation has been mercifully abandoned by all serious workers. If the ichnofabric approach is understood as a comprehensive way of analyzing bioturbated deposits, then the wealth of information that may be obtained is huge and not only restricted to paleoenvironmental reconstructions but also of significant potential in understanding reservoir properties, benthic paleoecology, and evolutionary paleoecology. German philosopher Immanuel Kant expressed that his reading of his British peer David Hume roused him from his dogmatic slumber and led him to become a "critical philosopher". In the same vein, the focus of this chapter, the ichnofabric approach, with its emphasis on taphonomic aspects, helps us to avoid taking the trace-fossil record at face value, permeating the whole interpretative process with some healthy criticism. We will start by providing the basics of the tiering concept before moving into a review of the ichnofabric concept, including aspects of quantifying the degree of bioturbation, visual strategies to present ichnofabric data, the paramount role of taphonomy, and the different types of ichnofabrics. Then, we will present the concept of ichnoguild, which, in our view, is central to the ichnofabric approach. Later, we will briefly review recent developments in the field of paleosol ichnofabrics. We will then address the general role of bioturbation, bioerosion, and biodeposition, before moving to the issue of bioturbation-enhanced permeability and reservoir characterization, a recently developed topic, which is having a strong impact in the petroleum industry. Finally, we will compare the ichnofacies and ichnofabric approaches.

5.1 TIERING

Tiering consists of the vertical partitioning of the habitat (Ausich and Bottjer, 1982; Bromley and Ekdale, 1986). It is in fact a synonym of ecological stratification (Seilacher, 1978), but this may be confused with the current use that geologists give to the term "stratification", and has not met with acceptance. Subaqueous substrates occupied by endobenthic communities are vertically zoned as a response to physical, chemical, and biological parameters (Bromley, 1990, 1996). Also, the water column displays vertical partitioning, and epifaunal and infaunal suspension-feeding animals obtain their food at several levels above the sediment surface (Ausich and Bottjer, 1982).

The tiering concept applied to the study of endobenthic communities has been incorporated in ichnology. The most important environmental factors that control tiering of endobenthic communities are consolidation of the substrate, organic matter, and oxygen (Bromley, 1990, 1996). Sediment compaction due to vertical accretion of the sea floor and progressive burial leads to dewatering and an increase in substrate consistency. As a result, shallow-tier organisms burrow in poorly compacted soft sediment, while deeper structures are emplaced in dehydrated and firm sediment (Bromley and Ekdale, 1986). The vertical distribution of organic matter displays a peak in abundance in the proximity of the sediment–water interface, resulting in the profusion of detritus and shallow-tier deposit feeders. Deeper within the sediment, organic matter decreases in abundance, resulting in a reduction of the biomass (Bromley, 1990, 1996). Oxygen content follows a similar trend, decreasing within the sediment; the redox discontinuity separates oxic from anoxic sediment.

Studies on modern ocean sediments allow reconstruction of the tiered structure of the infaunal community (Berger *et al.*, 1979; Ekdale *et al.*, 1984). The uppermost centimeters of the sediment are referred to as the mixed zone. In this zone, sediment is saturated in water and totally homogenized by bioturbation, but no discrete traces are recognized. Below this zone lies the transition zone, which is extremely heterogeneous due to the activity of deep burrowers, and displays tiered endobenthic communities (Savrda, 1992). The deepest sediment zone is the historical zone, which is located beyond the reach of even the deepest burrowers and, therefore, does not display active bioturbation. Because of continuous vertical accretion of sea-floor sediment, the mixed and transition zones of a given time are buried and become the historical zone. The typical record consists of an indistinctive burrow mottling formed in the mixed zone overprinted by well-defined discrete traces emplaced in the transition zone.

Unraveling the tiering structure of fossil examples can be a difficult task particularly in intensely bioturbated deposits in which trace fossils display complex cross-cutting relationships. The tiering structure and timing of emplacement in a given ichnofabric can be established by looking at cross-cutting relationships, burrow walls, and burrow fill, and by comparisons with modern examples (Bromley and Ekdale, 1986; Bromley, 1990, 1996; Taylor *et al.*, 2003). Under vertical accretion of the sea floor due to suspension fallout, deeper structures cross-cut shallow traces. If the rate of sedimentation is too low, the shallow-tier structures are totally obliterated by the activity of deep bioturbators. In addition, deep-tier trace fossils display well-defined morphologies and sharp boundaries as a result of their emplacement in stiffer substrates. Burrow-fills of these deep-tier structures tend to contrast with the host rock, reflecting active particle sorting by the organisms or material that is piped down from the surface (Bromley, 1990, 1996; Taylor and Goldring, 1993). Furthermore, deep-tier trace fossils are filled with chemically dynamic material (e.g. fecal sediment, surface material, metabolic products) within the reducing organic-poor host sediment, therefore promoting the formation of a digenetic microenvironment that helps to initiate mineralization, enhancing the visibility of the biogenic structures (Bromley, 1990, 1996). As a result, the preservation potential and visibility of deep-tier trace fossils is higher than those of shallower structures (Wetzel and Werner, 1981; Werner and Wetzel, 1982).

5.2 ICHNOFABRICS: CONCEPTS AND METHODS

An ichnofabric refers to any aspect of the texture and internal structure of a substrate resulting from bioturbation and bioerosion at any scale (Bromley and Ekdale, 1986). The related term bioturbate texture (Frey, 1973) shares many aspects in common with ichnofabric, but it does not include textures and structures resulting from bioerosion, and has not been extensively used. Application of the ichnofabric concept to paleoenvironmental reconstructions resulted in the so-called "ichnofabric approach". This approach represents a relatively new trend in ichnology that has been actively promoted since the organization of the first of a series of ichnofabric workshops in 1991. In more traditional ichnological studies, there is commonly a tendency to analyze only those structures that one can classify following current ichnotaxonomic procedures (i.e. discrete trace fossils). However, both discrete traces and poorly defined burrow mottling are taken into consideration in the ichnofabric approach (Bottjer and Droser, 1991). In addition, ichnofabric analyses are usually based on observations in cross-sections, where cross-cutting relationships and tiering structure can be evaluated. As with the ichnofacies model, the ichnofabric approach emphasizes the synecology of the endobenthic community, although an ichnofabric may represent the work of more than one community. However, tiering analysis is a key component of the ichnofabric approach, but has not been traditionally included within the ichnofacies paradigm.

5.2.1 QUANTIFYING BIOTURBATION AND ILLUSTRATING ICHNOFABRICS

Initially, a lot of effort was devoted to scaling degree of bioturbation. An early scheme was proposed by Moore and Scrutton (1957), but the proposal by Reineck (1963, 1967) is the one that has gained subsequent acceptance (e.g. Howard and Frey, 1975; Frey and Wheatcroft, 1989; Taylor and Goldring, 1993; Taylor *et al.*, 2003). In Reineck's scheme seven grades of bioturbation are distinguished, ranging from 0 for unbioturbated sediments to 6 for those that have undegone complete bioturbation. Subsequently, Droser and Bottjer (1986, 1989) put forward a semiquantitative field classification of ichnofabrics based on five ichnofabric indexes displayed by a series of flashcards designed for different environmental situations (e.g. high-energy clastics with *Ophiomorpha* or *Skolithos*, pelagic fine-grained sediments with mottlings). Although quite attractive in terms of providing a visual aid to evaluate bioturbation intensity, it needs to be used with caution because it does not address the composite nature of most ichnofabrics. More recently, Taylor and Goldring (1993) defined bioturbation indexes based on the categories established by Reineck. However, they noted that the original grades proposed by Reineck were based on a measurement of the percentage area bioturbated, although bioturbation should be measured as a unit volume per unit time, as stated by Frey and Wheatcroft (1989). Because such a procedure is extremely time consuming and difficult to follow, Taylor and Goldring (1993) favored a descriptive approach instead of a semiquantitative one. Accordingly, they maintained the original categories by Reineck, but based their definition in terms of burrow density, amount of burrow overlap, and the sharpness of the original fabric (Fig. 5.1). This scheme has been adopted in many ichnological studies because it is more precise and particularly appropriate for describing composite ichnofabrics (Ekdale and Bromley, 1991). In addition, as noted by Frey and Pemberton (1991), to characterize an unbioturbated layer with a bioturbation index of 0 (Taylor and Goldring, 1993) seems to be more logical than using an ichnofabric index of 1 (Droser and Bottjer, 1986, 1989). Another scheme by Miller and Smail (1997) is used to establish the density of biogenic structures along bedding planes, while that of Montague *et al.* (2010) has been proposed for microbioerosion.

Scaling of bioturbation is important because the establishment of well-defined grades conveys more information than simply stating that sediment is sparsely bioturbated or intensely bioturbated. However, other aspects, such as tiering or evaluation of successive bioturbation events, should not be overlooked.

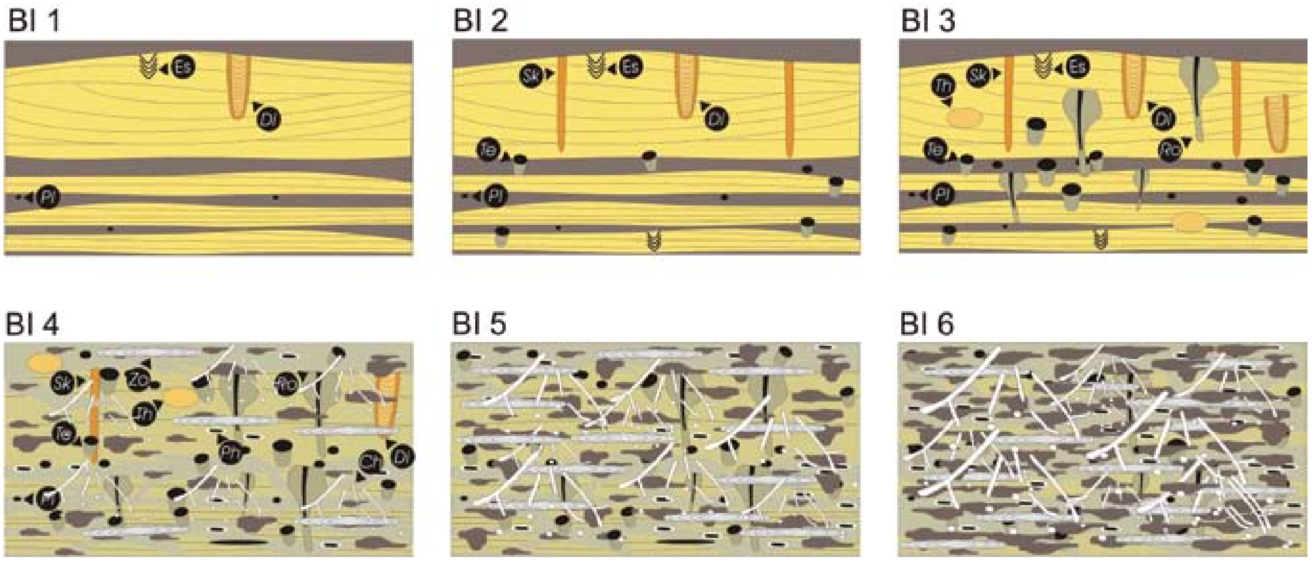


Figure 5.1 Graphic illustration of the different categories of bioturbation index of Taylor and Goldring (1993). BI = 0 is characterized by no bioturbation (0%). BI = 1 (1–4%) is for sparse bioturbation with few discrete traces. In the example illustrated, a few biogenic structures, such as *Planolites* (*Pl*), *Diplocraterion* (*Di*) and escape trace fossils (Es), exist in the storm and fair-weather deposits. BI = 2 (5–30%) is represented by low bioturbation in sediment that still has preserved sedimentary structures. This is illustrated by the presence of a number of burrows, including *Planolites* (*Pl*), *Diplocraterion* (*Di*), *Teichichnus*(*Te*), *Skolithos* (*Sk*), and escape trace fossils (Es), in both storm and fair-weather deposits. BI = 3 (31–60%) describes an ichnofabric with discrete trace fossils, moderate bioturbation and still distinguishable bedding boundaries. In addition to the ichnotaxa previously mentioned, *Thalassinoides* (*Th*) and *Rosselia* (*Ro*) are added in the example. BI = 4 (61–90%) is represented by intense bioturbation, high trace-fossil density, common overlap of trace fossils, and primary sedimentary structures are mostly erased. Some deep-tier trace fossils, such as *Zoophycos* (*Zo*) and *Chondrites* (*Ch*), are added in the example, together with undifferentiated burrow mottlings. BI = 5 (91–99%) is characterized by sediment with completely disturbed bedding and intense bioturbation. BI = 6 (100%) is for completely bioturbated and reworked sediment, related to repeated overprinting of trace fossils.

Visual graphics are useful to illustrate the main characteristics and origin of ichnofabrics. In particular, Taylor and Goldring (1993) proposed ichnofabric constituent diagrams as a way to illustrate the type and size of trace fossils, the percentage of bioturbated area, the depth and order of emplacement of each ichnotaxon, and the associated physical sedimentary structures in an ichnofabric. Although these diagrams summarized a large amount of data, they may be hard to visualize in some cases and their elaboration is rather time consuming. A more straightforward way of illustrating ichnofabrics was suggested by Bromley (1996), who combined ichnofabric icons, tiering diagrams, and estimation of degree of bioturbation for each tier (Fig. 5.2).

5.2.2 TAPHONOMY OF ICHNOFABRICS

One of the most important lessons learnt from the ichnofabric approach is the importance of taphonomy (Bromley, 1990, 1996). As in the case of body fossils, the fossilization barrier is a powerful taphonomic filter that separates the vast amount of biogenic structures produced in the sediment from the small proportion that become fossilized, passing to the trace-fossil record (Seilacher, 1967a). Trace fossils are subjected to their own taphonomic rules that result in a series of preservational biases. A careful evaluation of the taphonomic aspects involved helps to avoid the pitfalls associated with a naive reading of the trace-fossil record. The different biogenic structures produced in the sediment have variable preservation potential (Fig. 5.3a–c). Accordingly, the preserved ichnofabrics do not represent the exact copy of the original endobenthic community. As noted previously, although most of animal activity is concentrated in the uppermost centimeters of the substrate, the preservation potential of these shallow-tier structures is very low. In contrast, some deep-tier structures produced by mobile tracemakers represent the activity of key bioturbators that may obliterate any evidence of shallower tiers (Fig. 5.4a). Therefore, these deep-tier trace fossils are commonly the dominant component in an ichnofabric and have been referred to as elite trace fossils (Bromley, 1990, 1996). Also, elite trace fossils may be produced by preferential diagenesis. For example, *Thalassinoides* may be diagenetically enhanced due to the formation of minerals and associated concretionary growth (Bromley and Ekdale, 1984a) (Fig. 5.5). Unfortunately, shallow-tier traces are most sensitive to environmental fluctuations because they are formed close to the sediment–water interface, while deep-tier traces do not reflect sea-bottom conditions with such precision (Bromley and Ekdale, 1986). This problem lies at the core of the current controversies surrounding the paleoenvironmental implications of the *Zoophycos* ichnofacies (see Section 4.3.4). In fact, overlooking the taphonomic bias of some intensely bioturbated ichnofabrics may result in erroneous interpretations. Monospecific ichnofaunas are commonly linked to stress factors (e.g. dysaerobic or brackish-water conditions) typical of unstable environments. However, if monospecific ichnofaunas occur in intensely bioturbated ichnofabrics resulting from the activity of deep bioturbators, the low ichnodiversity may be a taphonomic artifact that reflects slow rates of sedimentation in a very stable environment.

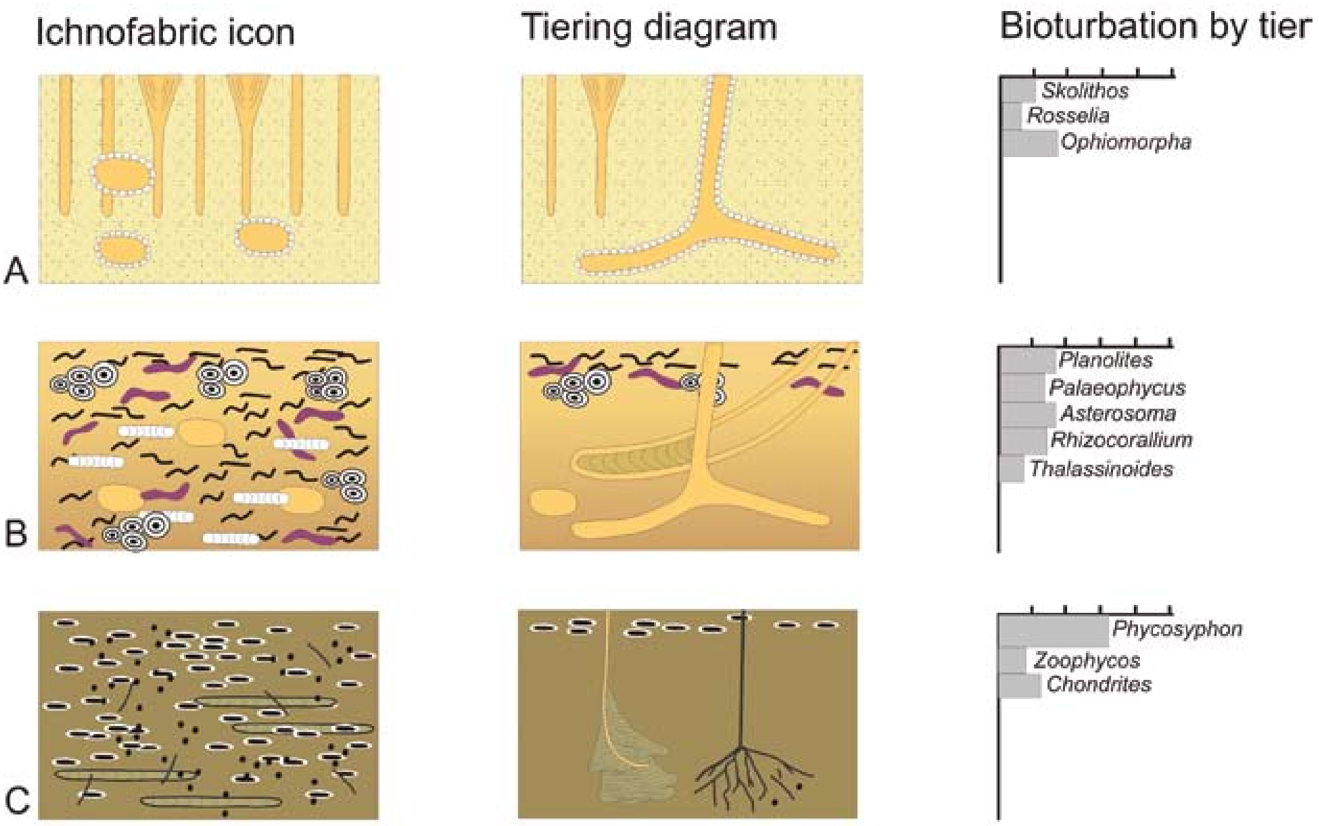


Figure 5.2 Visualization of ichnofabrics using ichnofabric icons, tiering diagrams and percentage of bioturbation per tier according to Bromley (1996). (a) Ichnofabric dominated by mid- to deep-tier vertical burrows in a high-energy middle-shoreface sandstone. (b) Ichnofabric characteristic of a low-energy offshore, displaying a complex tiering structure. (c) Ichnofabric of low-energy shelf deposits displaying low diversity of trace fossils and a combination of shallow and deep tiers.

In short, although degree of bioturbation and ichnodiversity are two different aspects (see Section 6.3), they should be considered in conjunction while performing an ichnological study.

Exceptionally shallow-tier structures may be preferentially preserved in the fossil record, commonly forming frozen-tiering profiles (Savrda and Bottjer, 1986). A typical example is related to episodic sedimentation that leads to cessation of bioturbation due to rapid burial (Orr, 1994) (Fig. 5.4b). Preservation of upper tiers is complete under no erosion and partial if some erosion is involved (Fig. 5.4c). The classic example is the preservation of shallow-tier graphoglyptids at the base of thin-bedded turbidites (e.g. Seilacher, 1962; Kern, 1980; Uchman, 1995). Similar situations may occur in distal tempestites of shallow-marine environments and ash fall deposits of volcanic terranes. When erosion occurs and the tiering structure of the endobenthic community is known, estimation of the minimum amount of erosion of the sea floor can be established based on the study of the washed-out tiers preserved as casts on the base of the event bed, thereby providing a measure of stratigraphic completeness (Wetzel and Aigner, 1986). A different way of generating frozen tiering profiles is due to a rapid deoxygenation event that leads to an immediate suppression of bioturbation and the preservation of all tiers, including those formed in the mixed zone (Savrda and Ozalas, 1993) (Fig. 5.4d). This situation is common in oxygen-depleted pelagic settings, typically shelf to deep-marine environments (see Section 6.1.3). Shallow-tier trace fossils can also be preserved in environments characterized by short breaks in sedimentation and, therefore, short duration of the colonization window (see Section 6.1.3). This is typical of slack-water deposition in intertidal settings, followed by minimal erosion during deposition of the subsequent flood or ebb event, as illustrated by tidal rhythmites in inner-estuarine settings (e.g. Buatois *et al.*, 1997b). Another excellent example of preservation of very shallow-tier structures occurs in Burgess Shale-type deposits. In this case, pristine preservation of subsuperficial structures results from the absence of deep-tier bioturbation (the *Zoophycos–Chondrites* ichnoguild) in dysoxic settings below storm wave base (Mángano, 2011) (see Sections 6.1.3 and 6.2).

5.3 TYPES OF ICHNOFABRICS

Two main types of ichnofabrics, simple and composite (Box 5.1), have been recognized by Bromley and Ekdale (1986). Simple ichnofabrics result from the activity of a single endobenthic community at a given moment and are, therefore, the product of a single bioturbation or bioerosion event (Fig. 5.6a). They are commonly characterized by single-tier colonization as a result of the activity of opportunistic forms (Taylor *et al.*, 2003). In this case, the associated colonization surface occurs at the top of the event bed. However, in other cases no colonization is involved and organisms may enter the event bed from

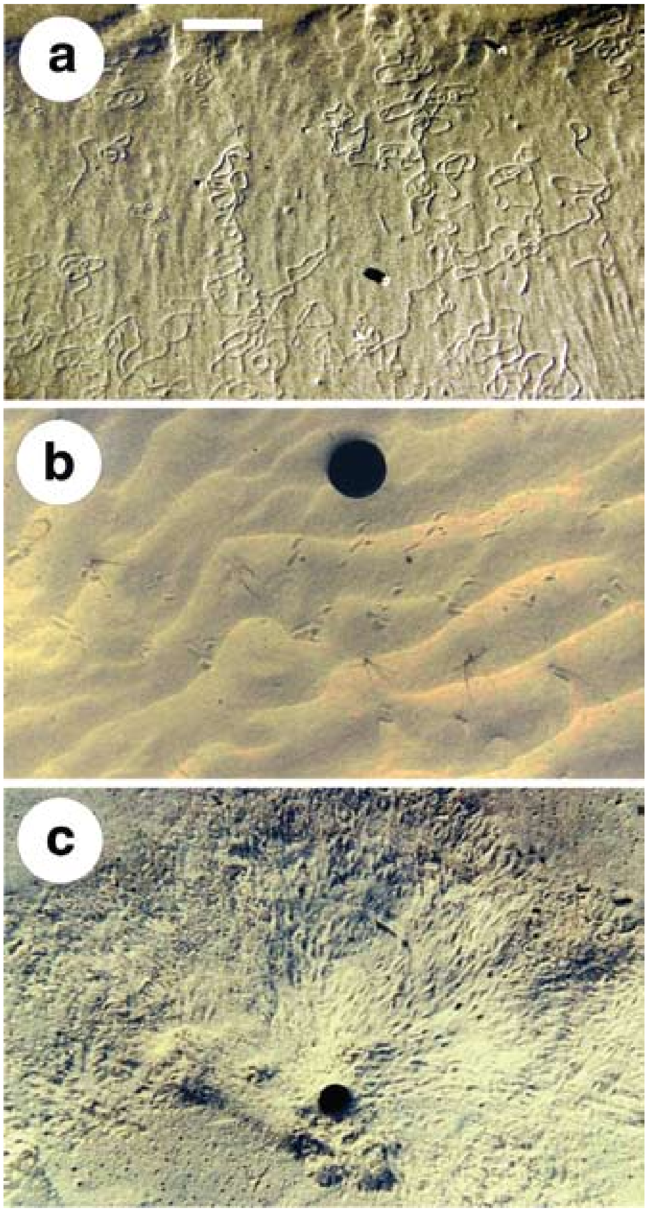


Figure 5.3 Variable preservation potential of intertidal biogenic structures. (a) Grazing trails produced on a tidal flat. Beach near Estancia Maria Luisa, Tierra del Fuego, Argentina. Scale bar is 2 cm. (b) Trackways produced by the crab *Uca* on a backshore. Aracaju, northeast Brazil. Lens cap is 5.5 cm. (c) Burrow entrance and scratch marks of the crab *Uca* in backshore sediments. Aracaju, northeast Brazil. Lens cap is 5.5 cm. The preservation potential of the trails, trackways, and scratch marks is essentially zero. The only structure with relatively high preservation potential is the *Uca* burrow (incipient *Psilonichnus*).

below by moving upwards, forming adjustment or escape trace fossils (Taylor *et al.*, 2003).

Composite ichnofabrics are much more common than simple ichnofabrics in the stratigraphic record, and are produced by the replacement of successive communities or by the upward migration of a tiered community. In the first case, community replacement results from a change in environmental conditions, such as a progressive increase in the degree of consolidation of a substrate, which is conducive to the cross-cutting of previously emplaced burrows by subsequent burrows and borings (e.g. Bromley, 1975; Mángano and Buatois, 1991; Lewis and Ekdale, 1992) (Fig. 5.6b). In the second case, vertical migration and trace-fossil cross-cutting reflect gradual accretion of the sea floor due to slow, steady sedimentation (Bromley and Ekdale, 1986; Orr, 1994) (Fig. 5.6c). An increase in substrate consistency results from compaction during vertical accretion of the substrate, leading to the emplacement of deeper burrows in a firmer substrate. However, no lithification is involved in the latter case and different tiers (deep-tiers cross-cutting shallower ones) are involved. Bedding planes displaying superposition of ichnocoenoses from successive communities are known as palimpsest surfaces.

A not always obvious case of composite ichnofabric is illustrated by a dense surface covered by *Lockeia siliquaria* in Carboniferous intertidal sandstones (Mángano *et al.*, 1998, 2002a). Detailed analysis of the surface reveals at least two colonization events, resulting in a palimpsest surface. The first bivalve population was eroded away, leaving only the basal resting structures. This was followed by sedimentation and a new colonization event. Cross-cutting relationships and burrow infill provide evidence for a composite ichnofabric in a monospecific trace-fossil assemblage. A similar situation may explain many occurrences of *Skolithos* and *Syringomorpha* ichnofabrics (e.g. Mángano and Buatois, 2004b; Desjardins *et al.*, 2010a) (Box 5.1). In the absence of clear colonization surfaces, the lack of lithological contrast in burrow infill from different populations makes it almost impossible to distinguish successive colonization events.

Although not always possible, establishing the colonization surface associated with each bioturbation or bioerosion event is of paramount importance in the analysis of composite ichnofabrics, because it allows the unraveling of the depositional history of the sedimentary unit and its associated environmental significance. In some cases, the environmental conditions operating at the time of deposition have little connection with those of the bioturbation or bioerosion event. The deeper a trace fossil is emplaced, the more cautious our approach should be in linking the colonization event with environmental conditions at the time of deposition. For example, coastal-eolian dune deposits may contain specimens of *Ophiomorpha*, penetrating from an overlying marine transgressive deposit. A careless examination of this situation may lead to the misinterpretation of *Ophiomorpha* as formed under terrestrial conditions. The problematic Lower Silurian fossil plant *Pinnatiramosus qianensis* has challenged our present knowledge on the origin and early evolution of vascular plants, which seem to have occurred by the Early Devonian. However, recent research suggests that the plant fossil is in fact a root system penetrating from overlying Permian deposits (Edwards *et al.*, 2007). Supposed Mesoproterozoic burrows have ended up as being identified as recent termite burrows emplaced within the Precambrian rocks (Cloud *et al.*, 1980).

5.4 THE ICHNOGUILD CONCEPT

Analysis of infaunal tiering structure suggests that organisms tend to group together within the same tier to exploit

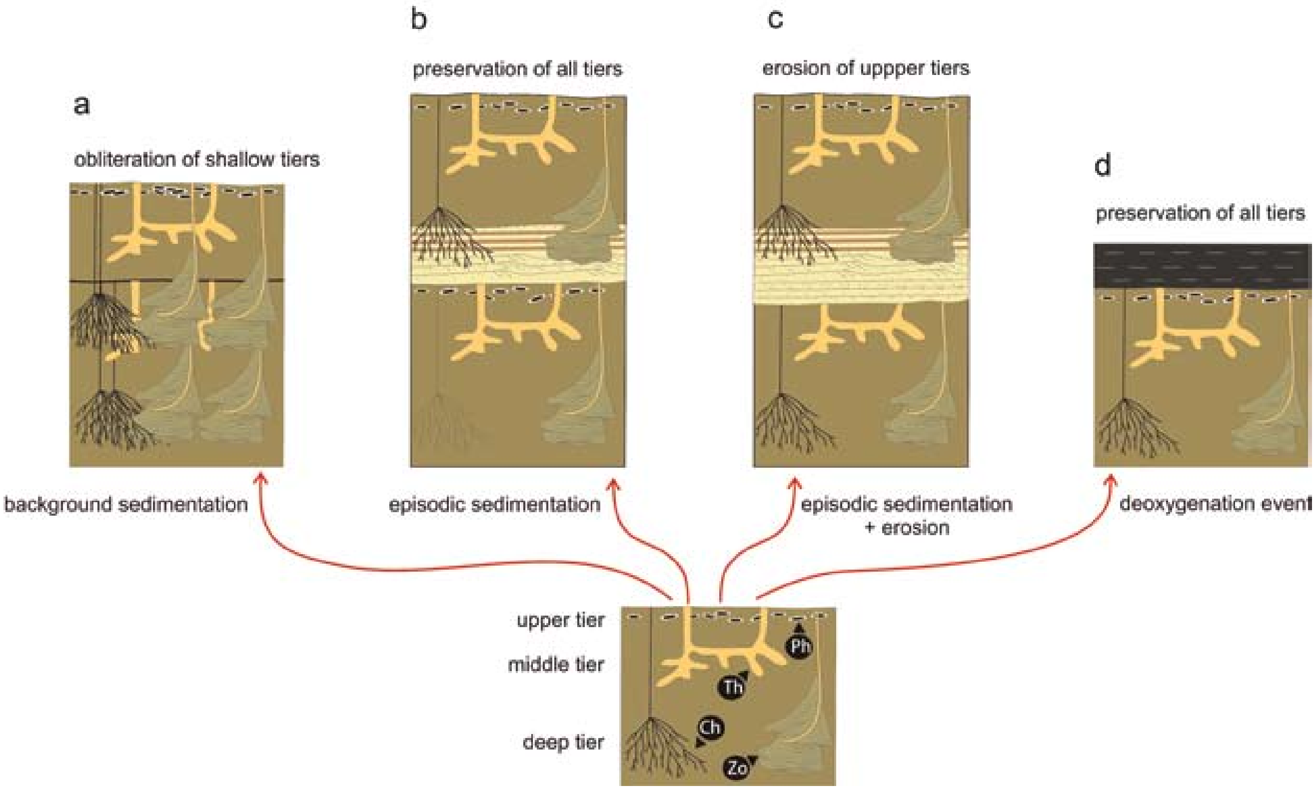


Figure 5.4 Formation of tiering profiles. (a) Tiering profiles formed during background sedimentation characterized by vertical accretion of the sea floor. Deep-tier structures migrate upwards to keep pace with sedimentation and obliterate shallow-tier structures. (b) Formation of frozen-tiering profiles associated with episodic sedimentation. In the absence of erosion, even the shallowest tiers are preserved. (c) With erosion, the upper tiers are removed. (d) Formation of frozen-tiering profiles associated with deoxygenation events that allow preservation of shallow tiers. *Phycosiphon* (*Ph*) represents the shallow tier, while *Thalassinoides* (*Th*) is a middle-tier form. *Chondrites* (*Ch*) and *Zoophycos* (*Zo*) make up the deep tier.

Figure 5.5 Nodular limestone containing *Thalassinoides* representing elite trace fossils. Upper Jurassic, Coralline Oolite Formation, Carr Naze, North Yorkshire Coast, England. Lens cap is 5.5 cm. see Fürsich (1972).

the same resources in similar ways. This fact led Bromley (1990, 1996) to propose the ichnoguild concept, following the utilization of the term guild in ornithology (Root, 1967) and invertebrate paleontology (Bambach, 1983). An ichnoguild reflects three parameters: (1) bauplan; (2) food source; and (3) use of space (Bromley, 1990, 1996) (Fig. 5.8). In terms of bauplan, biogenic structures are categorized as permanent to semi-permanent burrows produced by stationary organisms, or transitory structures made by vagile animals. Food source is reflected by trophic analysis of trace

Box 5.1 Simple and composite *Syringomorpha* ichnofabrics in Cambrian tidal flats and shorefaces

Lower to Middle Cambrian shallow-marine deposits of the Campanario Formation in northwest Argentina contain abundant *Syringomorpha* ichnofabrics. A high density of specimens occurs in intertidal areas, where they form a composite ichnofabric that records multiple colonization events (Fig. 5.7a). The composite nature of this ichnofabric is revealed by complex cross-cutting relationships of specimens. Pervasive bioturbation results from the activity of successive suites of deep-infaunal organisms. A high degree of bioturbation and preferential preservation of closely spaced, vertical components make this ichnofabric analogous to *Skolithos* pipe rock. Like *Skolithos* pipe rock, the *Syringomorpha* ichnofabric occurs in moderate- to high-energy settings, being particularly abundant in sand flats. Tide-dominated deposits are locally interbedded with storm-dominated facies. Bioturbation is sparse in these storm deposits. *Syringomorpha nilssoni* occurs in moderate to low densities in hummocky cross-stratified sandstone (Fig. 5.7b). This ichnofauna records opportunistic colonization after storms. Causative burrows extend from a colonization surface at the top of storm deposits, developing a wide spreite structure at the lower part of the tempestite. In contrast to tidal-flat examples, this ichnofabric is simple and represents a single bioturbation event following episodic sedimentation. The high density of vertical burrows in tidal-flat facies reveals that the "Agronomic Revolution" was not restricted to open-marine, shelfal environments (see Section 14.1.3). The depth and extent of bioturbation record colonization of a relatively deep-infaunal ecospace mostly by organisms feeding on epigranular microbes on sand grains and meiofauna.

Reference: Mángano and Buatois (2004b).

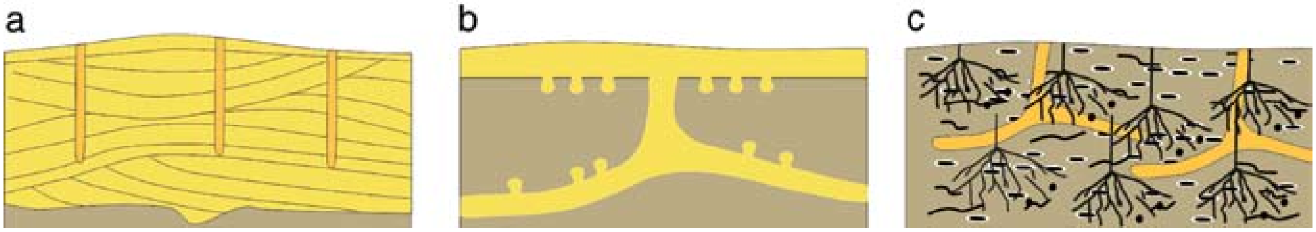


Figure 5.6 Types of ichnofabrics (a) Simple ichnofabric reflecting a single event of colonization after storm deposition. (b) Composite ichnofabric recording the replacement of a firmground trace-fossil suite by a hardground trace-fossil suite after substrate lithification. (c) Composite ichnofabric produced by the upward migration of a tiered community in response to vertical accretion of the sea floor.

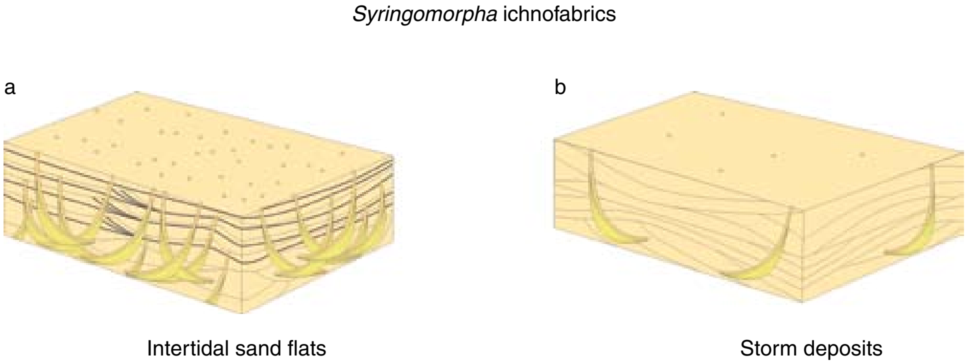


Figure 5.7 *Syringomorpha* ichnofabrics in Lower to Middle Cambrian shallow-marine deposits. (a) Composite ichnofabric recording multiple colonization events in tidal-flat deposits. (b) Simple ichnofabric recording single colonization events in lower-shoreface deposits.

fossils, including categories such as detritus feeding, deposit feeding, suspension feeding, gardening, and chemosymbiosis. Use of space is essentially equivalent to the vertical position within substrate recorded by the tiering structure. Ichnoguilds are named after their dominant ichnotaxa (Bromley, 1990, 1996). Bambachian guilds provide valuable information for understanding patterns of ecospace utilization through geological time (Bambach, 1983). Ichnoguild analysis may supply additional information to that recorded by body fossils. In the same way as guilds, ichnoguilds are useful tools to understand the adaptive strategies displayed by benthic organisms. As noted by Bromley (1990, 1996), ichnoguilds are well suited for characterizing the ecological complexity of ichnofaunas. Recognition and comparison of ichnoguilds from specific ecosystems through geological time become particularly useful in evolutionary paleoecology (e.g. Buatois *et al.*, 1998c).

The ichnoguild concept was originally applied to the study of chalk (Ekdale and Bromley, 1991; Bromley, 1996). Chalks are

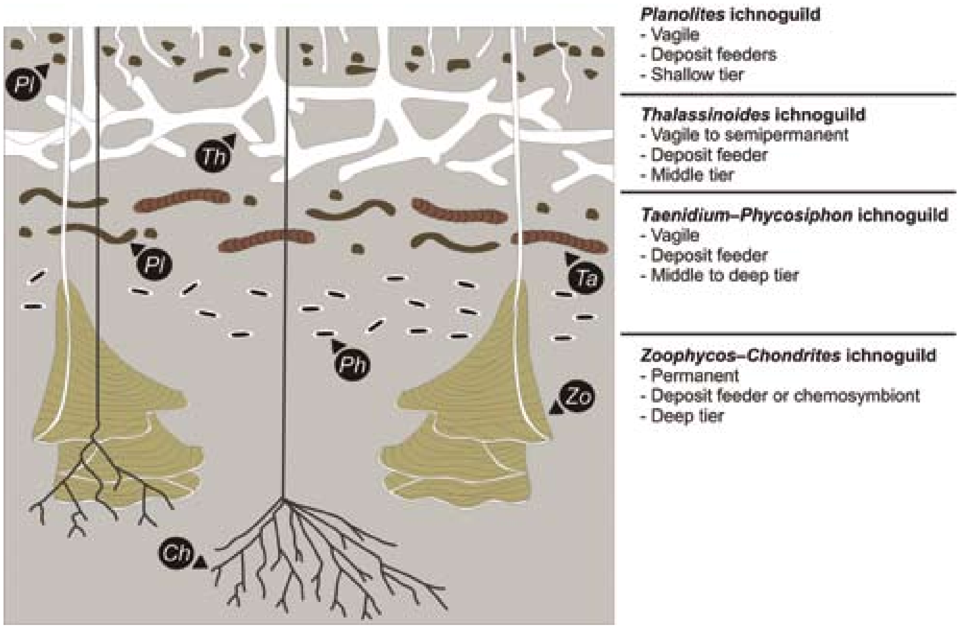


Figure 5.8 Ichnoguilds and tiering structure in Upper Cretaceous chalk of Denmark (modified from Ekdale and Bromley, 1991). Shallow tier is represented by *Planolites* (*Pl*), while *Thalassinoides* (*Th*) is a middle-tier form. The middle-to-deep tier is occupied by *Taenidium* (*Ta*) and *Phycosiphon* (*Ph*). The deep tier is represented by *Zoophycos* (*Zo*) and *Chondrites* (*Ch*).

Box 5.2 Composite ichnofabrics and ichnoguilds in Cretaceous chalk

Chalk ichnofabrics rank among the most complex of all. In particular, Cretaceous chalk ichnofabrics from Denmark have been thoroughly analyzed, and, in fact, represent the birthplace of the ichnofabric approach (Fig. 5.8). The rate of sedimentation in these pelagic environments was remarkably exceeded by the rate of bioturbation. The intensity of bioturbation in these shelf pelagic deposits is so high that virtually every grain of sediment has been processed by several animals. The resulting composite ichnofabrics represent the activity of multitiered endobenthic communities that moved upwards during continuous vertical accretion of the sea floor. The uppermost tier corresponds to indistinct burrow mottlings produced in the mixed layer by organisms that inhabited a soupground. The resulting structures are preserved as deformed and diffuse mottles that cannot be assigned to any particular ichnotaxa. Four ichnoguilds have been recognized. The *Planolites* ichnoguild typifies vagile, shallow-tier deposit-feeder structures. The *Thalassinoides* ichnoguild consists of semi-vagile and vagile, mid-tier deposit-feeder structures. The *Taenidium–Phycosiphon* ichnoguild is characterized by vagile, middle-to-deep-tier deposit-feeder structures. The *Zoophycos–Chondrites* ichnoguild is represented by non-vagile, deep-tier deposit-feeder or chemosymbiont structures. While the first three ichnoguilds were emplaced in softground, the deepest one records bioturbation in stiff, more compacted sediment. The zone of active bioturbation extended many centimeters below the sea floor.

Reference: Ekdale and Bromley (1991).

particularly appropriate for ichnoguild analysis because they are commonly intensely bioturbated and their tiering structure can be unraveled by careful analysis of cross-cutting relationships (Ekdale and Bromley, 1991) (Fig. 5.8; Box 5.2). Subsequently, ichnoguild analyses were expanded to include bioerosion structures (Bromley, 1994; Tapanila, 2008), tidal-flat ichnofaunas (Mángano *et al*., 2002a; Mángano and Buatois, 2004b; Baldwin *et al*., 2004), continental ichnofaunas (Buatois *et al*., 1998c), and earliest Cambrian ichnofaunas (Buatois and Mángano, 2003a, 2004b). In some settings, tiering and ichnoguild analysis is complicated due to different factors, such as temporal instability of community structure, time averaging of fossil faunas, and limited cross-cutting relationships (Mángano *et al*., 2002a). The ichnoguild concept is still an underutilized tool that has plenty of potential to illuminate paleoecological and evolutionary aspects of ichnofaunas (see Chapter 14).

5.5 PALEOSOL ICHNOFABRICS

Although the ichnofabric approach has become quite popular during the last two decades, still little is known about the characteristics and origin of continental ichnofabrics and review papers are almost exclusively based on marine examples (e.g. Taylor *et al*., 2003). More recently, a conceptual and methodological framework for the analysis of paleosol ichnofabrics has been advanced by Genise *et al*. (2004b). In subaqueously produced ichnofabrics, the sharpness of the primary sedimentary fabric is commonly a function of the degree of bioturbation. However, in terrestrial ichnofabrics, soil features may disrupt the primary fabric without the intervention of bioturbation, generating what is referred to as pedofabric (Genise *et al*., 2004b). Accordingly, these authors suggested that ichnofabric analysis in paleosols requires modifications to the standard methodology developed from marine examples. Genise *et al*. (2004b) proposed the construction of tiering diagrams, independent evaluation of the pedofabric and the ichnofabric, and construction of ternary diagrams showing percentages of bioturbation, pedofabric, and original bedding (Fig. 5.9). These authors illustrated their methodology with examples from Mesozoic and Cenozoic paleosols from Argentina, Uruguay, and Egypt.

5.6 THE ROLE OF BIOTURBATION, BIOEROSION, AND BIODEPOSITION

Organisms interact with and, therefore, affect the substrate in many different ways. Bioturbation involves all kinds of particle displacement and physicochemical sediment modifications resulting from the activity of organisms (Häntzschel and Frey, 1978). Bioturbation commonly leads to destruction of original sediment stratification and primary structures. However, the activity of organisms living in pore spaces may result in a localized displacement of sedimentary particles without actually destroying sedimentary structures, which results in so-called cryptobioturbation (Pemberton *et al*., 2008) (Fig. 5.10). In turn, bioturbation does not necessarily imply sediment homogenization. Rather, in many cases organisms may provide the substrate with a new structure, such as the concentration of fine-grained sediment within the concentric infill of burrows hosted in clean quartzose sandstone (e.g. *Rosselia* ichnofabric in sandstone bars). Another long-recognized example is the generation of biogenic graded bedding by upward advection by earthworms (Darwin, 1881). In marine settings, maldanid worms are also well known for their conveyor-belt activities, transporting subsurface particles to the surface (Mangum, 1964; Fauchald and Jumars, 1979) and from the surface to a feeding cavity at depth (Levin *et al*., 1997).

The bioturbation process has significant effects on sediment composition, stability, and texture (Ekdale *et al*., 1984). Chemical processes result in changes in composition, such as concentration of trace elements, fluctuations in redox potential, flow of chemicals, changes in organic content of sediments, concentration of metals on boring walls, and alteration of clay minerals as a result of ingestion (Pryor, 1975) (Box 5.3). For example, the structures of infaunal burrowers feeding on suspended particles result in an increase in oxygen circulation within the sediment with the redox-potential discontinuity being extended at depth. Sediment stability may increase or decrease as a result of bioturbation (see Section 6.7). Most mobile epifauna and infauna, involving both deposit- and detritus-feeders and some sedentary organisms, whose feeding and defecation activities provide a considerable number of suspended particles, cause substrate instability (Rhoads, 1974). In contrast, sedentary organisms building mucus-reinforced tubes cause reduction in resuspension and erosion, and behave as sediment-stabilizing elements. In turn, pellet development significantly alters sediment consistency, which may result in decreased substrate stability (Ekdale *et al*., 1984). Sediment texture may change in several ways as a result of bioturbation, particularly through the combination of sedimentary layers of varying grain size and mechanical sorting of sediment particles.

In addition, biodeposition, the production or concentration of sediment by the activities of an organism (Frey and Wheatcroft, 1989), also contributes to a change in sediment texture due to particle ingestion and excretion during the feeding process. For example, in carbonate sediments, pellet development and aggregation usually involves conversion of argillaceous and silty material into sand size. From the hydraulic viewpoint, these pellets behave like sand grains. Pryor (1975) noted that along the coast of Georgia and the Gulf of Mexico, *Callianassa major* annually generates pelletoidal material that is equivalent to a layer approximately 0.5 cm thick. Curran and Harris (1996) analyzed bioturbation by *Glypturus acanthochirus* in tidal-flat deposits of San Salvador Island, Bahamas, and estimated that this shrimp can move 118.6 kg sediment/m^2 to the surface every year (see also Section 6.2).

Bioerosion, every form of biological penetration and corrosion of hard substrates (Neumann, 1966; Bromley, 1992), also plays a major role in degrading lithified materials. For example, recent experiments in high-latitude settings demonstrated that foraminiferans are significant contributors during an early phase of bioerosion (Wisshak and Rüggeberg, 2006). During an advanced phase, sponges become dominant as agents of hard substrate degradation. Hardbottoms in the North Carolina continental margin are degraded by the activity of mechanical and chemical bioeroders (Riggs *et al*., 1998). The main bioeroders in this case are bivalves, shrimps, and macroalgal pluckers. As a result of bioerosion, the substrate is degraded, relief is developed on hardbottom surfaces, and significant volumes of new sediment are supplied to the continental shelf.

5.7 BIOTURBATION-ENHANCED PERMEABILITY AND RESERVOIR CHARACTERIZATION

The destruction of sediment porosity and permeability by bioturbation has been a dogma in reservoir characterization for many years. However, a number of recent studies demonstrated that this is not always the case. Buatois *et al*. (1999) documented porosity/permeability relations, and bioturbation types in Carboniferous clastic reservoirs of Kansas. These studies showed that reductions in permeabilities and porosities are common where sediment is affected by intense bioturbation by deposit feeders. In contrast, passively filled structures of suspension feeders may even result in a significant increase in porosity and permeability as the degree of interconnectivity between layers is increased. In some cases, hydrocarbons may even be held in such burrows (Fig. 5.11). Gingras *et al*. (1999a) documented dramatic differences between burrow-fill permeabilities and matrix

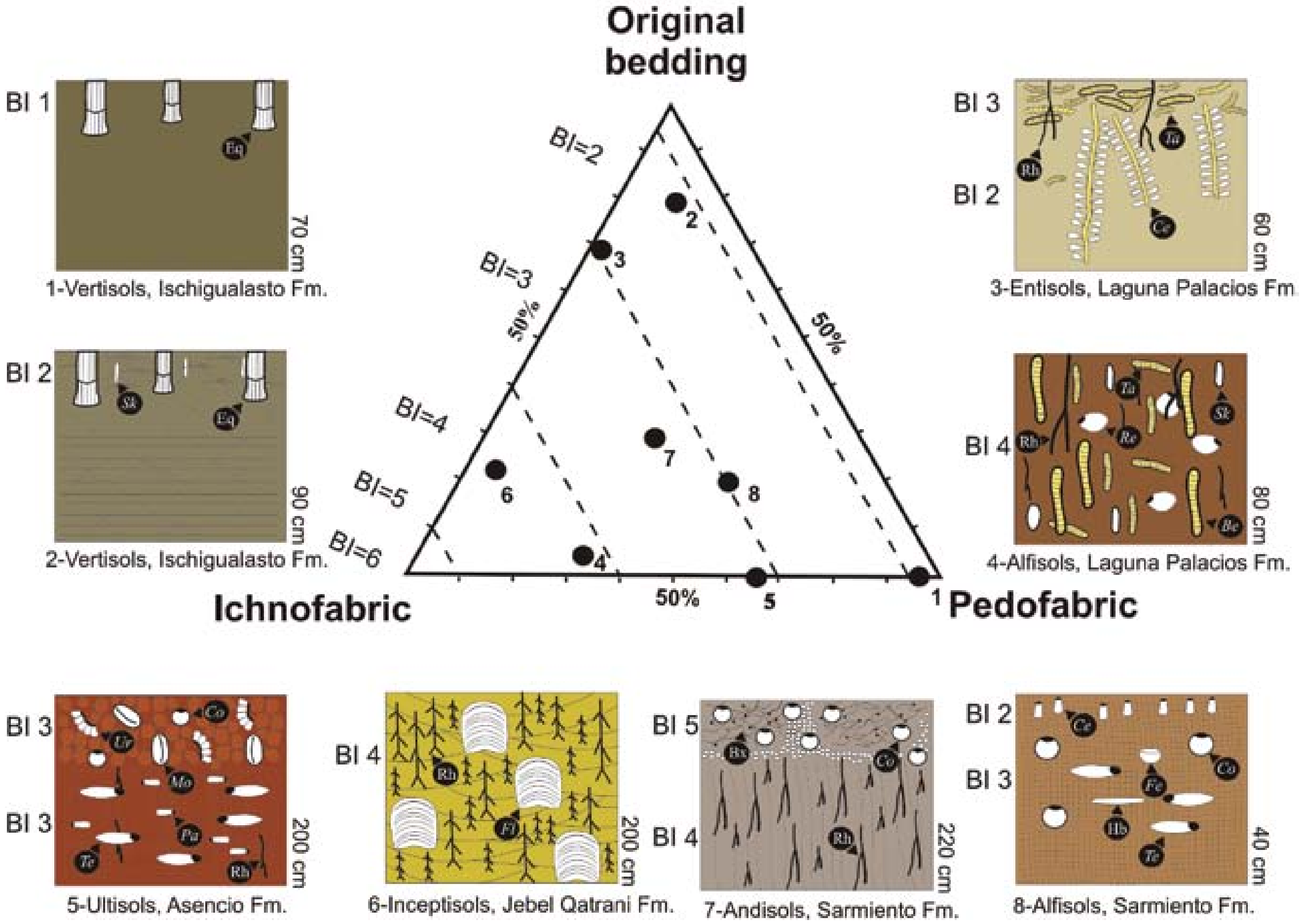


Figure 5.9 Ternary diagram for assessing paleosol ichnofabrics, pedofabric, original bedding, and grades of bioturbation (modified from Genise *et al.*, 2004b). Vertisols from the Triassic Ischigualasto Formation of western Argentina show different degrees of maturity. Example 1 is a well-developed vertisol with a uniform pedofabric characterized by small, angular blocky peds and closely spaced slickensides. No original bedding is preserved and stems of equisetales (Eq) in life position represent the only biotic evidence. Example 2 is a less-developed vertisol with primary fabric still preserved. Equisetales (Eq) stems and *Skolithos* (*Sk*) are present. Examples 3 and 4 from the Cretaceous Laguna Palacios Formation of Patagonia, Argentina, include an entisol and an alfisol. Example 3 is an entisol developed in tuff. The upper tier consists of *Taenidium barretti* (*Ta*), and the lower tier consists of the bee nest *Cellicalichnus chubutensis* (*Ce*). Rhizoliths (Rh) are present. Pedofabric is absent and the original bedding is relatively well preserved. Example 4 is a well-developed alfisol in tuffaceous sandstone. It is intensely bioturbated and the original bedding is only scarcely preserved in the upper horizon. The paleosol shows a well-developed upper elluvial horizon with platy peds, and a lower illuvial horizon with angular to subangular blocky peds. The ichnofauna consists of the probable coleopteran nest *Rebuffoichnus casamiquelai* (*Re*), *Taenidium barretti* (*Ta*), *Skolithos linearis* (*Sk*), and *Beaconites coronus* (*Be*). Thin rhizoliths (Rh) are present. Example 5 is an ultisol from the Paleogene Asencio Formation of Uruguay. Two interfingered horizons are present in this paleosol, one nodular and poorly consolidated, and the other one well indurated displaying columnar structures and total disturbance of the primary sedimentary fabric. Bioturbation is moderate in both horizons. The nodular horizon is dominated by the beetle nests *Coprinisphaera* (*Co*) and *Monesichnus* (*Mo*), and the bee cell *Uruguay* (*Ur*). The indurated horizon contains the bee ichnotaxon *Palmiraichnus* (*Pa*) and the probable coleopteran pupation chamber *Teisseirei* (*Te*). Rhizoliths (Rh) occur in this horizon. Example 6 is a poorly developed inceptisol from the Eocene–Oligocene Jebel Qatrani Formation of Egypt. This paleosol developed in a meandering channel point-bar sandstone, and relict trough cross-bedding is preserved. No horizons or soil structures are recognized. The ichnofauna is dominated by the termite nest *Fleaglellius pagodus* (*Fl*) and small rhizoliths (Rh). Examples 7 and 8 from the Eocene–Miocene Sarmiento Formation of Patagonia, Argentina, include an andisol and an alfisol. Example 7 is a weakly to moderately developed andisol present in a tuff. Two horizons have been recognized. The upper horizon is indurated and intensely bioturbated, and contains scattered specimens of the beetle nest *Coprinisphaera* (*Co*). The intense bioturbation is due to a boxwork of sinuous interconnected burrows (Bx) that resemble termite nests. The lower horizon shows columnar structures and sparse bioturbation. Very thin long root trace fossils (Rh) are present. Example 8 is a moderately developed alfisol associated with an erosive unconformity. Relict preservation of the primary fabric is noted. The pedofabric consists of subangular blocky peds with ferruginous crusts at the top. The ichnofabric consists of two tiers. The upper tier is represented by the bee nest *Celliforma* (*Ce*), while the lower tier includes *Coprinisphaera* (*Co*), *Teisseirei barattinia* (*Te*), *Feoichnus* (*Fe*) and large horizontal burrows (Hb). Bioturbation is low in the upper tier and moderate in the lower one.

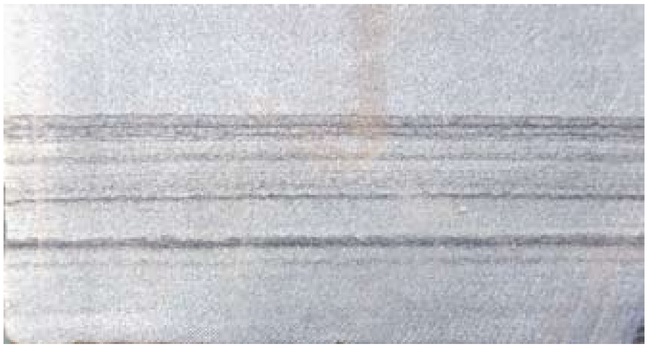


Figure 5.10 Cryptobioturbation in delta-front hummocky cross-stratified sandstone. Note the fuzzy lamination. Lower Miocene, Tácata Field, Eastern Venezuelan Basin. Core width is 9 cm. See Buatois *et al*. (2008).

permeabilities in a discontinuity surface at Willapa Bay. Substrates were colonized by crustaceans producing gallery systems representing the *Glossifungites* ichnofacies. Buatois and Mángano (2000) suggested that burrows passing through several layers, or multi-layer colonizers, generally cause an increase in permeability in the vertical direction to the bedding plane (Fig. 5.12). For example, crustacean galleries passing through sand turbidites provided pathways for fluid migration through mudstone intercalations, which would have normally acted as impermeable barriers (Schuppers, 1993). Similar situations occur in intertidal heterolithic facies where vertical *Skolithos* burrows pass through mud partings and connect sand layers (Buatois *et al*., 1999). Gerard and Bromley (2008) illustrated spectacular examples of the contribution of three-dimensional *Thalassinoides* burrows to reservoir heterogeneity and of *Ophiomorpha* systems to fluid circulation. Tomkin *et al*. (2010) documented an increase of porosity and permeability associated with *Thalassinoides* burrows, but a decrease linked to *Ophiomorpha* systems.

Certainly, the role of bioturbation in enhancing permeability extends beyond the field of petroleum geology. Muñoz (1994) demonstrated that extensive *Thalassinoides* systems caused leaking in a dam, and Martin *et al*. (1994) established correlations between bioturbation and porosity fluctuations in aquifers. More recently, Cunningham *et al*. (2009) evaluated the impact of post-depositional *Ophiomorpha* burrows in increasing macroporosity in karst aquifers. These authors noted that burrow systems provide an alternative pathway for concentrated groundwater flow that differs from the standard model for karst aquifers, which is based on the role of fractures and cavernous dissolution features.

This emerging view on the relationships between permeability and bioturbation has received a more systematic treatment (Pemberton and Gingras, 2005). In a seminal paper, these authors recognized five different situations: (1) surface-constrained textural heterogeneities; (2) non-constrained textural heterogeneities; (3) weakly defined textural heterogeneities; (4) diagenetic textural heterogeneities, and (5) cryptic bioturbation (Fig. 5.13).

Surface-constrained textural heterogeneities occur in connection with discontinuity surfaces delineated by the *Glossifungites* ichnofacies. These heterogeneities are represented by high-permeability burrows that penetrate a low-permeability firm substrate. Therefore, elements of the *Glossifungites* ichnofacies introduce discretely packaged coarse-grained sediment into the underlying matrix, enhancing vertical permeability and creating a dual porosity-permeability system. Although permeability enhancement is

Figure 5.11 *Ophiomorpha* saturated in oil. No hydrocarbons occur in the impermeable pelletoidal wall. Lower Miocene, Oficina Formation, Oritupano Field, Eastern Venezuela Basin. Core width is 7 cm.

Box 5.3 Burrowing, accelerated weathering, and mineral authigenesis

Experiments with the annelid *Arenicola marina* have illustrated the importance of bioturbation and biodeposition in changing the chemical properties of the substrate. Two experimental tanks containing mature sand and mud consisting of quartz, chlorite, and muscovite were prepared. *Arenicola marina* was introduced into one and the other one was kept separate as a control. The annelids introduced into the experimental tank constructed J-shaped burrows penetrating up to 20 cm below the sediment–water interface, and significantly mixing the sediment. After 20 weeks, the mud in the control tank remained unchanged. In contrast, sediment in the tank populated with *A. marina* underwent significant mineralogical changes. Chlorite was preferentially destroyed during digestion and neoformed minerals were detected in the cast samples. It has been suggested that the lowered pH microenvironment in the organisms' guts accelerated mineral dissolution and precipitation processes during digestion. This experiment demonstrated that burrowing significantly changes substrate properties. By causing the growth of authigenic clays, digestive processes of *A. marina* influence the porosity and permeability of potential reservoir facies. Attempts to predict rates of mineral weathering and authigenesis without taking biogenic processes into account are unlikely to be accurate.

Reference: McIlroy *et al.* (2003).

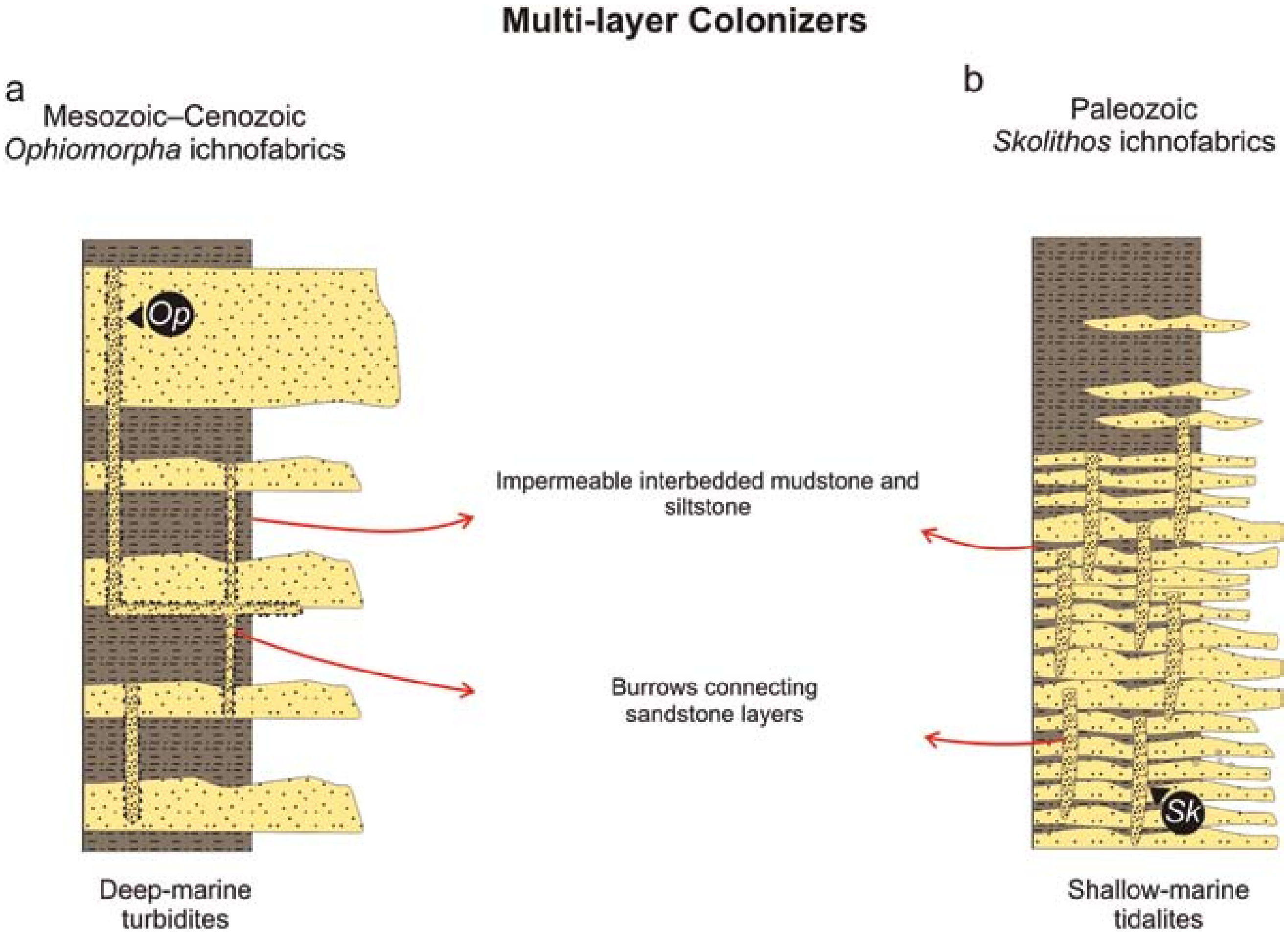


Figure 5.12 Multilayer colonizers and their role on vertical transmissivity of fluids. (a) *Ophiomorpha* (*Op*) ichnofabric in Mesozoic and Cenozoic thin-bedded turbidites. (b) *Skolithos* (*Sk*) ichnofabrics in lower Paleozoic intertidal heterolithic facies. Burrows passing through several layers may cause an increase in vertical permeability. Modified from Buatois and Mángano (2000).

limited in thickness, some of these surfaces (e.g. wave ravinement surfaces) have remarkable lateral extension. In some cases (e.g. Ghawar field of Saudi Arabia), firmground *Thalassinoides* burrows represent a biogenic plumbing system, conducive to stratiform super-permeability (Super-K).

Non-constrained textural heterogeneities are represented by discrete, sediment-filled burrows, encased by low-permeability sediment, which are not associated with a discontinuity surface. The host sediment commonly records low-energy background deposition, while the coarser-grained burrow-fill is delivered

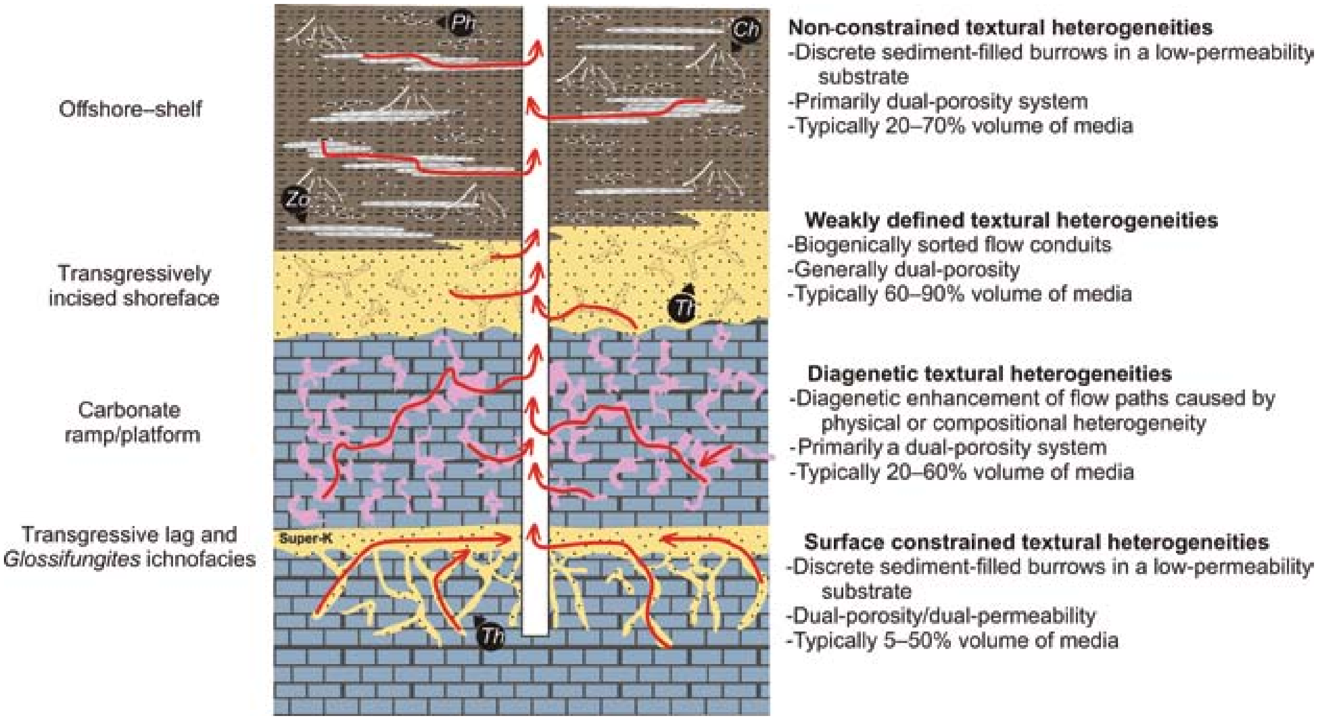


Figure 5.13 Relationships between permeability and bioturbation In the case of non-constrained textural heterogeneities, selective feeding in *Zoophycos* (*Zo*), *Chondrites* (*Ch*), and *Phycosiphon* (*Ph*) results in coarser-grained burrow fill in comparison with the host low-permeability silt-dominated sediment. Weakly-defined textural heterogeneities are illustrated by coarser sand-filled *Thalassinoides* (*Th*) penetrating into a finer-grained sandy matrix. Permeability contrast is subtler than in the previous case. Diagenetic textural heterogeneities are typically associated with diagenetic processes induced by bioturbation, resulting in the formation of tortuous pathways for fluid transmission in mottled carbonates. Surface-constrained textural heterogeneities are associated with discontinuity surfaces delineated by the *Glossifungites* ichnofacies, in which *Thalassinoides* (*Th*) burrow systems introduce discretely packaged coarse-grained sediment into the underlying low-permeability matrix, enhancing vertical permeability (Super-K). Modified from Pemberton and Gingras (2005).

during high-energy sedimentation events or results from selective feeding. Vertical burrows that penetrate into the substrate may interconnect permeable layers separated by low-permeability interbeds that may otherwise serve as barriers to fluid migration. A typical example is represented by vertical burrows of the *Skolithos* ichnofacies connecting thinly bedded sandstone and mudstone successions. In some cases (e.g. Terang–Sirasun field of Indonesia), a similar effect is attained by *Zoophycos* filled with empty globigerinid tests that penetrates into pelagic carbonates, increasing vertical permeability and breaching possible barriers. Another example is illustrated by *Macaronichnus*. In this case, the host sediment records high-energy conditions and the tracemaker causes significant mineralogical heterogeneity, leading to significant changes in permeability (Gingras *et al.*, 2002). Selective feeding in *Nereites missouriensis* and *Phycosiphon incertum* may play a key role in promoting gas transmissivity in low permeability gas-prone reservoirs (Fig. 5.14).

Weakly defined textural heterogeneities consist of discrete burrows infilled with sediment that slightly differs from the encompassing sediment. This situation is commonly illustrated by coarser sand-filled *Thalassinoides* penetrating into a finer-grained sandy matrix. Flow paths are tortuous as a result of the chaotic distribution of burrow conduits. Although the contrast between the burrows and the matrix is subtler than in previous scenarios, permeability contrasts may still influence production from these burrowed units.

Diagenetic textural heterogeneities typically result from dolomitization in bioturbated limestone. Burrowing in carbonates creates significant physical and compositional heterogeneities. The former includes changes and redistribution of grain size, sorting, and compaction. Compositional heterogeneities are caused by the concentration of organic material in the form of mucous or fecal material. Burrowing creates a microenvironment that is conducive to bacterial colonization. Diagenetic processes induced by bioturbation result in changes in porosity and permeability. Typical examples are represented by burrow systems, such as *Thalassinoides*, which create tortuous pathways for fluid transmission in mottled carbonates.

Cryptic bioturbation is a very subtle type of permeability enhancement characterized by non-discrete biogenic structures that completely alter the sediment, mostly resulting from the activity of meiofauna or small infauna. The high intensity of cryptic bioturbation may create zones of high permeability in sediment that in other aspects (e.g. grain size) shows little heterogeneity. Cryptobioturbation is common in shallow- to marginal-marine clastic deposits where it may affect considerable volumes of sediment.

The study by Pemberton and Gingras (2005) demonstrated that bioturbation has been commonly overlooked as a process that enhanced permeability in clastic and carbonate reservoirs. Of most importance, petrophysical studies are not usually focused at the trace-fossil scale. While the applications of ichnology in facies analysis and sequence stratigraphy are currently

Figure 5.14 High-density of *Nereites missouriensis* in offshore-transition deposits illustrating an example of non-constrained textural heterogeneities. Presence of this ichnofabric promotes gas and light oil transmissivity in low permeability reservoirs in many fields in North America. Upper Devonian–Lower Mississippian, Bakken Formation, Saskatchewan, Canada. Core width is 9.5 cm. See Angulo and Buatois (2009).

taken into consideration in the petroleum industry, the role of bioturbation as a modifying agent of porosity and permeability has been essentially neglected.

5.8 CRITICAL EVALUATION: ICHNOFABRICS VERSUS ICHNOFACIES OR ICHNOFABRICS AND ICHNOFACIES?

We believe that ideas derived from the ichnofabric approach should be used within the broader framework of the ichnofacies model. Both research strategies may be employed in conjunction, resulting in a more comprehensive and consistent view of the trace-fossil record. A well-balanced eclecticism may be a healthy approach to the ichnological record. As noted by McIlroy (2008), the confrontation between the ichnofabric approach and the ichnofacies model is misleading. The notion that ichnofabric analysis should replace ichnofacies put forward by Goldring (1993, 1995) is not supported by present developments in the field.

The ichnofabric approach is ideally suited to the study of cores (e.g. Bockelie, 1991; Martin and Pollard, 1996; McIlroy, 2004b; Gerard and Bromley, 2008). However, ichnofacies have proved to be extremely successful in paleoenvironmental and sequence-stratigraphic studies in cores (e.g. Pemberton *et al.*, 2001). In addition, both approaches have been routinely employed in outcrops. The ichnofabric approach is particularly useful in fully bioturbated deposits, as illustrated by chalk facies (e.g. Ekdale and Bromley, 1991), and some fine-grained shallow-marine units, such as the Jurassic Fulmar Formation of the North Sea (Martin and Pollard, 1996; Gowland, 1996; Gerard and Bromley, 2008) or the Miocene Chenque Formation of Patagonia (Buatois *et al.*, 2003; Carmona *et al.*, 2008). In contrast, many depositional settings are characterized by limited development of ichnofabrics. For example, delayed evolutionary innovations of the terrestrial and freshwater biotas constrained the development of continental ichnofabrics (Buatois and Mángano, 1998, 2007). Paleozoic fluvio-lacustrine and fluvio-estuarine ichnofaunas are dominated by bedding-plane, very shallow trace fossils, mostly grazing trails and arthropod trackways that produce little or no bedding disruption. Consequently, trail- and trackway-bearing deposits are commonly seen in cross-section as unbioturbated, fine-grained, thinly laminated rocks, precluding traditional ichnofabric analysis (Buatois *et al.*, 1998d). Ediacaran to earliest Cambrian deposits also contain bedding-plane trace fossils with almost no disturbance of primary fabric (see Sections 14.1.2 and 14.1.3). To a lesser degree, the same is shown by thinly bedded turbidites, which contain highly diverse graphoglyptid ichnocoenoses (e.g. Książkiewicz, 1977; Leszczyński and Seilacher, 1991; Uchman, 1995, 1998).

It has been emphasized that the ichnofabric approach provides a finer paleoenvironmental resolution because there are more ichnofabrics than ichnofacies. Although this is theoretically true, in practice the strategy to be undertaken is largely dependent on the scale of analysis. In addition, it is unclear if a large number of ichnofabrics recognized in a studied interval results in a more precise paleoenvironmental characterization. For example, Goldring *et al.* (1991) recognized seven different *Phycosiphon* ichnofabrics, but they mostly occur between the offshore transition and the upper offshore. This fact may point to the existence of several ichnocoenosis and the commonly overlooked issue of spatial heterogeneity (e.g. Mángano *et al.*, 2002a; McIlroy, 2007a). Moreover, ichnofacies practitioners do not restrict themselves to mere ichnofacies recognition; in fact, ichnofacies are subdivided in case-by-case studies allowing detailed subdivision of different environments (e.g. MacEachern *et al.*, 1999a).

The strength of the ichnofacies model relies on its archetypal nature (see Sections 4.1 and 4.6). The strength of the ichnofabric approach resides in the evaluation of the taphonomic controls that filter the biogenic signal through the fossilization barrier. Accordingly, taphonomy may illuminate the nature of some ichnofacies (taphofacies of Bromley and Asgaard, 1991). Analysis of tiering structure and ichnoguild characterization are strong conceptual and methodological tools derived from the ichnofabric approach. These tools are particularly useful to evaluate composite ichnofabrics that result from successive bioturbation events. Also, ichnoguilds provide a conceptual approach to the study of ecospace utilization through geological time, yielding valuable insights into evolutionary paleoecology (see Chapter 14).

Part II Spatial trends

6 Trace fossils and paleoecology

> Decían que había como mil pichis escondidos en la tierra, ¡enterrados! Que tenían de todo: comida, todo. Muchos decían tener ganas de hacerse pichis cada vez que se venían los Harrier soltando cohetes.
>
> Rodolfo Foghill
> *Los Pichiciegos* (1994)

Organisms burrow in response to many biotic and environmental factors. Ichnological studies provide detailed information on environmental parameters involved during sediment deposition and, therefore, serve as a basis for sedimentary environment and facies analysis. To that end, ichnological analysis should focus on the paleoecological aspects of trace-fossil associations (e.g. ethology, feeding strategies, ichnodiversity) and should avoid the simple use of a checklist approach because this may lead to paleoenvironmental misinterpretations. The paleoecological approach needs to be integrated with facies analysis, and should never aim to replace it. Many factors define the niche and survival range of animal species. However, the key to the analysis is the identification of major control factors, which are called limiting factors (Brenchley and Harper, 1998). In this chapter, we revise the response of benthic organisms to different environmental parameters, evaluate the role of taphonomy, and address a set of concepts that should be employed in paleoecological analysis of trace fossils, such as ichnodiversity and ichnodisparity, population strategies, and the notion of resident and colonization ichnofaunas. Then, based on the concept of ecosystem engineering, we discuss how organisms affect the environment. Finally, we address what biogenic structures can tell us about organism–organism interactions and spatial heterogeneity.

6.1 RESPONSE TO ENVIRONMENTAL PARAMETERS

As organism behavior is highly sensitive to certain parameter fluctuations (e.g. salinity, oxygen), biogenic structures may provide information that cannot be derived from conventional facies analysis strictly based on physical evidence (e.g. Gerard and Bromley, 2008). Ideally, sedimentological and ichnological data should be integrated with paleoecological information derived from the associated body fossils (e.g. Scasso *et al*., 1991; Mángano and Buatois, 1996). In any case, integrated paleoenvironmental studies have shown that the level of resolution obtained using trace fossils commonly supersedes those based on palynofossils and foraminifers (MacEachern *et al*., 1999b; Aquino *et al*., 2001). Also, it has been suggested that sedimentary and ichnological features should be carefully analyzed in order to provide constraints to guide geochemical sampling and interpretation (Schieber, 2003).

Although in this chapter environmental factors are considered separately, it is important to understand that the limits of tolerance of benthic organisms are defined in terms of multi-variable responses, rather than in terms of isolated factors (Newell, 1979). For example, in tidal-flat environments, salinity, temperature, and exposure to subaerial conditions are intimately linked, and are strongly dependent on latitudinal position and climate (Mángano *et al*., 2002a). On the other hand, hydrodynamic energy and substrate conditions are also interconnected and dependent on coastal topography and physiography. The resultant ichnofauna is therefore shaped by the interplay of key environmental parameters overprinted by taphonomic factors (see Section 6.2).

6.1.1 HYDRODYNAMIC ENERGY

Hydrodynamic energy is one of the most common limiting factors in trace-fossil distribution, influencing both the behaviors of the tracemakers, as well as the preservation potential of their respective biogenic structures. Trace-fossil associations from low- and high-energy settings are remarkably different (Fig. 6.1). Ichnofaunas developed under low-energy conditions are dominated by horizontal traces of deposit and detritus feeders, as well as active predators. In deep-marine environments, other more sophisticated feeding strategies, such as farming and capture of microorganisms, are commonly involved (Seilacher, 1977a). Overall, marine low-energy trace-fossil associations display high ichnodiversity and are typically included in the *Cruziana* and *Nereites* ichnofacies. In the freshwater realm, associations are less varied, and represented by the *Scoyenia* and *Mermia* ichnofacies.

High-energy ichnofaunas are typically characterized by the dominance of vertical dwelling structures of infaunal suspension feeders and/or passive predators, forming low-diversity suites that are commonly included in the *Skolithos* ichnofacies. Burrow systems, such as *Thalassinoides* and *Ophiomorpha*, tend to show a higher proportion of vertical components under conditions of increasing energy (Howard and Frey, 1984; Anderson and Droser, 1998). The high energy of tides, waves, and currents strongly

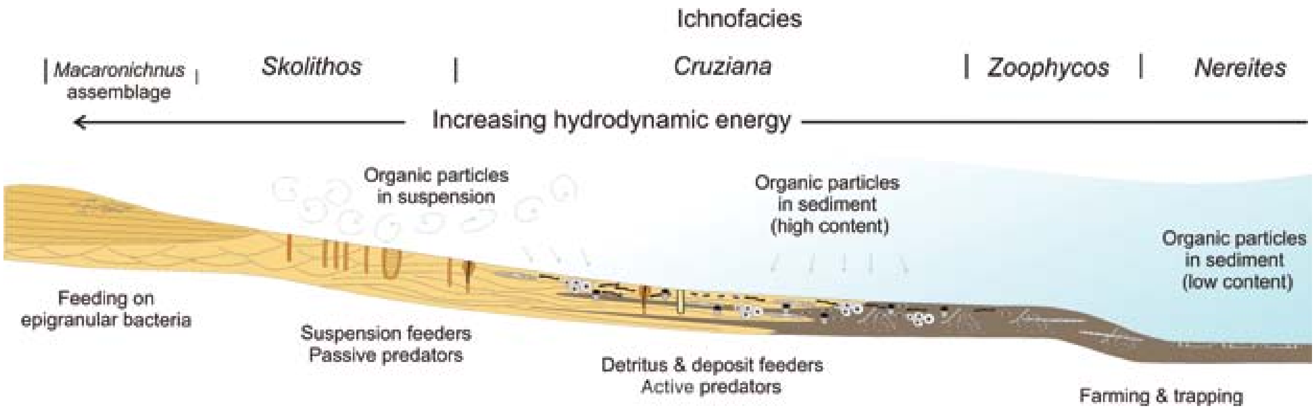


Figure 6.1 Relationship between trace-fossil associations, hydrodynamic energy, and food supply. Episodic sedimentation (i.e. storms and turbidity currents) generates environmental disturbances and may introduce organic particles in suspension favoring seaward displacement of suspension-feeding infauna. A wave-dominated regime is assumed.

Box 6.1 Response of the polychaete *Euzonus* to beach morphodynamics

Some sandy beaches of central Japan are characterized by wave dominance and high energy. The opheliid polychaete *Euzonus* is abundant at mid intertidal levels of the foreshore, producing incipient *Macaronichnus*. A detailed study was conducted during almost every spring tide from June to December in 2006. Distribution of *Euzonus* and orientation of its traces were plotted along a transect line. During fair-weather conditions, beach sediments accumulate landward, with the beach face developing as a steep slope. During storm conditions, the beach face is eroded by large waves, generating a gentle slope. *Euzonus* moves horizontally seaward and landward within the substrate in response to the shifting beach face as a result of changes in wave conditions. Under fair-weather conditions this polychaete burrows horizontally without any preferential direction. In contrast, under heavy erosion due to storm waves, *Euzonus* moves landward. The infaunal mode of life prevents *Euzonus* from excessive burial and washing out due to beach morphodynamics.

References: Seike (2008, 2009).

controls patterns of trace-fossil distribution along tidal shorelines. High-energy zones of tidal flats are typically dominated by vertical burrows, such as *Diplocraterion* or *Skolithos* (e.g. Cornish, 1986; Simpson, 1991). Deposits formed in these settings commonly contain deep gutter casts, flute marks, truncated vertical shafts, palimpsest surfaces, and transported burrows, which result from events of high energy that sculpt the tidal-flat surface and move a considerable amount of sediment (Mángano *et al.*, 2002a).

Overall features of high-energy ichnofaunas are strongly influenced by taphonomic controls. Modern coastal high-energy environments may contain a moderate number of horizontal trails and burrows. However, their preservation potential in these settings is very low. For example, any enthusiastic diver knows that modern high-energy subtidal environments of tropical-carbonate systems, such as those in the Bahamas, are plagued with horizontal biogenic structures of starfish, large heavy gastropods, and crawling crabs, but their Pleistocene counterparts are commonly dominated by vertical *Ophiomorpha* burrows (Curran, 1994).

Interestingly, under very high-energy conditions, some ichnofaunas display characteristics that are in sharp contrast to those of the *Skolithos* ichnofacies. These ichnofaunas are dominated by horizontal trace fossils produced by mobile deposit feeder polychaetes assigned to the ichnogenus *Macaronichnus* (Pemberton *et al.*, 2001; Seike, 2008, 2009; Quiroz *et al.*, 2010) (Box 6.1). These organisms feed on epigranular bacteria around sand grains and inhabit well below the sediment–water interface as a result of strong infiltration that produces well-oxygenated and nutrient-rich environments within the sediment. In contrast to shallow- to mid-tier horizontal traces, the deep emplacement of *Macaronichnus* provides high preservation potential under high-energy conditions (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001).

In shallow-marine environments, local fluctuations in hydrodynamic energy are recorded by the alternation of the *Cruziana* and *Skolithos* ichnofacies. In storm-dominated settings, the former represents fair-weather conditions, while the latter is storm related (Pemberton and Frey, 1984a; Pemberton *et al.*, 1992c; Pemberton and MacEachern, 1997). In tide-influenced environments, the *Cruziana* ichnofacies may be associated with slack-water periods, while the *Skolithos* ichnofacies is more typical of higher-energetic traction sedimentation (Mángano and Buatois, 2004a, b). An analogous situation occurs in deep-marine environments where the *Nereites* and *Skolithos* ichnofacies alternate due to repeated times of pelagic and turbidite sedimentation, respectively (Crimes, 1977).

6.1.2 SUBSTRATE

Whereas the anatomy of body fossils is controlled by inherited genetic factors, the morphology of trace fossils is strongly influenced by extrinsic factors in addition to the constraints imposed by animal anatomy (Goldring *et al*., 1997). Substrate type and consistency are important external factors in determining both burrowing technique and infaunal community composition (Bromley, 1990, 1996). Substrate consistency embraces the intricate interplay of multiple factors (e.g. grain size, sorting, water content, organic matter content, mucus binding) that define the mechanical properties of the sediment (Bromley, 1990, 1996). In turn, sediment composition directly influences substrate consistency. The degree of substrate consolidation may change laterally, vertically, or temporally. Lateral changes occur along a sediment surface at different scales as a response to environmental heterogeneity (e.g. intertidal areas having both emergent zones and submerged pools). Vertical changes result from a decrease in sediment water content and increase in compaction within the sediment, thereby influencing infaunal tiering. Temporal changes result from a progressive increase of substrate consolidation either as a result of desiccation (e.g. overbank sediment) or early diagenesis (e.g. carbonate substrates).

Carbonate substrates may be subjected to progressive dewatering, and a series of stages based on degree of consolidation have been defined. These include soupground, softground, firmground, and hardground, which are associated with increasing compaction and cementation (Ekdale *et al*., 1984; Ekdale, 1985; Lewis and Ekdale, 1992). These categories also apply for siliciclastic substrates, although hardgrounds are exceedingly rare in siliciclastic rocks. To this list we should add xylic substrates or woodgrounds (Bromley *et al*., 1984). Substrate-controlled ichnofacies are defined based on these substrate categories (see Section 4.3). In the case of modern sediments, a series of field methods have been developed to determine substrate firmness (e.g. Gingras and Pemberton, 2000; Rodríguez-Tovar and Delgado, 2006).

Soupgrounds are saturated in water and incompetent. Organisms may move in these substrates; in many cases they swim through them using undulatory movements (Bromley, 1990, 1996). However, the preservation potential of these structures is nearly zero (Ekdale, 1985). Softgrounds represent unconsolidated sediment, and are inhabited by a large number of burrowers, becoming the most appropriate substrate for production and preservation of biogenic structures. Most of the established ichnotaxa typically belong to softgrounds. Goldring (1995) introduced the term "looseground" for soft sand and gravel as distinct from soft mud and silt (softground). Loosegrounds commonly contain robust burrows with reinforced walls (e.g. *Ophiomorpha*). Wetzel and Uchman (1998b) introduced the concept of stiffground, which has been further expanded by Lettley *et al*. (2007a) to include stiff, but not fully compacted mud, commonly developed along inclined surfaces in heterolithic sediment. Stiffgrounds contain medium- to small-sized unlined burrows that may suffer significant compaction after emplacement. Firmgrounds are compacted and dewatered sediment that have not yet undergone cementation. They typically contain abundant burrows and pseudoborings, although ichnodiversity is rather low. Burrows are typically unlined, display bioglyphs, and do not suffer significant compaction (Bromley, 1975). Hardgrounds are cemented substrates, which may contain bioerosion structures (see Section 1.1). In contrast to the rigidity of hardgrounds, woodgrounds are flexible, formed by organic matter, and experience rapid biodegradation (Bromley *et al*., 1984). Bivalves and insects are typical tracemakers in xylic substrates. In recent years, increased attention has been paid to sediment surfaces stabilized my microbial action, referred to as matgrounds (Seilacher, 1999; Baucon, 2008; Buatois and Mángano, 2003a, 2010). Some grazing trails and feeding traces (e.g. *Oldhamia*) may reflect strategies to exploit microbial mats (see Section 14.1.2).

Most studies concerning substrate-controlled trace fossils have focused on the evolution of carbonate substrates and how this affects community composition (e.g. Bromley, 1975; Goldring and Kaźmierczak, 1974; Mángano and Buatois, 1991; Bromley and Allouc, 1992; Lewis and Ekdale, 1992; Taylor and Wilson, 2003), or on the erosional exhumation of firm siliciclastic sediments and its implications in sequence stratigraphy (e.g. MacEachern *et al*., 1992; Pemberton *et al*., 2004). However, recent work emphasizes that the process of dewatering, and the concomitant changes in substrate properties, is a continuum rather than a series of compartmentalized stages, allowing the establishment of a scale of morphological variation of ichnofossils depicting substrate evolution (e.g. Buatois *et al*., 1997a; Lobza and Schieber, 1999; Mángano *et al*., 2002a; Schieber, 2003; Uchman and Pervesler, 2006; Davis *et al*., 2007; Carmona *et al*., 2010). Therefore, trace fossils serve as useful tools for evaluating substrate properties. In defining a range of substrate conditions, the presence of impregnated walls, sharpness of delicate morphological details, and degree of deformation are important observations (Goldring, 1991). In addition, changes in burrowing mechanisms, from swimming through sediment (soupground) and sediment feeding with active backfilling (softground) to sediment feeding with passive filling (firmground) occur as a response to increasing substrate consistency (Schieber, 2003) (Fig. 6.2). Although in theory it should be possible to identify ichnotaxa irrespective of substrate effects, occasionally deformation is so severe that accurate identification cannot be achieved. In soupgrounds, only biodeformational structures can be identified.

Morphological changes in trace fossils due to different degrees of substrate consolidation are common in water bodies and floodplain environments subject to desiccation or stabilized by microbial mats. Buatois *et al*. (1997a) documented changes in morphology in Permian floodplain trace fossils due to increased consolidation of the substrate. Morphological details are very poorly preserved in specimens of *Cochlichnus anguineus*, which were emplaced in a water-saturated substrate (Fig. 6.3a). These poorly preserved traces may be cross-cut by better-defined softground trace fossils, reflecting increasing compaction. This second suite includes *Helminthoidichnites tenuis*, *Helminthopsis abeli*, and another generation of *Cochlichnus*

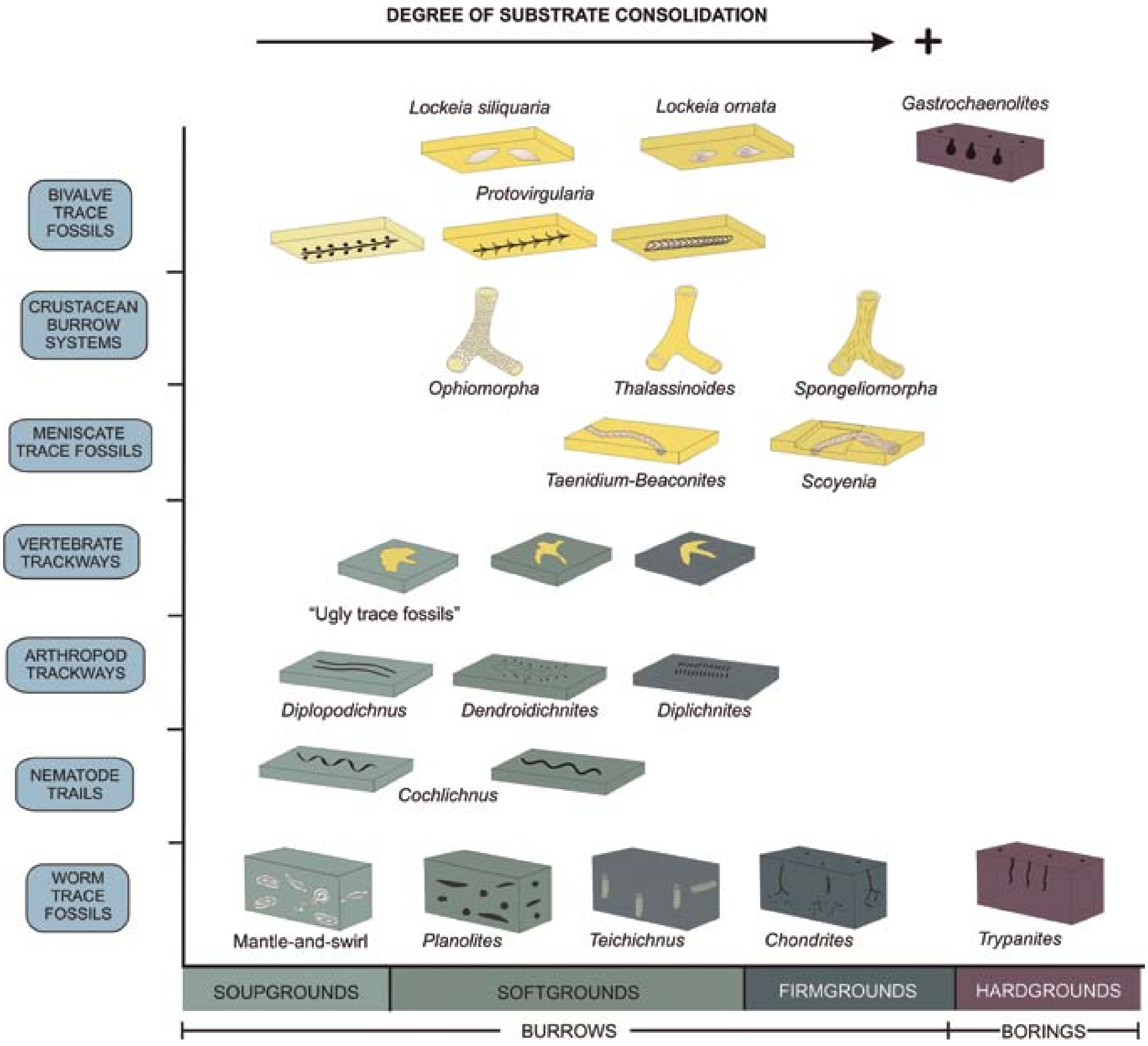


Figure 6.2 Relationship between morphology of different groups of trace fossils and degree of substrate consolidation. In general, quality of morphological definition increases parallel to increased cohesiveness.

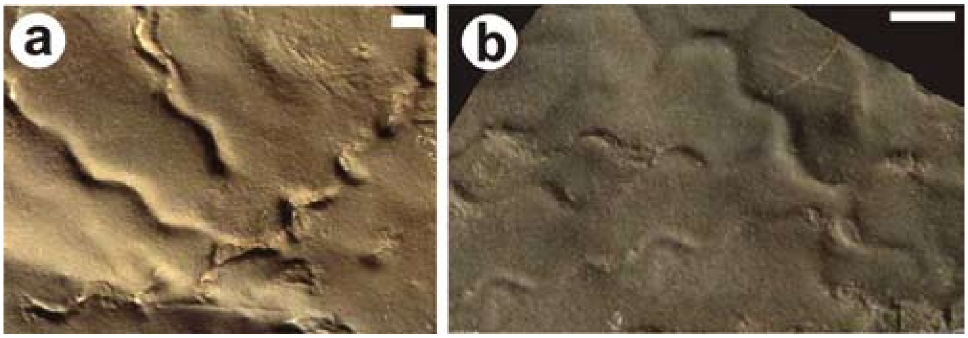


Figure 6.3 Trace-fossil morphology and degree of substrate consolidation in Permian overbank deposits, La Golondrina Formation, Patagonia, Argentina. See Buatois *et al.* (1997a). (a) Extremely deformed *Cochlichnus anguineus*. Note bedding-plane expression of *Ctenopholeus kutscheri* shafts cross-cutting *C. anguineus*. (b) Well-preserved specimens of *C. anguineus*. Scale bars are 1 cm.

anguineus (Fig. 6.3b). The dwelling traces *Ctenopholeus kutscheri* and *Palaeophycus striatus* were emplaced in slightly stiffer substrates. The overall features of this ichnofauna reflect subaqueous emplacement in a water body. Other ancient floodplain deposits exhibit suites formed in even more compacted sediment. The softground suite is characterized by meniscate, backfilled structures without ornamentation (e.g. *Taenidium*, *Beaconites*), and the firmground suite is typified by striated trace fossils (e.g. *Scoyenia*, *Spongeliomorpha*), cross-cutting the former. The resulting palimpsest surfaces reflect progressive desiccation of sediment accumulated along the margins of freshwater bodies (Buatois and Mángano, 2002, 2004a).

Tidal-flat trace fossils also display striking morphological variations depending on the degree of consolidation of the substrate (Mángano *et al.*, 1998, 2002a; Uchman and Pervesler, 2006). Studies on marine benthic ecology demonstrate that vertical and horizontal differences in substrate conditions influence the diversity, abundance, and distribution of intertidal organisms (Newell, 1979; Reise, 1985). Because tidal flats are regularly exposed and submerged by the tides, the concomitant pore-fluid content within the sediment will vary during a tidal cycle. On the other hand, the low-tide landscape is commonly characterized by the presence of tide pools within a generally emerged area, resulting in a range of substrate conditions along an isochronous surface.

Trueman *et al.* (1966) analyzed the effects of substrate, particularly grain size, on the rate of burrowing by soft-bodied animals, concluding that the easier the penetration, the worse the anchorage, and vice versa. A dilatant medium becomes firm and more resistant to shear as increased force is applied, whereas a thixotropic system shows reduced resistance to increased rates of shear. As a consequence, anchorage requires a substance with dilatant qualities, whereas motion is facilitated by a thixotropic system (Trueman and Ansell, 1969). Factors involved in the penetration and protraction phase tend to compensate one another so that the difference in the rate of burrowing may not be determined solely by grain size. However, Trueman *et al.* (1966) noticed that compacted sediment is stiffer, which results in a decreased burrowing rate. Accordingly, the frequency of the digging cycle and depth of penetration in each sequential movement decrease as burrowing into deeper levels proceeds (Ansell, 1962). Within any given grain-size range, a more compacted sediment will be less fluid and stiffer, offering increased resistance to penetration.

Several studies have investigated controls by substrate fluidity on the morphological variability of protobranch bivalve trace fossils (Mángano *et al.*, 1998, 2002a; Carmona *et al.*, 2010). These structures exhibit a complex array of relationships controlled by bivalve behavior, substrate character, and toponomy. In bivalve chevron locomotion traces (i.e. *Protovirgularia*), the distance between two chevrons represents each sequential set of movements, the chevron indicating the site the foot flaps were anchored within the sediment. Sharp, closely spaced chevrons account for short steps, with the animal struggling to advance in stiff, resistant sediment (Fig. 6.4a). Mángano *et al.* (1998) documented striking changes in the morphology of *Protovirgularia* in a Carboniferous tidal flat. The sharp chevrons of *Protovirgularia bidirectionalis* provide evidence of penetration in relatively firm, dewatered substrates. Structures with sharp, closely spaced chevrons represent what can be characterized as the firmer end of the softground range. Longer distances between chevrons, such as those observed in some delicate *Protovirgularia dichotoma* may reflect relatively coherent, but less resistant substrates, resulting in lower shell friction, and allowing smoother and easier movement during the protraction phase. Fluid sediment is conducive to the formation of irregular and highly deformed biogenic structures, reflecting complications in obtaining a secure anchorage (Fig. 6.4b). Similar substrate controls on the morphology of *Protovirgularia* have been documented in Miocene tide-dominated deltaic deposits (Carmona *et al.*, 2010).

Uchman and Pervesler (2006) analyzed how substrate properties influence amphipod and isopod structures in a modern tidal flat. As in the previous cases, they noted that a variety of biogenic structures reflects the stiffness of the substrate and the organism's ability to cope with it. Semi-fluid substrates prevent preservation of biogenic structures, while increasing stiffness leads to preservation of morphological details. Interestingly, on stiff and very stiff substrates these crustaceans move by jumping rather than penetrating into the substrate.

Substrate consistency also plays a major role in the morphological fidelity of arthropod and vertebrate trackways. Davis *et al.* (2007) conducted detailed neoichnological experiments that addressed trackway formation in substrates of various grain sizes and degrees of consolidation simulating subaerial and transitional subaerial–subaqueous environments. These authors noted that with increased firmness of the substrate there is a tendency to increased definition of individual tracks, decreased track width, and loss of tracks within series. Locomotion by heavier arthropods resulted in trackways formed across a broader spectrum of grain size and moisture.

Recently, Scott *et al.* (2010) investigated controls exerted on vertebrate track morphology by wetting and drying cycles in substrates containing different clay minerals in an attempt to evaluate the taphonomy of biogenic structures around saline lakes. These studies suggested that track morphology in smectitic substrates is altered rapidly by wetting and drying, particularly

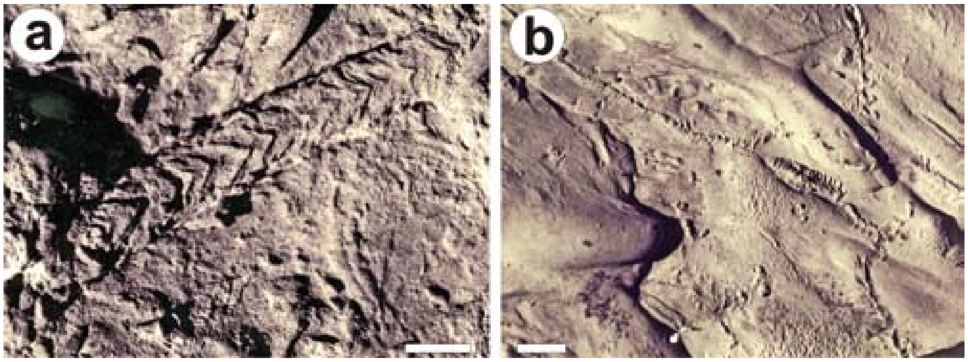


Figure 6.4 Relationship between morphology of bivalve locomotion trace fossils (*Protovirgularia rugosa*) and degree of substrate consolidation, Stull Shale, Waverly trace-fossil site, Kansas, United States. See Mángano *et al.* (1998, 2002a). (a) Sharp, closely spaced chevrons recording relatively stiff sediment. (b) Delicate, poorly defined chevrons. Note flute casts that suggest relatively fluid, poorly cohesive sediment. Scale bars are 1 cm.

in the case of substrates containing saline pore waters. In contrast, track morphology is less affected in non-swelling clays (e.g. kaolinite). These authors also noted that the degree of morphological alteration and/or resistance to wetting and drying is controlled by the rate of substrate drying and the type of resulting salt efflorescence (e.g. interstitial versus surficial crust).

Bromley (2001) noted that if the substrate is too rigid and the animal is not too heavy, no vertebrate footprints are preserved, while, in relatively firm substrates, tracks preserve very delicate structures of the track-making limb (e.g. hairs, scales, claws). With increasing fluidity and softness, however, morphological features become blurred, and the impression of the limb causes significant sediment flow and disruption. Bromley (2001) coined the name "ugly trace fossils" for this type of footprint. Assigning these tracks to specific producers may be difficult due to the lack of diagnostic features. In some cases, track misinterpretations are far from trivial. This is the case of elongate indistinct Cretaceous trackways in Texas that were attributed to humans in pseudoscientific and creationist circles, including some popular movies during the seventies. More serious analysis indicated that these are deformed theropod dinosaur tracks (Kuban, 1989)! In any case, Bromley (2001) noted that these footprints convey significant environmental information, particularly with respect to sediment shear strength and pore-water content, and ultimately the environmental setting of formation (e.g. Marsicano *et al.*, 2010). This situation is reminiscent of taphonomy's motto of the late eighties "Ecology's loss is sedimentology's gain" (Thomas, 1986). In the case of trackways, it is "Anatomy's loss is sedimentology's gain."

6.1.3 OXYGENATION

The importance of oxygen content as a limiting factor has been outlined in different ichnological studies (Bromley and Ekdale, 1984b; Ekdale and Mason, 1988; Savrda and Bottjer, 1986, 1989, 1991; Wignall, 1991; Leszczyński, 1991a; Savrda, 1992, 2007a; Martin, 2004). Rhoads and Morse (1971) proposed a subdivision of marine waters and associated biofacies in three categories based on their oxygen content. These studies indicated that aerobic or fully oxygenated water contains oxygen in excess of 1.0 ml O_2/l H_2O, dysaerobic or poorly oxygenated water contains between 1.0 and 0.1 ml O_2/l H_2O, and anaerobic or anoxic water is characterized by less than 0.1 ml O_2/l H_2O. Subsequent studies slightly modified this scheme and suggested separate terms for the oxygenation regime and the biofacies (Tyson and Pearson, 1991). This revised scheme of oxygenation levels includes oxic (8.0–2.0 ml O_2/l H_2O), dysoxic (2.0–0.2 ml O_2/l H_2O), suboxic (0.2–0.0 ml O_2/l H_2O), and anoxic (0.0 ml O_2/l H_2O). The corresponding biofacies for these four categories are aerobic, dysaerobic, quasi-anaerobic, and anaerobic.

Studies in modern environments demonstrate that diverse shelly faunas tend to flourish under aerobic conditions, while dysaerobic associations are commonly dominated by poorly diverse, small soft-bodied organisms (Rhoads and Morse, 1971; Byers, 1977; Savrda *et al.*, 1991; Tyson and Pearson, 1991). It has been a tenet that quasi-anaerobic biofacies lacks macrofauna, but has *in situ* benthic meio- and microfauna (Neira *et al.*, 2001). The 0.2 ml O_2/l H_2O boundary seems to mark the disappearance of infaunal bioturbation (Tyson and Pearson, 1991). Traditionally, in ichnological models the quasi-anaerobic zone has been considered together with the anoxic zone. Anoxic settings are essentially devoid of metazoan life. The so-called "exaerobic zone" was further introduced based on the presence of calcified invertebrates (Savrda and Bottjer, 1987), and is now regarded as corresponding, at least in part, to the quasi-anaerobic biofacies. In addition, it has been noted that these divisions do not account for rapid seasonal changes (Oschmann, 1993). Recent studies documented intense bioturbation in near-anoxic sediment (0.02–0.03 ml O_2/l H_2O), suggesting that the oxygen limit of macrofaunal bioturbation may be significantly lower than previously estimated (Levin *et al.*, 2003). Bacterial communities have also been reported as blooming under anoxic conditions (e.g. Caumette, 1986; Jorgensen, 1996).

Several attempts have been made to link trace-fossil suites to specific conditions of oxygen content in both the bottom waters and the interstitial waters of a given sediment. Some of these models are very general (e.g. Ekdale and Mason, 1988), while others are exclusive for pelagic (e.g. Savrda and Bottjer, 1986, 1989, 1991) or turbiditic sedimentation (e.g. Leszczyński, 1991a). All these models generally agree that the density of bioturbation, trace-fossil diversity, maximum penetration, and burrow size tend to decrease with decreasing oxygen (Fig. 6.5). However, some of these conclusions have been challenged by studies in modern environments revealing no correlation between decreasing oxygen and depth of bioturbation and burrow size in the Arabian Sea (Smith *et al.*, 2000), and documenting intense bioturbation by symbiont-bearing oligochaetes in a nearly anoxic basin on the Peru margin (Levin *et al.*, 2003). However, two important issues are critical to extrapolate information from modern studies to assess the validity of trace-fossil models: the elusive macroevolutionary component and the time-averaged constraint. It is clear that oxygen-controlled communities have changed through time (Martin, 2004; Mángano, 2011). The issue of whether modern marine oligochaetes record a recent invasion of an underexploited niche deserves further exploration. Although posing a cautionary note on established ichnological models, its implications for the geological record may be limited. Also, oxygen fluctuations at the ecological timescale may not be reflected in the fossil record. Time-averaging is inherent to trace fossils and may represent a complication because short-term redox cycles or events may not be revealed (Savrda, 2007a).

In addition, it has been suggested that in some cases, it is difficult to discriminate between oxygen and substrate controls, particularly in the case of a very low diversity of trace fossils, which may reflect either dysaerobic conditions or soupy substrates (Wignall, 1993; Savrda, 2007a). Careful analysis of trace-fossil morphological details is the key in this case (see Section 6.1.2).

Ekdale and Mason (1988) proposed a general model that attempts to link certain ethological categories with oxygen content. Although some objections were raised (e.g. Wheatcroft,

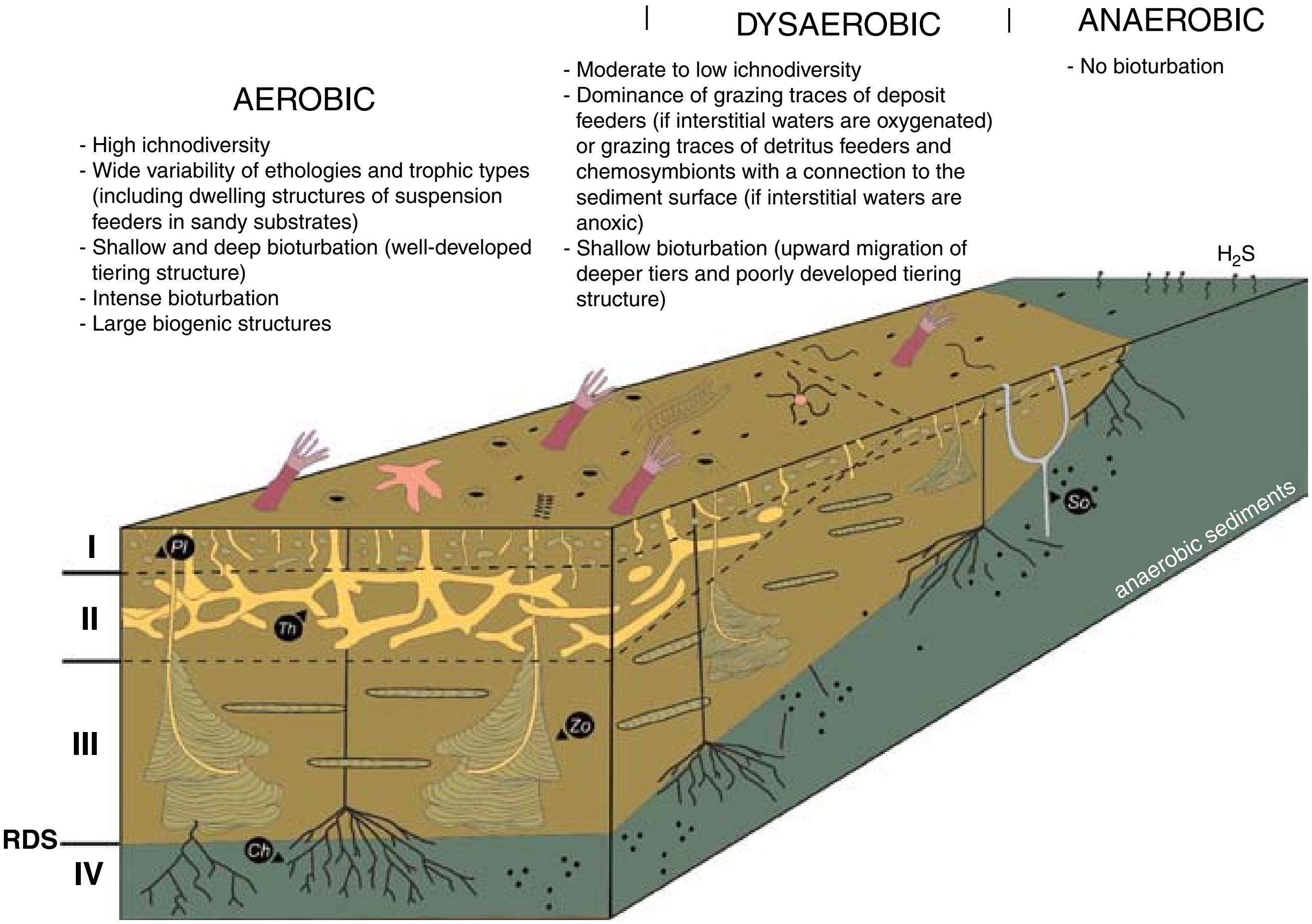


Figure 6.5 Relationship between trace fossils and oxygen content. Aerobic, dysaerobic, and anaerobic refer to oxygenation of bottom waters. Under aerobic conditions in both the interstitial and bottom waters, endobenthic communities tend to display complex tiering structures. Four tiers, shallow (I – *Planolites* or *Pl*), mid (II – *Thalassinoides* or *Th*), deep (III – *Zoophycos* or *Zo*), and very deep (IV – *Chondrites* or *Ch*, *Solemyatuba* or *So*), are illustrated in the example. Burrows maintaining a connection with the oxygenated sediment surface are able to penetrate in anaerobic sediment below the redox discontinuity surface (RDS). No bioturbation develops under anaerobic bottom waters.

1989; Martin, 2004), the model is useful for the study of ancient marine successions and modern sediments, particularly if other controlling factors are taken into consideration (Buatois and Mángano, 1992; Levin *et al.*, 2003). According to this model, if both the bottom and interstitial waters are anoxic, no bioturbation occurs and the sediment is typically dark and well laminated. If anoxic conditions exist in interstitial waters, but bottom waters are at least dysoxic, fodinichnia is the dominant ethology, essentially represented by permanent burrow systems that maintain a connection with the sediment–water interface allowing the circulation of the more oxygenated waters into the anoxic sediment. Ichnodiversity is typically low, and monospecific associations are common. *Zoophycos* and *Chondrites* (Fig. 6.6a) (and, in some cases, *Teichichnus* and *Trichichnus*) are the classical components. If the interstitial waters are dysoxic and the bottom waters are either dysoxic or oxic, pascichnia becomes dominant. The assumption here is that grazing trails are temporary structures formed by infaunal deposit feeders. Because these organisms backfill their structures, no connection is maintained with the sea bottom, and the sediment cannot be totally anoxic. Although grazing trails are also produced at the sediment–water interface, and thereby they do not require oxygen within the sediment, their preservation in marine environments is very low. Finally, under fully oxic conditions in both the bottom and interstitial waters, domichnia is the dominant ethological group. Permanent domiciles of suspension feeders, such as *Skolithos*, represent the typical structures.

Savrda and Bottjer (1986, 1987, 1991) proposed a model that attempts to explain trace-fossil distribution in pelagic or hemipelagic sediments unaffected by sediment gravity flows. They characterized oxygen-related ichnocoenoses (ORI), which occur in stratal units that accumulate under similar conditions of oxygenation of bottom waters. Their method allows the construction of oxygenation curves for sedimentary successions. The general trend under decreasing oxygen content is a decrease in ichnodiversity, burrow diameter, and burrowing depth. Accordingly, structures that occupy deep tiers in oxygenated sediments tend to move upwards as a result of the upward migration of the redox discontinuity under oxygen-depleted conditions. Under extreme dysoxic conditions monospecific

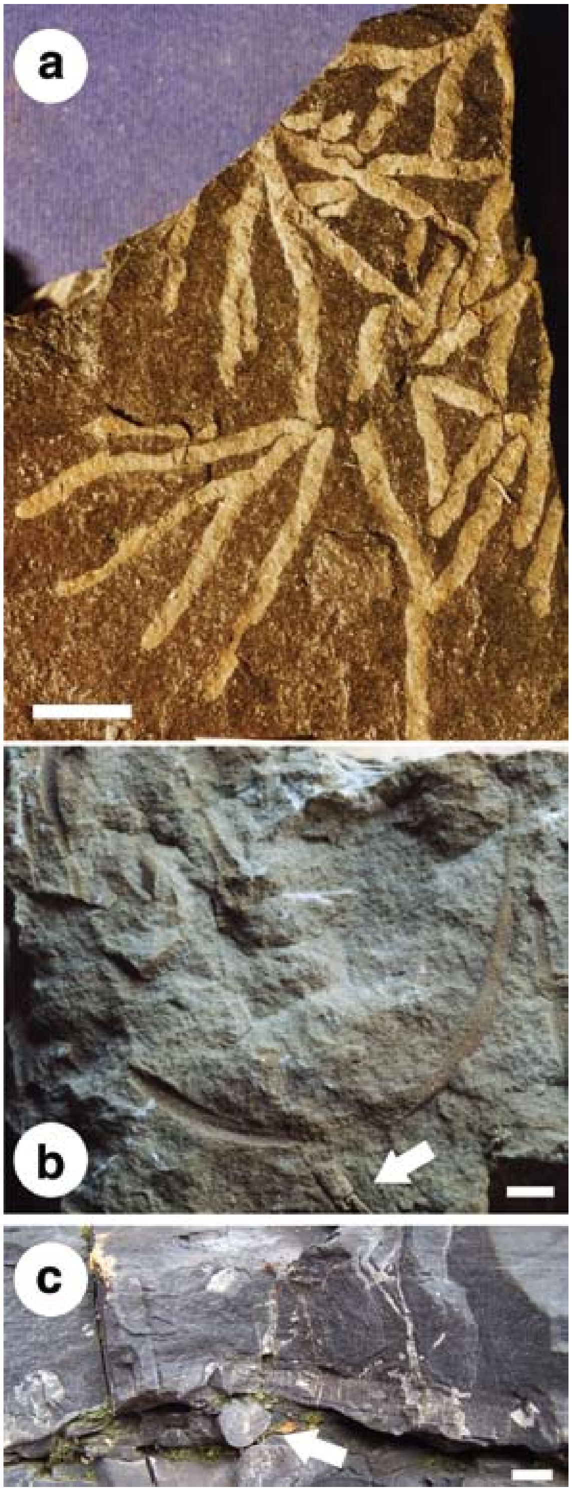


Figure 6.6 Typical ichnotaxa of oxygen-depleted conditions. (a) *Chondrites* isp. Upper Carboniferous, near Eudora town, Eudora Shale, eastern Kansas, United States. (b) *Solemyatuba ypsilon* showing lower extension tube (arrow). Upper Triassic, Rhaetian Sandstone, Olgahain, southern Germany. See Seilacher (1990a). (c) Cross-section view of *Protovirgularia obliterata* (arrow) at the base of a turbidite. Veřovice Beds, Lower Cretaceous, Zagórnik, Outer Carpathians, Poland. See Uchman (2004b). All scale bars are 1 cm.

suites of deep-tier traces in shallow-tier positions occur, with *Chondrites* being the typical ichnotaxon (see also Bromley and Ekdale, 1984b). Under totally anoxic conditions, no bioturbation occurs. These ideas have been applied to the study of a large number of pelagic successions (e.g. Savrda and Bottjer, 1989, 1994; Savrda *et al.*, 1991; Savrda and Ozalas, 1993; Ozalas *et al.*, 1994; Locklair and Savrda, 1998a, b; Savrda, 1998; Olóriz and Rodríguez-Tovar, 2002; Martin, 2004).

Leszczyński (1991a) proposed a model to examine the links between oxygen conditions and trace-fossil distribution in turbidite successions. He distinguished five ichnocoenoses reflecting progressive oxygenation of the deep sea that are revealed by trace fossils preserved at the base of thin-bedded turbidites. Some of the trends under increasing oxygen content are an increase in ichnodiversity and size of the trace fossils. Graphoglyptids (agrichnia) reach their climax in relatively well-oxygenated settings, while turbidites formed under poorly oxygenated conditions display undifferentiated biogenic structures. Subsequent studies, however, suggest that food supply and sedimentation rate may have also played a role in trace-fossil distribution in this case (Wetzel and Uchman, 1998a).

The model developed by Wignall (1991), based on a single case study (the Jurassic Kimmeridge Clay of England), does not agree with some tenets of the more general models. For example, *Chondrites* does not correspond to his dysoxic end member, being replaced by the supposed Pascichnion *Astacimorphichnus etchesi*. However, this ichnotaxon is only known from this unit and its overall morphology does not agree with a grazing trace ethology.

In addition to *Chondrites* (Fig. 6.6a), other ichnotaxa have been suggested to reflect particular adaptations to oxygen-depleted settings. Some of these are produced by chemosymbiotic bivalves (Seilacher, 1990a). The U-shaped burrow *Solemyatuba* (Fig. 6.6b) has been regarded as the dwelling structure of relatives of the modern bivalve *Solemya*, which endosymbiotically farms bacteria in its gills (Seilacher, 1990a). Deep-tier occurrences of *Protovirgularia* (Fig. 6.6c) have been also attributed to the work of chemosymbiotic bivalves in anoxic sediment (Uchman, 2004b).

While previous models attempt to explain behavioral adaptations to oxygen deficiency, there are cases of animals living in nearshore well-oxygenated settings that are transported basinward into anoxic settings via sediment gravity flows or hyperpycnal flows. These are the so-called “doomed pioneers” of Föllmi and Grimm (1990), and Grimm and Föllmi (1994). Doomed pioneers construct burrows in completely anoxic sediments, but do not persist in such settings, dying from suffocation (Fig. 6.7a–d). Decapod crustaceans, having skeletonized resistant body parts, are typical doomed pioneers. Commonly, sandy substrates with *Thalassinoides* or *Gyrolithes* intercalate with totally anoxic mudstone reflecting short-term burrowing events. The ability of crustaceans to survive for short periods under anoxic conditions has been inferred from the presence of “dying” trackways (mortichnia) associated with their body fossils in the Jurassic Solenhöfen Limestone of Germany (e.g. Janicke, 1969; Viohl, 1990; Barthel *et al.*, 1990). The same situation has been proposed for Cretaceous lacustrine limestones of

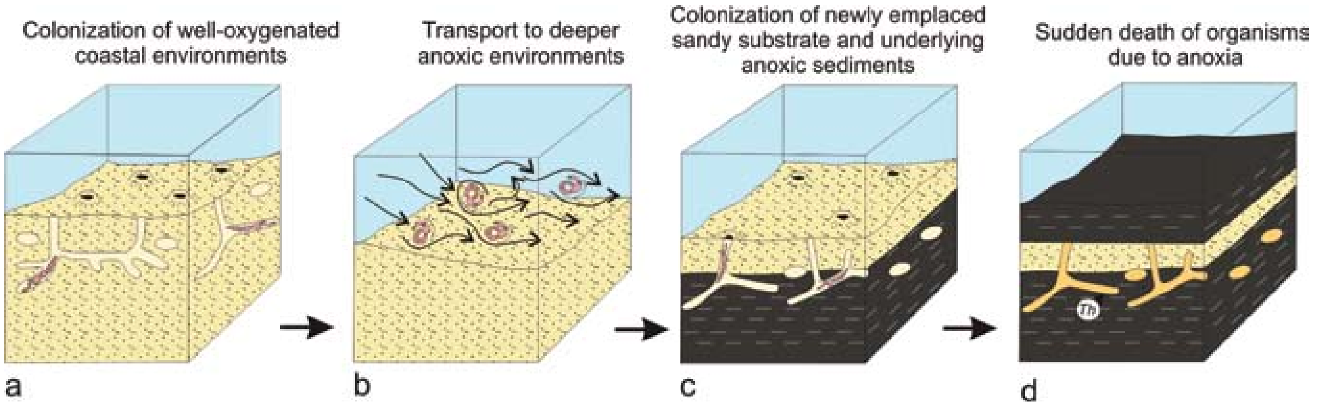


Figure 6.7 Doomed pioneers model (based on Föllmi and Grimm, 1990, and Grimm and Föllmi, 1994). (a) A benthic community in established in well-oxygenated nearshore environments. (b) Sediment gravity flows or hyperpycnal flows transport these nearshore components to deeper-water anoxic environment. (c) These anoxic sediments are colonized by the doomed pioneers and *Thalassinoides* (*Th*) burrows are emplaced. (d) The organisms die rapidly due to anoxia.

Spain that contain deep-water anoxic sediments with the crustacean trackway *Hamipes* (Gibert *et al*., 2000).

6.1.4 SALINITY

The importance of salinity as a limiting factor in coastal areas has been emphasized in different studies (e.g. Howard and Frey, 1975; Howard *et al*., 1975; Wightman *et al*., 1987; Pemberton and Wightman, 1992; Rindsberg, 1992; MacEachern and Pemberton, 1994; Buatois *et al*., 1997b, 2010a; Mángano and Buatois, 2004a; MacEachern and Gingras, 2007). In particular, it has been noted that while the distribution of physical sedimentary structures is mainly salinity-independent, the distribution of benthos is not and, accordingly, ichnology represents a powerful tool to reconstruct paleosalinity (Buatois *et al*., 1997b). Salinity levels are classified into limnetic (less than 0.5‰), oligohaline (0.5–5‰), mesohaline (5–18‰), polyhaline (18–30‰), and euryhaline (30–40‰) (Remane and Schlieper, 1971; Knox, 1986). Limnetic is equivalent to freshwater, while oligohaline, mesohaline, and polyhaline correspond to brackish water. Fully marine conditions fall within the euryhaline category with mean seawater salinity at approximately 35‰ (McLusky, 1989). Bromley and Asgaard (1991) emphasized that behavioral convergence leads some ichnotaxa to occur on both sides of the salinity barrier, although this does not imply the identity of the producers. The classic example is that of *Cruziana* and *Rusophycus*, which are commonly produced by trilobites in marine environments (Seilacher, 1970, 1985) and by branchiopods or notostracans in freshwater (Bromley and Asgaard, 1972b; Pollard, 1985). In any case and regardless of behavioral convergence, salinity is of paramount importance in trace-fossil distribution (Fig. 6.8).

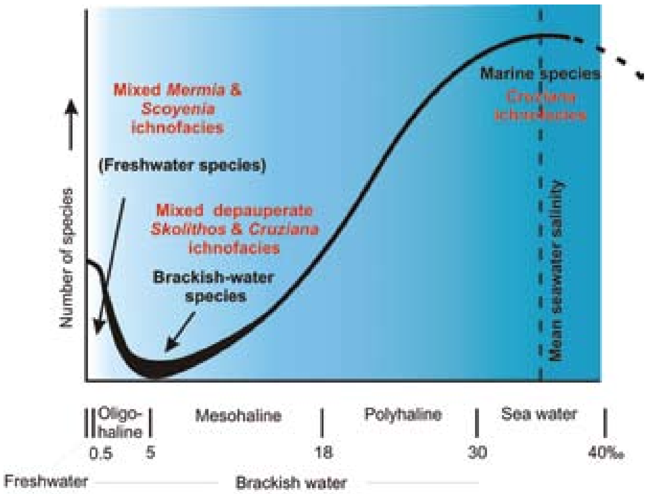


Figure 6.8 Relationship between trace-fossil associations, ichnodiversity, and salinity Modified from Buatois *et al*. (1997b), and Mángano and Buatois (2004a).

Ichnofaunas developed under normal-marine salinity conditions in nearshore to offshore zones are characterized by: (1) high ichnodiversity; (2) marine ichnotaxa produced by both euryhaline and stenohaline organisms; (3) onshore–offshore trends displayed by the *Skolithos* and *Cruziana* ichnofacies; (4) presence of both infaunal and epifaunal traces; (5) presence of simple and complex structures produced by presumed trophic generalists and specialists, respectively; (6) presence of multispecific associations, which become more common towards distal settings; (7) high density; and (8) wide size ranges (Mángano and Buatois, 2004a). These ichnofaunas reflect the activity of benthic organisms that inhabited shallow-marine areas dominated by euryhaline conditions. These benthic faunas experience less salinity stress than those developed in brackish-water ecosystems, characterized by steep salinity gradients. Fully marine deposits are typically extensively bioturbated, and contain a wide range of ethological categories and ichnotaxa. Ichnodiversity commonly reaches a maximum peak under euryhaline conditions (Buatois *et al*., 1997b). Although it is difficult to pinpoint ichnotaxa exclusive of fully marine conditions in shallow-marine areas, *Chondrites*, *Phycosiphon*, *Scolicia*, and *Zoophycos* are common indicators.

A large number of studies have focused on the diagnostic features of brackish-water benthic faunas. Valuable information has been obtained from studies of marine benthic ecology in modern estuaries and bays (e.g. Remane and Schlieper, 1971; Croghan, 1983; McLusky, 1989; Hudson, 1990), and ichnological studies of marginal-marine ecosystems as well (e.g. Howard and Frey, 1975; Howard *et al.*, 1975; Rindsberg, 1992; Gingras *et al.*, 1999b). This ecological and neoichnological information has been subsequently integrated with data from the fossil record, initially from the Mesozoic of the Canadian region of the Western Interior Seaway (e.g. Wightman *et al.*, 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994, 1997; MacEachern and Gingras, 2007), resulting in the so-called "brackish-water model".

Very few animals have the physiological adaptations necessary to survive in brackish water (Croghan, 1983). This reflects the harsh conditions of brackish-water ecosystems that result from fluctuating environmental parameters, mostly salinity but also temperature, oxygen, and water turbidity. In modern estuaries, salinity fluctuations from 30‰ to 10‰ in one hour have been documented (Ferguson *et al.*, 1981). Therefore, brackish-water faunas are less diverse than their marine and freshwater equivalents (e.g. Croghan, 1983; McLusky, 1989; Hudson, 1990; Pickerill and Brenchley, 1991). As a result, the abundance and particularly the diversity of biogenic structures in brackish-water settings are very low, reaching a minimum under mesohaline to oligohaline conditions (Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Buatois *et al.*, 1997b; Mángano and Buatois, 2004a).

Some marine organisms referred to as euryhaline are usually capable of colonizing brackish-water environments, as they are highly tolerant to changes in salinity. In contrast, continental organisms living in freshwater are not physiologically fit to survive in a brackish ecosystem. Diversity of freshwater animals tends to decline rapidly, even with slight increases in salinity, whereas marine organisms experience a more gradual decrease in number under dilution of normal-marine salinity (Pemberton and Wightman, 1992; Buatois *et al.*, 1997b; Mángano and Buatois, 2004a). As a result, the ichnofauna from estuarine environments is represented by an association of biogenic structures produced by an impoverished marine fauna rather than from a combination of fully marine and freshwater forms. This is reflected by ichnofacies distribution, with brackish-water ecosystems characterized by a mixed of depauperate *Skolithos* and *Cruziana* ichnofacies (Wightman *et al.*, 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994).

Burrowing is a key strategy intended to minimize salinity variations as salinity fluctuations are considerably lower a few centimeters into the substrate than at the water–sediment interface because the presence of impermeable fine sediment slows down the exchange of pore water (Sanders *et al.*, 1965; Johnson, 1967; Rhoads, 1975). Thus, brackish-water associations tend to be dominated by structures of infaunal organisms rather than surface epifaunal trails.

Organisms able to foray into brackish-water settings are commonly opportunistic (see Section 6.4). Accordingly, ichnofaunas from brackish-water settings contain very simple forms produced by nonspecialized r-selected animals, which are typically adapted to environments of high physiological stress (Miller and Johnson, 1981; Ekdale, 1985; Pemberton and Wightman, 1992; Beynon and Pemberton, 1992). In terms of trophic types, euryhaline animals are either omnivorous or trophic generalists (Wolff, 1973).

It has been noted that reduced size is one of the most notable features of brackish-water associations (Hakes 1976, 1985). Although Taylor *et al.* (2003) have expressed doubts on the connection between size reduction and brackish water, this link is in agreement with studies of marine benthic ecology and observations from the ichnological record, which have documented reduced size in brackish-water faunas, particularly ophiuroids, bivalves, and some worms (Remane and Schlieper, 1971; Spaargaren, 1979, 1995; Mángano *et al.*, 1999; Gingras *et al.*, 1999b; Mángano and Buatois, 2004a). However, Gingras *et al.* (1999b) noted that crustaceans do not display size reduction in brackish-water environments. It has further been postulated that size reduction in response to salinity occurs either as a morphological adaptation or as a result of population dynamics (Gingras *et al.*, 1999b). In the first case, decreasing size allows the organism to increase its surface area to mass ratio to control osmotic transfer. In the second case, large populations of small forms that attain full growth result in the same biomass.

In short, brackish-water trace-fossil associations are characterized by: (1) low ichnodiversity; (2) forms typically found in marine environments; (3) mixture of vertical and horizontal trace fossils from the *Skolithos* and *Cruziana* ichnofacies; (4) dominance of infaunal traces rather than epifaunal trails; (5) simple structures produced by trophic generalists; (6) variable abundance; (7) presence of monospecific associations; and (8) small size (Wightman *et al.*, 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Mángano and Buatois, 2004a). Typical components of brackish-water environments are *Teichichnus* (Fig. 6.9) (Buatois *et al.*, 2005) and the spiral burrow *Gyrolithes* (Wetzel *et al.*, 2010), together with *Skolithos*, *Diplocraterion*, *Palaeophycus*, *Protovirgularia*, *Lockeia*, and *Planolites*.

In contrast, freshwater ichnofaunas, such as those present at the fluvio-estuarine transition, are characterized by: (1) moderate to relatively high diversity; (2) forms typically present in continental environments; (3) a mixture of trace fossils belonging to the *Scoyenia* and *Mermia* ichnofacies; (4) the dominance of surface trails and meniscate trace fossils; (5) temporary structures produced by mobile detritus and deposit-feeding fauna; (6) moderate density of individual ichnotaxa; (7) presence of multispecific associations; and (8) small size (Buatois *et al.*, 1997b; Mángano and Buatois, 2004a). The relatively high ichnodiversity records a secondary peak in diversity typically associated with the activity of freshwater, and terrestrial organisms along a salinity gradient (Buatois *et al.*, 1997b). The freshwater benthos inhabiting this zone does not have the special adaptations necessary to survive in the brackish environment. While fully marine ichnofaunas gradually decrease in diversity into brackish-water settings, freshwater ichnofaunas from fluvio-estuarine transitions do not intergrade with those from brackish water. Arthropods are the

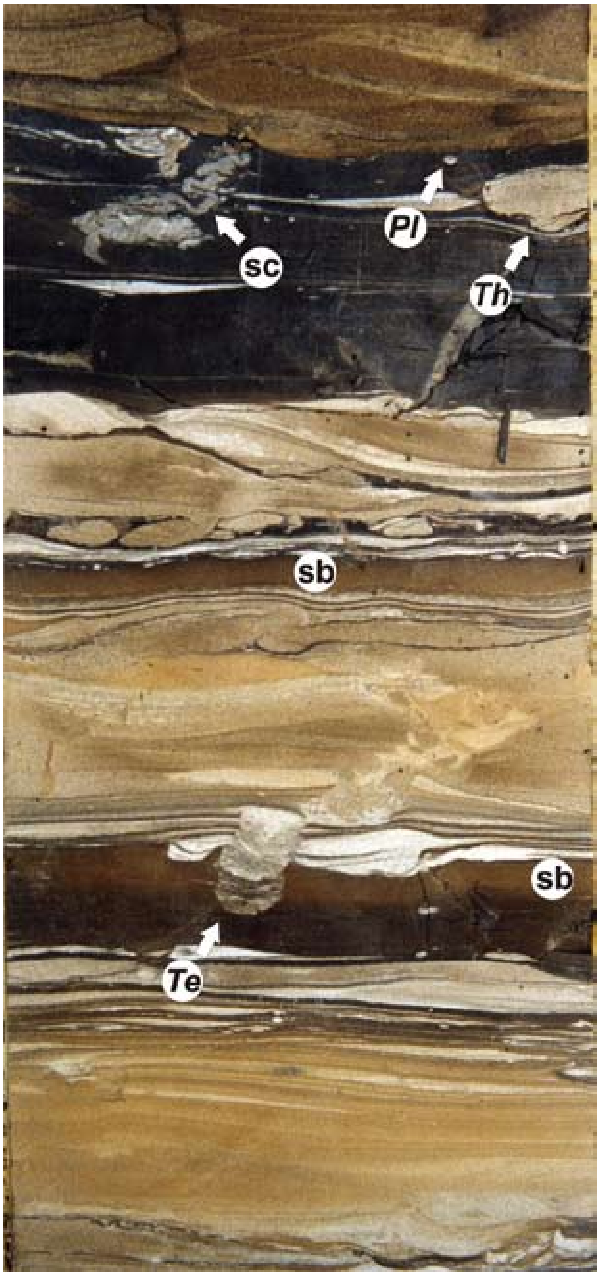


Figure 6.9 Typical aspect of a brackish-water deposit as expressed in core. Bioturbation intensity and ichnodiversity is low. The trace-fossil association consists of *Teichichnus* (*Te*), small *Planolites* (*Pl*), and *Thalassinoides* (*Th*). Synaeresis cracks (sc) and siderite bands (sb) are common. Lower Miocene, Oficina Formation, Oritupano Field, Eastern Venezuelan Basin. Core width is 7 cm.

dominant tracemakers. Typical elements are trackways (e.g. *Dendroidichnites*, *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Stiallia*, *Stiaria*) and resting traces (e.g. *Tonganoxichnus*), as well as grazing (e.g. *Gordia*, *Helminthoidichnites*, *Helminthopsis*) and feeding traces (e.g. *Circulichnis*, *Treptichnus*). Vertebrate trace fossils are represented by fish trails (*Undichna*) and tetrapod trackways (e.g. *Serpentichnus*), and illustrate the *Serpentichnus* ichnocoenosis of Hunt and Lucas (2006a, 2007).

Suppressed erosion during rising tides allowed excellent preservation of delicate surface structures (Archer *et al.*, 1994). Additionally, the absence of pervasive burrowers in such settings (particularly in Paleozoic examples) improves the preservation potential of surface traces because the activity by infaunal organisms would have lead to the destruction of the uppermost tiers (Bromley, 1990, 1996; Buatois *et al.*, 1997b).

Finally, stressful conditions linked to salinity are extreme under hypersaline conditions, such as those typical of sabkhas and saline lakes (e.g. Price and McCann, 1990). Ekdale *et al.* (1984) noted that hypersaline lakes and thermal pools generally have no benthic fauna and, therefore, no biogenic structures. However, Scott *et al.* (2007a) noted that hot springs provide favorable sites for insects, mammals, birds, and reptiles. In saline lakes, freshwater inflow is higher around ephemeral streams, hot springs, and ground-water seepage, allowing a concentration of animals that produce trackways, trails, and burrows. Ichnofaunas from restricted, hypersaline seas described from the fossil record are dominated by small, poorly specialized trace fossils (Gibert and Ekdale, 1999). Typically marine hypersaline deposits are scarcely bioturbated and contain low-diversity trace-fossil associations (Jaglarz and Uchman, 2010).

6.1.5 SEDIMENTATION RATE

Ichnological evidence commonly reflects the complex interplay between sedimentation rate, erosion, and biogenic activity, therefore revealing information on depositional rhythms. Continuous and slow sedimentation usually allow for intense bioturbation and destruction of physical sedimentary structures, particularly in the absence of any other stress factor (Howard, 1978; Howard and Reineck, 1981; Monaco, 1995). Application of this simple principle allows re-examination of Cretaceous-Tertiary deposits attributed to tsunami events that were in fact intensely bioturbated, suggesting slow rates of sedimentation rather than episodic deposition (Savrda, 1993; Ekdale and Stinnesbeck, 1998). Episodic deposits commonly contain burrows only in the top of layers, revealing post-event colonization (Howard, 1978; Frey and Goldring, 1992). Where storm deposits alternate with intensely bioturbated background sedimentation units, these deposits are characterized by the so-called "Lam-Scram" pattern (see Section 7.1.5).

Pollard *et al.* (1993) introduced the notion of the colonization window or time available for occupation of the substrate to understand burrowing in high-energy settings. Colonization of shifting sands, such as those forming subtidal bars, is impossible under high-energy conditions, but may occur during short periods of quiescence, revealing brief colonization windows. In contrast, under slow accretion (e.g. lower offshore) the colonization window is more or less continuously open. In fluvial successions, it is not unusual that the only trace fossils occur in fine-grained overbank and pond deposits interbedded within unbioturbated, stacked channel deposits, recording brief colonization windows (Buatois *et al.*, 1997a) (see Section 10.2.2). In any case, in some settings brief periods of sedimentation breaks may be enough for benthic

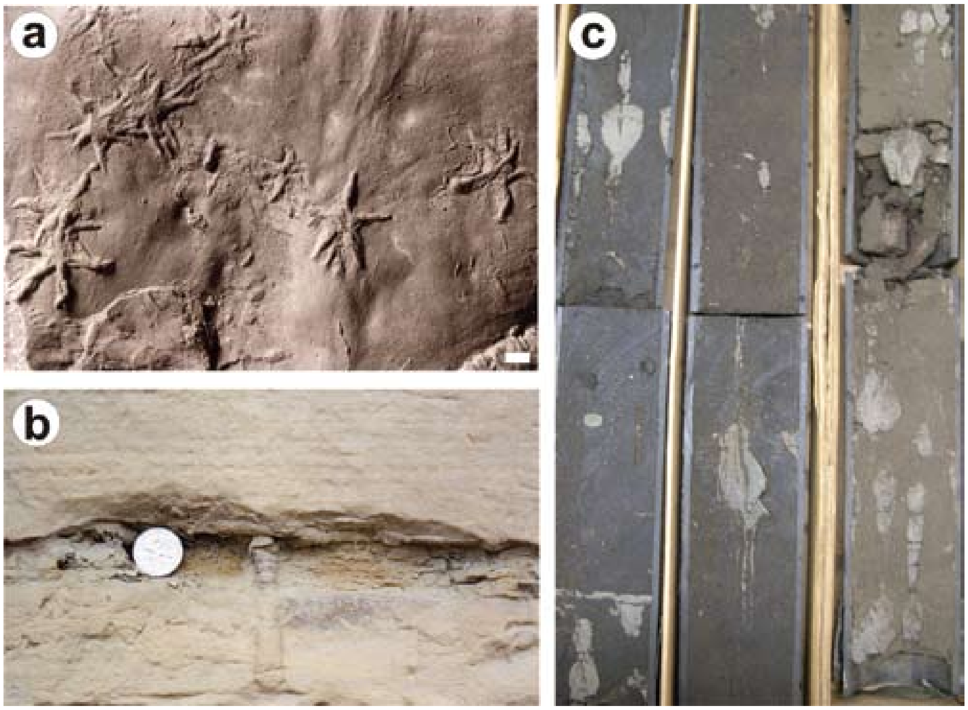


Figure 6.10 Trace fossils and sedimentation rate. (a) *Asteriacites lumbricalis* in tidal-flat deposits forming imbricated structures that document vertical movement though the sediment (from lower left to upper right). Pennsylvanian, Rock Lake Shale, Stanton Formation, Western Missouri, United States. See Mángano *et al.* (1999). Scale bar is 1 cm. (b) Truncated *Ophiomorpha* in hummocky cross-stratified sandstone recording storms in offshore-transition deposits. Intense storm scouring truncated the top of the burrow. Upper Cretaceous, Desert Member, Blackhawk Formation, Book Cliffs, Utah, United States. Coin is 1.4 cm wide. (c) Stacked *Rosselia socialis* in lower-shoreface deposits, reflecting re-equilibration of burrows after storm deposition. Lower Cretaceous, Grand Rapids Formation, Alberta, Canada. Core is read from base at lower left to top at upper right. See Pemberton *et al.* (2001). Core width is 9 cm.

organisms to graze on the substrate. Sedimentation rates of 3.8 m/yr were estimated for Carboniferous tidal-flat deposits formed in a fluvio-estuarine transition (Lanier *et al.*, 1993). However, clay drapes along bedding planes are covered by trackways and trails, reflecting arthropod ability to use available resources during short-term slack-water periods (Buatois *et al.*, 1997b).

Some ichnotaxa, particularly those regarded as equilibrium structures, are useful to detect changes in the balance between deposition and erosion. Goldring (1964) illustrated the upward and downward movements of *Diplocraterion yoyo* in response to aggradation and degradation of the substrate, respectively. Burrowing sea anemones slowly move upwards during gradual vertical accretion of the substrate, but move faster if sedimentation is episodic (Schäfer, 1962). Horizontal and vertical repetition is recorded by multiple impressions of the ophiuroid resting trace *Asteriacites lumbricalis*. These structures record slight horizontal relocation and the punctuated upward motion of the animal through the sediment, and most likely document an escape strategy (Seilacher, 1953b; Mángano *et al.*, 1999) (Fig. 6.10a). In high-energy nearshore settings, truncated specimens of *Ophiomorpha* indicate erosive events (Howard, 1978) (Fig. 6.10b).

The ichnogenus *Rosselia* commonly reflects adjustments of the burrow as a response to sedimentation events (Nara, 1997, 2002; Pemberton *et al.*, 2001; Campbell *et al.*, 2006). Nara (1995, 1997) described Pleistocene funnel- and spindle-shaped specimens of *Rosselia*, attributed to terebellid polychaetes that are vertically stacked reflecting upward migration to avoid burial due to episodic sedimentation in a storm-dominated shallow-marine setting. Pemberton *et al.* (2001) illustrated up to seven Cretaceous stacked *Rosselia* reflecting burrow readjustments after storms in a lower shoreface (Fig. 6.10c). Identically, Howell *et al.* (2007) documented seven stages of upward migration and readjustment in *Rosselia* throughout an approximately 1-m thick amalgamated sandstone unit, resulting from repeated storms in a delta-front environment. These findings provide a new source of data to estimate sedimentation rate and frequency of storms in wave-dominated shallow-marine environments. Campbell *et al.* (2006) analyzed Pleistocene specimens of *Rosselia* displaying a simple morphology that were regarded as extreme-event end members. These specimens occur in mudstone and siltstone interpreted as oceanic-flood deposits from an adjacent river system, and record adaptation of terebellid polychaetes to allow them to thrive under conditions of very high sedimentation rates that caused the exclusion of any other benthic fauna.

6.1.6 FOOD SUPPLY

The type and amount of food supply ranks among the most important controlling factors in determining feeding strategy (Fig. 6.1) (see Section 3.1). Suspension feeders tend to be dominant in high-energy settings where organic particles are kept in suspension by waves or currents. In contrast, organic particles accumulate in the sediment in tranquil waters and animals tend to develop deposit- and detritus-feeding strategies. Food supply tends to vary in a predictable way along onshore–offshore trends, resulting in what has been termed the food resource paradigm by Pemberton *et al.* (2001). Another gradient occurs within the sediment in relation to the vertical distribution of organic matter (see Section 5.1). Organic matter is more abundant close to the sediment–water interface, which results in a peak of available food for detritus and deposit feeders occupying superficial to shallow tiers (Fig. 6.11).

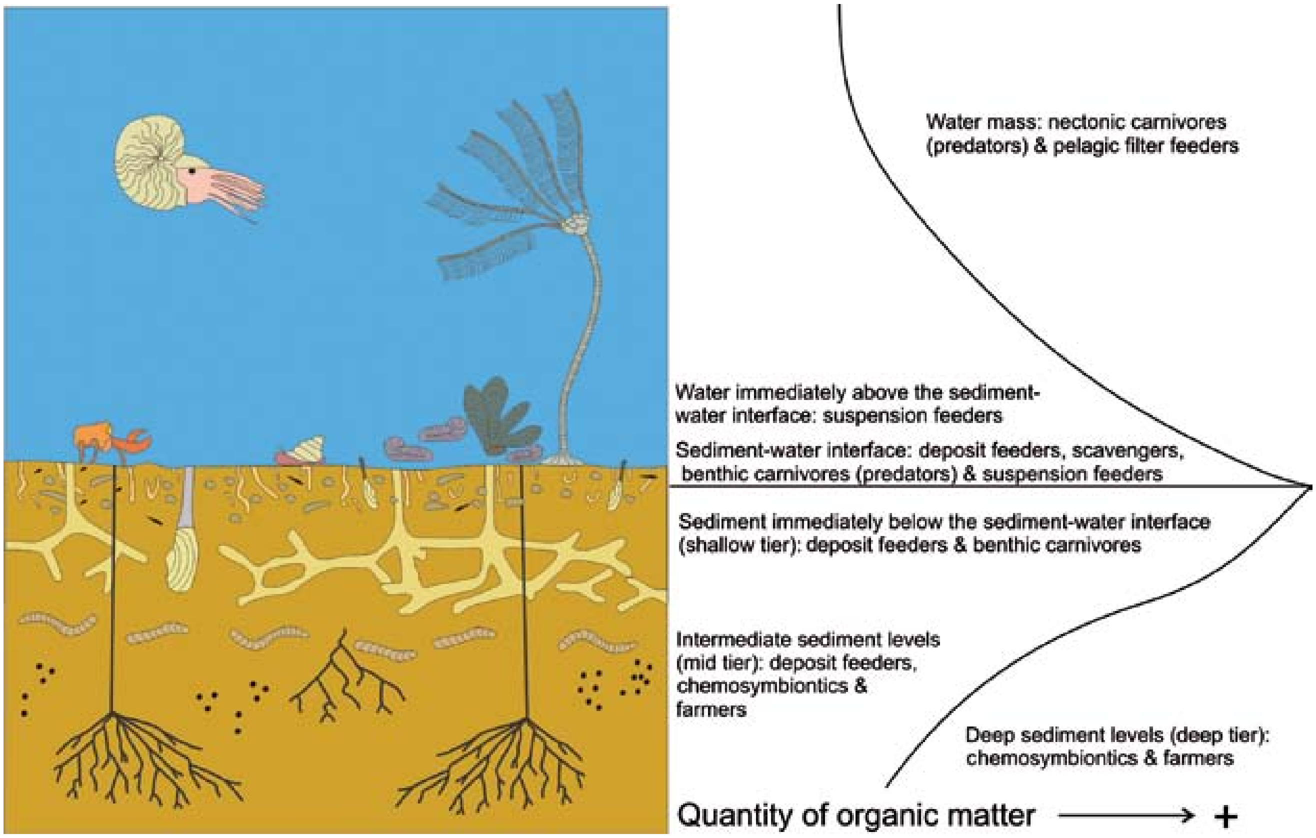


Figure 6.11 Relationship between tier position, feeding strategies, and quantity of organic matter. Note that the highest amount of organic matter is near the sediment–water interface. In deep-marine environments burrows produced by chemosymbionts and farmers (i.e. graphoglyptids) occupy a very shallow tier. Modified from Mángano and Buatois (1999a).

Under conditions of scarce food supply, animals developed sophisticated feeding strategies, including gardening and chemosymbiosis. This is the case of deep-marine environments, which are dominated by graphoglyptids and complex grazing trace fossils, typical of the *Nereites* ichnofacies (Seilacher, 1977a; W. Miller, 1991a). Conversely, it has been argued that high frequency of sediment gravity flows supplying organic detritus to deep-marine ecosystems precludes the development of ichnofaunas dominated by agrichnia and ornate pascichnia (Buatois and López Angriman, 1992b).

The importance of food supply in deep-marine ichnofaunas has been emphasized by Wetzel and Uchman (1998a). These authors suggested that high amounts of food supply are indicated by: (1) dark-colored sediments, (2) complete bioturbation, (3) high density of shallow-tier trace fossils, (4) rarity or absence of graphoglyptids, and (5) deep tiers totally bioturbated by feeding traces that have a connection to the surface. Also, in settings with seasonal strongly fluctuating input of organic matter (e.g. under monsoonal regimes), a double nutritional strategy is adopted by some organisms, detritus feeding during bloom times and deposit feeding during non-bloom times (Wetzel, 2008, 2010). During times of benthic food richness, oxygenation of interstitial water decreases and, as a result, organisms move upward. In areas of marked seasonality of organic matter input, biogenic structures tend to show pronounced upward and downward movements (Wetzel, 2010). On the other hand, predominance of horizontal burrows without evidence of vertical displacement indicates a more constant input of organic matter. Up-and-down movements of endobenthic organisms affect near-surface burrowers. Consequently, graphoglyptids tend to be absent in deep-sea regions affected by pronounced seasonality of primary production (Wetzel, 2010).

In lacustrine environments, grazing patterns are nonspecialized, as exemplified by the ichnogenus *Mermia*, which displays looping and a high level of self-overcrossing, recording the repeated passage of the tracemaker across the same portion of sediment. Such nonspecialized trophic strategies most likely reflect the abundance and accessibility of food in lacustrine systems (Buatois and Mángano, 1998). A similar situation has been recorded in modern tidal flats with grazing trails of the isopod *Chirodotea coeca* (Hauck *et al.*, 2008). These authors documented an increase in trail tortuosity and self-overcrossing parallel to an increase in food content.

6.1.7 BATHYMETRY

Originally, bathymetry was emphasized in earlier ichnological studies that attempted to establish links between trace-fossil associations and depositional environments (e.g. Seilacher, 1967b). However, it soon became clear that ichnofacies and trace-fossil distribution reflect sets of environmental factors rather than sedimentary environments and specific bathymetric zones (see Section 4.6). Exceptions to the standard bathymetric model are countless (e.g. Henbest, 1960; Crimes, 1977; Crimes *et al.*, 1981; Pemberton and Frey, 1984b). As noted by Frey *et al.* (1990), bathymetry per se is only very rarely a governing factor. As a consequence, bathymetric implications should be established with caution. In any case, the relative success of the ichnofacies model in bathymetric assessments is based on the fact that in some cases most direct controls (e.g. substrate type, food supply, energy) vary parallel to water depth (Fig. 6.1). A very general bathymetric trend is the dominance of dwelling structures in shallow water, the abundance of feeding, locomotion, and resting traces at intermediate depths and the dominance of farming and grazing traces in food-starved deep-water sediments (Ekdale, 1985).

A different picture emerges from the study of microborings produced by microendolithic algae, bacteria, and fungi. Because many microborers are photosynthetic, they reflect adaptations to different light intensities and wave frequencies and, therefore, display a direct relationship with water depth (Glaub, 1994, 2004; Vogel *et al.*, 1995, 1999, 2000; Glaub *et al.*, 2001, 2002, 2007; Perry and MacDonald, 2002; Vogel and Marincovich, 2004; Glaub and Vogel, 2004). Microborings can be used to differentiate euphotic, dysphotic, and aphotic zones, and index ichnocoenoses have been defined (Glaub, 1994; Glaub *et al.*, 2001, 2002) (Fig. 6.12). Although this scheme was originally based on bathymetric studies in modern environments and Mesozoic–Cenozoic successions, further studies demonstrated that it is applicable in the Paleozoic (Glaub and Vogel, 2004). The lower limit of the euphotic zone is located where the surface light is reduced to approximately 1%. This zone includes the supratidal, intertidal, and the well-illuminated subtidal (Liebau, 1984). The euphotic zone is essentially dominated by photoautotrophic endoliths, such as cyanobacteria, green algae, and red algae.

Analysis of microbioerosion allows us in turn to subdivide the euphotic zone into four subzones, three for the shallow euphotic region and one for the deep euphotic region (Glaub *et al.*, 2001, 2002; Glaub, 2004). Shallow euphotic subzone I is more or less equivalent to the supratidal zone, and is dominated by microborings of cyanobacteria that protect themselves from sunburn damage by sheath pigmentation. No index ichnocoenose has been defined from this zone because no ancient counterparts are known. Shallow euphotic subzone II is coincident with the intertidal zone, and is dominated by cyanobacterial microborings oriented perpendicular to the substrate. The index ichnocoenose of this subzone is the *Fasciculus acinosus*/*Fasciculus dactylus* ichnocoenose. The changing level in hydrodynamic energy is also a significant controlling factor in the intertidal zone. Shallow euphotic subzone III includes the well-illuminated portion of the subtidal area, and is dominated by microborings of cyanobacteria, red algae, and green algae that commonly display perpendicular orientations but may include parallel components, particularly with increasing water depth. The index ichnocoenose of this subzone is the *Fasciculus dactylus*/*Palaeoconchocelis starmachii* ichnocoenose. The deep euphotic subzone represents the less illuminated region of the euphotic zone, and is dominated by red and green algal microborings that are oriented parallel to the substrate. The index ichnocoenose of this subzone is the *Palaeoconchocelis starmachii*/*Reticulina elegans* ichnocoenose.

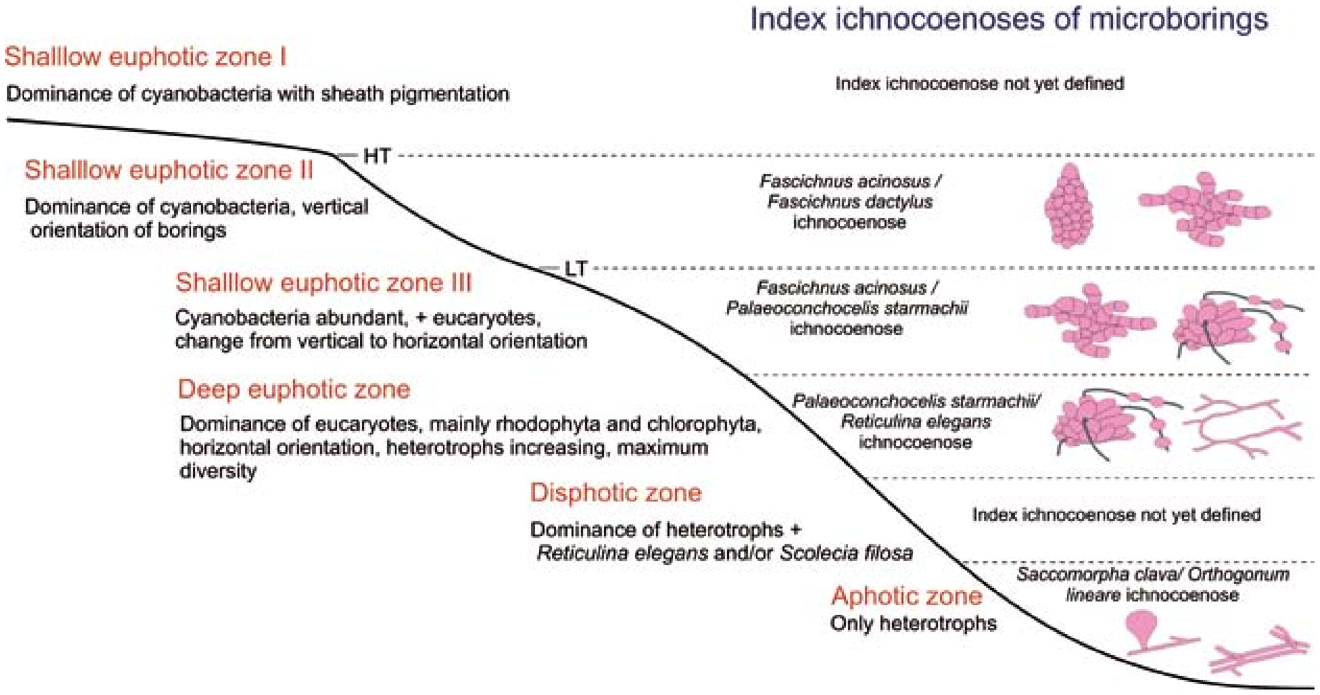


Figure 6.12 Bathymetric zonation based on microborings. HT = High tide. LT = Low tide. Vertical scale greatly exaggerated. Modified from Glaub (2004).

The dysphotic zone extends from the 1% level to approximately 0.01% or 0.001% of surface light. This zone is dominated by chemoheterotrophic endoliths, mostly fungi. However, two traces of photoautotrophs (*Scolecia filosa* and *Reticulina elegans*) are present because their producers can cope with less than 1% of surface light. No index ichnocoenose has been defined from this zone. The aphotic zone is characterized by the lack of light and, therefore, includes heterotrophs only. The index ichnocoenose of this zone is the *Saccomorpha clavata*/*Orthogonum lineare* ichnocoenose.

The bathymetric distribution of macroborings is less well understood. Bromley and D'Alessandro (1990) analyzed the distribution of borings in shallow- and deep-marine coral materials from the Pliocene to the Recent in the Mediterranean Sea. They noted that ichnodiversity is higher in shallow water than in deep water. The sponge boring *Entobia* was dominant in both shallow- and deep-water materials, but the latter are typified by less distinctive forms and greater morphological variability. This may result from areally restricted substrates that lead to constrained development of the boring system with more mature chambers crowded into the corners of the substrate. While the abundance of other borings decreases in deep water, that of sponge borings increases dramatically, with coral substrates locally reduced to a filigree. However, the underlying control in degree of bioerosion is certainly not depth per se, but low rates of sedimentation in deep-sea settings.

Comparative analysis of shallow- to deep-water macrobioerosion in the Pleistocene carbonates of Rhodes also indicates higher ichnodiversity in shallow-marine settings (Titschack *et al.*, 2005). The shallowest-water facies is dominated by the bivalve boring *Gastrochaenolites torpedo* and the sponge boring *Entobia gonioides*. With increasing water depth, *Gastrochaenolites* disappears and the association is dominated by several ichnospecies of *Entobia*. The deepest-water ichnofabrics are dominated by the simple borings of polychaetes (*Trypanites*). However, relatively diverse macroboring associations were documented in the deep-water coral *Lophelia* in the Pleistocene of Rhodes (Bromley, 2005). Rasping traces that are dominant in shallow-water corals, such as *Radulichnus* (produced by mollusks) or *Gnathichnus pentax* (produced by regular echinoids), are patchily distributed or absent, supporting an aphotic environment for the *Lophelia* bioerosion association. Associated microborings belong to the *Saccomorpha clavata*/*Orthogonum lineare* ichnocoenose, further supporting aphotic settings.

6.1.8 WATER TURBIDITY

The role of water turbidity is beginning to be recognized as an important controlling factor for benthic faunas (e.g. Gingras *et al.*, 1998; MacEachern *et al.*, 2005). In coastal areas affected by fluvial discharge, buoyant mud plumes extend in a seaward direction particularly under hypopycnal conditions (Bates, 1953; Wright, 1977; Kineke *et al.*, 1996). Because high suspended loads of fine-grained material close to the sediment–water interface clog the filter-feeding apparatus of suspension feeders, this trophic type tends to be inhibited under such conditions (Perkins, 1974). As a result, there is an impoverishment or direct suppression of the *Skolithos* ichnofacies, and associations are dominated by deposit-feeding traces (Gingras *et al.*, 1998; MacEachern *et al.*, 2005; Buatois *et al.*, 2008). However, primary production can be severely affected in settings characterized by high water turbidity, resulting in a general impoverishment of both suspension and deposit feeders (Leithold and Dean, 1998). Therefore, on occasions, water turbidity may be conducive to an overall reduction in ichnodiversity and burrow density (MacEachern *et al.*, 2005).

Estuaries are commonly turbid due to the amounts of silt and clay in the water, particularly in the low-energy estuary basin (Vernberg, 1983). Turbidity at the sediment surface typically excludes suspension feeders, which are sensitive to clogging (Rhoads and Young, 1970). Estuary-basin deposits, therefore, tend to be dominated by trace fossils of deposit feeders (Buatois *et al.*, 2002b). In particular, turbidity may be extreme in tide-dominated estuaries, with nonbioturbated mudstone typically characterizing the turbidity-maximum zone (Bechtel *et al.*, 1994; MacEachern and Gingras, 2007; Lettley *et al.*, 2007b).

Water turbidity also plays an important control in microboring distribution (Perry and MacDonald, 2002). The depth-related microboring zonation (see Section 6.1.7) may display some departure from the typical model depending on water turbidity. These authors noted that in turbid waters the euphotic zone is extremely compressed, and elements of the dysphotic zone (mostly fungi microborings) may occur at only 30 m depth.

6.1.9 CLIMATE

The application of ichnology in paleoclimatology is still in its infancy. The first studies were conducted in paleosols, using insect trace fossils (e.g. Genise and Bown, 1994a; Genise *et al.*, 2000). These authors noted that insects are extremely sensitive to local ecological constraints, and emphasized the importance of microclimate as an environmental limiting factor. Microclimate includes different aspects, such as temperature, radiation, humidity, and wind speed near the ground (Unwin and Corbet, 1991). In turn microclimate depends on local vegetation, and these two factors are ultimately controlled by climate. Therefore, insect trace fossils are powerful indicators of climate conditions at the time of nest formation. In fact, archetypal and potential paleosol ichnofacies are indicators of paleoclimatic conditions rather than depositional environments (Genise *et al.*, 2000, 2010a). In particular, insect nests (calichnia) contain larvae that are provisioned with organic matter by the adults; both larvae and provisions are sensitive to microclimatic conditions, such as moisture and soil temperature (Michener, 1979; Grassé, 1984; Genise, 1999; Genise *et al.*, 2004b). Excessive moisture inside cells results in the decay of provisions, while insufficient moisture results in the dehydration of larvae (Genise *et al.*, 2000). More recently, Hasiotis *et al.* (2007) addressed the relationship between tiering and availability of water, suggesting that tiers become progressively shallower as a response to increasing humidity.

A close relationship exists between Scarabaeinae dung beetles (producers of *Coprinisphaera*, *Fontanai*, and *Monesichnus*) and herbaceous communities, because these beetles provision their nests with excrement of vertebrate herbivores (Halffter and Edmonds, 1982; Genise *et al.*, 2000). The nests of most solitary bees (e.g. *Celliforma*, *Palmiraichnus*) are produced on bare, well-drained, light soil exposed to sun rather than humid tropical areas (Batra, 1984; Michener, 1979; Genise and Bown, 1994a). Clustered bee cells, such as *Corimbatichnus*, *Uruguay*, and *Palmiraichnus*, most likely display similar preferences (Genise and Verde, 2000). This distribution is related to the fact that the larval food is commonly exposed to fungal attack or hygroscopic liquefaction in humid environments (Michener, 1979; Roubik, 1989; Genise *et al.*, 2000, 2004b). Bee nesting in poorly drained soils is, therefore, very rare (e.g. Roubik and Michener, 1980). Ants (producers of *Attaichnus*) also favor bare soil, although they may move eggs and larvae from one site to another to avoid submersion during flooding (Hölldobler and Wilson, 1990; Genise *et al.*, 2004b). Ecological preferences of dung beetles, bees, and, to a lesser extent, ants explain the association of the *Coprinisphaera* ichnofacies with herbaceous communities that range from dry and cold to relatively humid and warm climates. The climatic affinities of coleopteran pupal chambers (e.g. *Teisseirei*, *Rebuffoichnus*, *Fictovichnus*) are less well understood, although they tend to be associated with bee nests (e.g. Genise *et al.*, 2002).

In contrast, termite nests (e.g. *Termitichnus*, *Vondrichnus*, *Fleaglellius*, *Tacuruichnus*) tend to be more abundant in more humid environments, including waterlogged soils (Grassé, 1984). Paleosols dominated by termite nests commonly developed under higher-moisture conditions and more frequent flooding events than those dominated by dung beetle and bee nests (Genise and Bown, 1994b; Genise *et al.*, 2000, 2004b). Genise (1997) used the presence of *Tacuruichnus* (a nest very similar to that of the extant species *Cornitermes cumulans*) to infer warm and wet conditions in Pliocene deposits. In some cases, termite nests may be associated with dung beetle nests (e.g. Sands, 1987). However, these termite nests are assigned to the Macrotermitinae, whose distribution ranges from tropical rain forest to semiarid steppes. In the Miocene Pinturas and Santa Cruz formations of Patagonia, the lower paleosols contain abundant termite nests (*Syntermesichnus*), while the upper ones display bee and dung beetle nests (*Celliforma*, *Palmiraichnus*, and *Coprinisphaera*), reflecting increasingly arid conditions and deforestation after ash fall events (Bown and Laza, 1990; Genise and Bown, 1994a). Climatic fluctuations characterized by the presence of relatively wet periods within more permanent semiarid conditions have been inferred from the presence of bee nests and coleopteran pupal nests in Quaternary paleosols of the Canary Islands (Alonso-Zarza and Silva, 2002; Genise and Edwards, 2003).

Tidal-flat environments commonly exhibit rapid changes in temperature related to periodic subaerial exposure that have strong impact on animal–sediment interactions (Mángano *et al.*, 2002a). In addition, tidal-flat faunas experience important latitudinal changes in connection to temperature gradients (e.g. Green and Hobson, 1970; Yeo and Risk, 1981; Aitken *et al.*, 1988). Upper-intertidal zones in tropical settings are characterized by very high temperatures, long durations of subaerial exposure, and abnormal salinities, representing an extremely inhospitable habitat for marine organisms. As a result, the highest density of biogenic structures in tropical tidal flats is in the lower intertidal zone (Terwindt, 1988). In particular, arid climates cause more extreme upper-intertidal conditions and correspondingly impoverished communities than humid climates. In general, benthic organisms tend to be less specialized in their diet, often being trophic generalists. On the other hand, high-latitude tidal flats commonly exhibit dense concentrations of biogenic structures in the upper-intertidal zone (e.g. Yeo and Risk, 1981). As documented by Reise (1985), bathymetric displacement of certain species along latitudinal gradients is common. For example, Green and Hobson (1970) noted that the bivalve *Gemma gemma* lives in intertidal areas in northern North America and in subtidal areas in the south to avoid high temperatures on tidal flats. Aitken *et al.* (1988) documented a dominance of vertical domiciles of bivalves and polychaetes in modern subarctic tidal flats. These authors compared subarctic and temperate tidal flats in terms of biogenic structures and noted that some species (e.g. *Corophium volutator*) are abundant in temperate tidal flats but are absent from subarctic intertidal areas. Tidal flats that are exposed to regular winter freeze contain lower ichnodiversity than their warmer counterparts (Gingras *et al.*, 2006). As noted by Mángano *et al.* (2002a), application of modern observations to the stratigraphic record is complicated. However, these authors extensively documented a Carboniferous equatorial tidal-flat ichnofauna that displays the highest density and diversity of biogenic structures in lower-intertidal deposits close to low tide. Therefore, they concluded that high temperatures and increased desiccation in the upper-intertidal zone were probably major limiting factors.

The topic of climatic controls on shallow-marine ichnofaunas has been explored also by Goldring *et al.* (2004). These authors proposed the existence of three climatic zones: (1) tropical and subtropical with *Ophiomorpha*, echinoid trace fossils as well as other ichnotaxa; (2) temperate with echinoid trace fossils and *Thalassinoides*; and (3) arctic with only molluscan and worm trace fossils. Partial support for this model comes from observations in modern environments by Gingras *et al.* (2006), although they extended the dominance of mollusk and worm burrows to the temperate zone. Burrowing bivalves and worms tend to occur in bare intertidal deposits of temperate to cold climates, while crabs mostly burrow in vegetated intertidal sediments of tropical to subtropical settings (Eisma, 1998). However, both *Ophiomorpha* and *Scolicia* are abundant in Miocene mid-latitude shallow-marine settings under temperate to cold climates, suggesting an anomaly in the proposed pattern (Buatois *et al.*, 2003; Carmona *et al.*, 2008).

In particular, the ichnogenus *Macaronichnus* tends to occupy cold to temperate zones (Gingras *et al.*, 2006; Pemberton *et al.*, 2006). Interestingly, *Macaronichnus* has been recently documented in Miocene tropical foreshore deposits, but associated

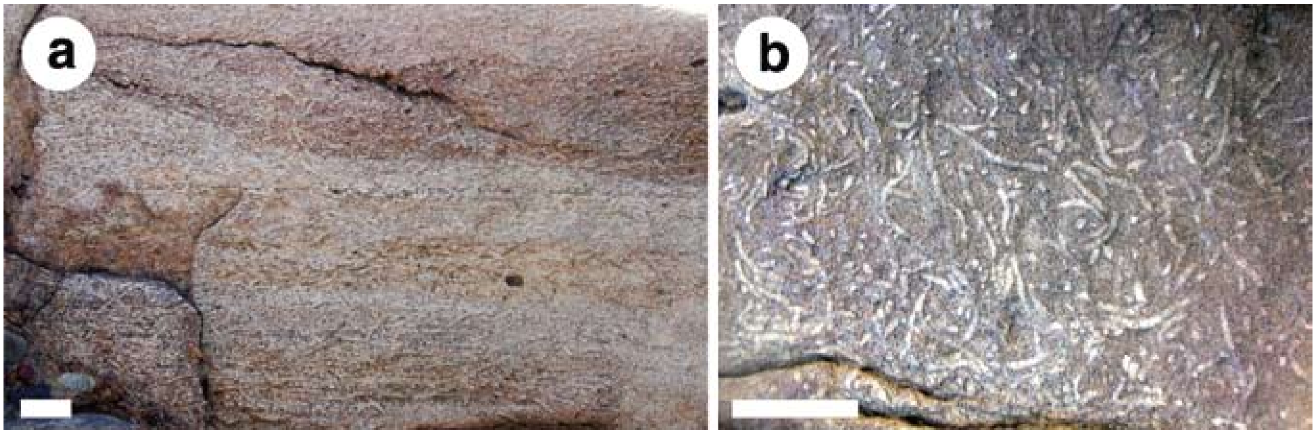


Figure 6.13 *Macaronichnus* in tropical settings, but linked to upwelling conditions, Upper Miocene, Urumaco Formation, Urumaco, northwest Venezuela. See Quiroz *et al.* (2010). (a) Foreshore deposits with *Macaronichnus segregatis* (cross-section). (b) Close-up of specimens showing light colored sand fill that contrasts with the dark colored surrounding mantle (bedding-plane view). Scale bars are 4 cm.

with upwelling conditions (Quiroz *et al.*, 2010) (Fig. 6.13a–b). Preliminary data also suggest an increase in trace-fossil size towards high latitudes (Gingras *et al.*, 2006; Pemberton *et al.*, 2006). In addition, deep-infaunal burrowers tend to be more abundant in mid and high latitudes (Aberhan *et al.*, 2006; Bush *et al.*, 2007; Carmona *et al.*, 2008).

It has long been suggested that the evolution of deep-sea benthic biotas has been influenced by water temperature (Wolf, 1960). Comparative analysis of trace-fossil diversity in the deep sea through the Phanerozoic (Seilacher, 1974; Uchman, 2004a) seems to support this view (see Section 14.2.2). Uchman (2004a) noted that the lowest ichnodiversities tend to occur in times of cold deep-seawaters, such as the late Paleozoic and the Oligocene. The role of the Late Ordovician glaciation is still unclear, but some authors have suggested that there is an associated drop in ichnodiversity (McCann, 1990).

A different dataset comes from carbonate ichnofaunas. Most ichnological studies on carbonates focus on tropical environments, particularly in the Bahamas, Grand Cayman, and Florida (e.g. Pemberton and Jones, 1988; Curran and White, 1991, 2001; Curran, 1992, 1994, 2007). Terrestrial suites in tropical settings include relatively diverse insect ichnofaunas, mostly produced by sphecid wasps and halictid bees, and pervasive root traces as well (Curran and White, 2001; Curran, 2007). Intertidal and subtidal tropical carbonates are dominated by crustacean burrows, including *Ophiomorpha* (Curran, 1994, 2007). However, *Ophiomorpha* is apparently rare in temperate carbonates. Large specimens of *Conichnus* seem to be common in both tropical and temperate carbonates (e.g. Curran and White, 1997).

Bioerosion also displays some specific patterns in response to climate and latitude (Johnson, 2006). While most studies concentrate in tropical and subtropical environments (e.g. Bromley, 1978; Bromley and D'Alessandro, 1983; Bromley and Asgaard, 1993a, b; Vogel *et al.*, 2000; Glaub *et al.*, 2001; Perry and MacDonald, 2002), there is a growing dataset on cold-temperate and polar regions (e.g. Akpan, 1986; Akpan and Farrow, 1984; Glaub *et al.*, 2002; Vogel and Marincovich, 2004; Wisshak *et al.*, 2005; Wisshak, 2006). Some studies (e.g. Glaub *et al.*, 2002; Vogel and Marincovich, 2004) have pointed to overall similarities between microbioerosion in high and low latitudes, indicating a widespread applicability of schemes originally established for tropical and subtropical areas. However, some differences were noted by Wisshak *et al.* (2005) and Wisshak (2006) in their study of bioerosion along the Swedish coast. The index ichnotaxa of the euphotic zone were either rare or absent, and this zone was very compressed in comparison to low latitudes. In fact, the boundary between the euphotic and dysphotic zones occurs at only 15 m. Some ichnotaxa (e.g. *Flagrichnus baiulus*) have been suggested to occur only in non-tropical settings (Wisshak and Porter, 2006).

6.1.10 WATER TABLE

The position of the water table and the degree of substrate humidity is one of the most fundamental controls in trace-fossil formation and preservation in continental environments (Gierlowski-Kordesch, 1991; Hasiotis *et al.*, 1993a; Hasiotis and Honey, 2000; Buatois and Mángano, 2002, 2004a; Genise *et al.*, 2004b). Sediment water content strongly influences the degree of substrate consolidation, which in turn controls trace-fossil morphology and preservation (Buatois and Mángano, 2002, 2004a). In fact, the position of the water table is essential to understand distribution of the *Mermia* and *Scoyenia* ichnofacies. The *Mermia* ichnofacies is formed in subaqueous freshwater environments and, therefore, characterizes a high water table that results in the formation of water bodies, such as lakes and ponds (see Section 4.4.2). In contrast, the *Scoyenia* ichnofacies is formed in transitional settings, such as lake-margin environments (see Section 4.4.1), and corresponds to areas of relatively low water table. This is particularly so in the case of the firmground suite of the *Scoyenia* ichnofacies, which is associated with subaerial desiccated substrates. Links between the architecture of crayfish burrows (*Camborygma*), and the position of the water table have been established (Hobbs, 1981; Hasiotis

Figure 6.14 Roots of a modern quiver tree in arid environment, Gannabos Farm, South Africa. Note horizontally extended root systems to follow the water table generated close to the sediment surface after sporadic torrential rain.

and Mitchell, 1993; Hasiotis *et al*., 1993a, 1998; Hasiotis and Honey, 2000). Complex architectures with many branches and chambers are constructed by primary burrowers in areas with a high water table, while deep simple burrows are dominant in areas with a low and/or highly fluctuating water table.

Genise *et al*. (2004b) reviewed the relationships between different insect nests and the position of the water table in paleosols. Bee and dung beetle nests are commonly associated with low water tables. Hasiotis *et al*. (1993b) explored the links between a fluctuating water table and the scarabeid nest *Scaphichnium* in hydromorphic paleosols developed in a distal floodplain. They noted that the appearance of *Scaphichnium* was coincident with a decrease in gray root traces and meniscate traces, suggesting that the nest was emplaced during periods of low water table. The significance of coleopteran pupal chambers is unclear, but they are definitely constructed in subaerial substrates above the water table (Genise *et al*., 2002). Ant and termite nests are constructed in well-drained to seasonally flooded soils (Genise *et al*., 2004b). In the case of seasonally flooded soils, termites use a series of devices, such as chimneys or special walls, which allow them to deal with a higher water table (Genise *et al*., 2004b). Finally, earthworm burrows (e.g. *Edaphichnium*, *Castrichnus*) commonly occur in moist substrates, such as gleyed paleosols (Genise *et al*., 2004b; Verde *et al*., 2007).

Root traces are particularly useful to evaluate position of the water table (Sarjeant, 1975; Cohen, 1982; Bockelie, 1994; Kraus and Hasiotis, 2006). Roots tend to be shallow and horizontally extended in poorly drained soils with a high water table as a response to lack of aeration (Sarjeant, 1975; Cohen, 1982). These roots are typically filled with carbonaceous material and branch at distinct intervals (Bockelie, 1994). Goethite rims commonly surround root traces formed in poorly drained paleosols; some rhizoliths are preserved as tubular bodies of Fe and Mn oxides and jarosite (Kraus and Hasiotis, 2006). In contrast, environments with a low water table are characterized by penetrative, deep root traces (Cohen, 1982; Bockelie, 1994). These well-drained paleosols are characterized by calcareous rhizocretions, or elongate gray mottles surrounded by hematite rims (Kraus and Hasiotis, 2006). In arid environments affected by sporadic torrential rains, root systems can be horizontally extended to follow the rapidly generated water table close to the sediment surface (Fig. 6.14)

6.2 ROLE OF TAPHONOMY

Parallel to the detailed analysis of the limiting ecological factors, the role of taphonomic aspects should be clarified. Information derived from benthic ecology cannot be directly translated into the fossil record without a careful evaluation of the fossilization barrier (Seilacher, 1967a; Bromley, 1990, 1996), a taphonomic filter that separates the plethora of biogenic structures produced from the few that are preserved in the fossil record (see Section 5.2.2). In addition, different diagenetic processes provide a final overprint that may enhance ichnofossil visibility (see Section 1.3.2).

Savrda (2007b) noted that two factors are involved in trace-fossil taphonomy: completeness of the preserved record of biogenic activity or ichnological fidelity, and degree of ichnofossil preservation or trace-fossil visibility. He noted that these two factors may be independent of one another. For example, some ichnofabrics may have high fidelity, but some or all trace fossils may be difficult to discern, while other ichnofabrics may have low fidelity, but discrete ichnotaxa may be well expressed.

The concept of fossil-lagerstätten has been used extensively for body fossils and refers to "any rock containing fossils that are sufficiently well preserved and/or abundant to warrant exploitation" (Seilacher *et al.*, 1985). Some studies attempt to apply this concept to the ichnological record, stressing the importance of taphonomic aspects in the final shaping of ichnofaunas (Bromley and Asgaard, 1991; Savrda *et al.*, 1993; Savrda and King, 1993; Savrda and Ozalas, 1993; Mángano and Buatois, 1995a; Fornós *et al.*, 2002; Savrda, 2007b). This has resulted in the adaptation of the classification framework of body-fossil lagerstätten of Seilacher *et al.* (1985) to the analysis of ichnofaunas (Mángano and Buatois, 1995a; Savrda, 2007b). Seilacher *et al.* (1985) distinguished concentration and conservation deposits, and divided the latter into obrution and stagnation deposits, these being the categories that can be easily translated into ichnofossil-lagerstätten.

Concentration lagerstätten are characterized by an abundance of fossils that results either from transport, commonly in connection with episodic processes, or from condensation due to sediment starvation. Both situations are detected in connection with concentrations of wood fragments with *Teredolites*. Although transport is exceedingly rare in the case of trace fossils, secondary displacement is common with *Teredolites* logs, and concentration lagerstätten commonly occur in transgressive lags (Savrda *et al.*, 1993) (see Box 12.1). In addition, dense occurrences of logs with *Teredolites* result from the combination of increased rate of wood introduction during transgression and concentration of logs that have drifted via sediment starvation, delineating maximum flooding surfaces (Savrda and King, 1993; Savrda *et al.*, 2005). Other examples of condensation ichnofossil-lagerstätten occur in omission surfaces developed in carbonates. In hardgrounds, very low sedimentation rates and early cementation result in intensely bioeroded surfaces that record ecological succession and changes in the degree of substrate consolidation (Mángano and Buatois, 1995a).

Conservation lagerstätten involve exceptional preservation. Obrution deposits result from the episodic smothering of the sea floor that strongly affects benthic biotas (Seilacher *et al.*, 1985). Obrution ichnofossil-lagerstätten are relatively common. The best example is represented by the delicate preservation of graphoglyptids as predepositional trace fossils on the base of thin-bedded turbidites (e.g. Seilacher, 1962; Uchman, 2007). In continental settings, a similar situation is represented by delicate superficial trails preserved in underflow-current lacustrine deposits (Buatois and Mángano, 1993a).

Stagnation deposits are formed under anoxic conditions that favor delicate preservation of body fossils (Seilacher *et al.*, 1985). Because anoxia prevents the establishment of macrobenthic organisms, the emplacement of biogenic structures is commonly restricted (see Section 6.1.3). However, meiofaunal subsuperficial trails have been recorded in Cambrian conservat lagerstätten. Tiny micrometric to millimetric trails (e.g. *Helminthoidichnites*, *Helminthopsis*, *Cochlichnus*) are directly associated with soft-bodied organisms in the Burgess Shale (Mángano and Caron, 2008; Caron *et al.*, 2010; Mángano, 2010), Sirius Passet (Williams *et al.*, 1996), Chengjiang (Y. Zhang *et al.*, 2006), and Kaili (X. Wang *et al.*, 2009; Lin *et al.*, 2010) biotas. Interestingly, non-mineralized carapaces of *Tuzoia* and other organisms serve as sites of preferential preservation of biogenic structures. Dying trackways (mortichnia) formed under anoxic conditions and associated with the body fossils of their producers have been documented in stagnation fossil lagerstätten of Jurassic lithographic limestone (see Section 6.1.3).

An ichnofossil-lagerstätten analogous to stagnation deposits is represented by a pelletal mixed layer preserved as a result of a deoxygenation event (Savrda and Ozalas, 1993) (see Section 5.2.2). Preservation of mixed-layer biogenic structures is commonly inhibited by the interplay of physical and biological processes, including bioturbation by deep-tier infaunal organisms, and low sediment-shear stress. In the case analyzed by Savrda and Ozalas (1993), deoxygenation led to the cessation of bioturbation and, in the absence of physical and biogenic reworking, mixed-layer traces became part of the historical layer.

Ideally, taphonomic overprints should be analyzed in the context of depositional settings. In an attempt to evaluate the interplay between depositional and taphonomic processes in specific sedimentary environments, the concept of taphonomic pathways has been applied to ichnology (Buatois and Mángano, 2004a, 2007; Desjardins *et al.*, 2010a). Analysis of trace-fossil preservational styles in continental deposits suggests that ichnofaunas result from various taphonomic pathways that reflect depositional conditions (subaqueous versus subaerial) and time spans between flooding events (Buatois *et al.*, 1997b, 2007a; Zhang *et al.*, 1998; Buatois and Mángano, 2002, 2004a, 2007; Minter *et al.*, 2007b). Additionally, taphonomic pathways help to explain the role of substrate and rapid environmental fluctuations as main controlling factors in ichnofacies development and replacement (Buatois and Mángano, 2002, 2004a, 2007). In fluvial systems, a variety of taphonomic pathways results from channel abandonment, overbank deposition, and establishment of ponded areas that may desiccate or be filled by overbank vertical accretion without experiencing desiccation (see Section 10.2). In lakes, taphonomic pathways commonly reflect shoreline fluctuations, and associated changes in substrate consolidation (see Section 10.3). Ichnofaunas formed in subaerially exposed overbank and lake-margin deposits are commonly represented by palimpsest surfaces recording taphonomic pathways due to progressive desiccation. The concept of taphonomic pathways has been applied also to the study of subtidal sand-dune complex dynamics (Desjardins *et al.*, 2010a) and storm-dominated shallow-marine (see Section 7.1) and deep-marine (see Section 9.2.1) enviroments.

6.3 ICHNODIVERSITY AND ICHNODISPARITY

In trace-fossil studies, ichnodiversity simply refers to the number of ichnotaxa present. Most studies use ichnodiversity at ichnogenus rather than at ichnospecies level because trace-fossil taxonomy is more firmly established at the ichnogenus level. As noted by Ekdale (1985), by no means should one establish equivalence between species diversity and ichnodiversity. Because ichnodiversity essentially reflects the different interactions of organisms and the substrate, it depends on factors that are different from those that determine species diversity or, in the case of paleontological studies, body-fossil diversity (Bromley, 1990, 1996). Also, while some of the taphonomic filters that operate in trace-fossil preservation are shared by body fossils, trace-fossil taphonomy has its own peculiarities (see Sections 5.2.2 and 6.2).

However, if used with caution, ichnodiversity may provide some information on general trends in species richness along depositional environments and through geological time (Ekdale, 1988; Buatois *et al.*, 1997b; Mángano and Buatois, 2004b). Low ichnodiversity may be associated with some stress factors (e.g. brackish water, oxygen depletion, high energy). In contrast, high ichnodiversity is commonly linked to stable and predictable environmental conditions. Some ichnofacies as a whole illustrates this principle. While the poorly diverse *Skolithos* ichnofacies develops under unstable conditions (e.g. high energy, fluctuating rates of deposition and erosion), the highly diverse *Nereites* ichnofacies corresponds to the more stable conditions of the deep sea. Accordingly, trends in ichnodiversity may follow the hypothesis put forward by Sanders (1968) for species diversity that states that high stability or predictability of the environment is conducive to high species diversity. However, low ichnodiversity may, in some cases, be a simple taphonomic artifact resulting from intense bioturbation of deep-tier organisms (see Section 5.2.2).

In ecological and macroevolutionary studies, global diversity has been divided in three components: alpha, beta, and gamma (Whittaker, 1972; Sepkoski, 1988). Alpha diversity measures the richness of taxa at a single locality or in a particular community; beta diversity refers to taxonomic differentiation between sites or communities; and gamma diversity records the taxonomic differentiation between regions. Alpha and beta diversity reflect species differentiation of niche and habitat, respectively, while gamma diversity reflects provinciality (Whittaker, 1972; Sepkoski, 1988). Ichnological studies oriented towards macroevolution (see Chapter 14) deal mostly with global diversity, essentially changes in ichnodiversity during certain times of Earth history (e.g. Crimes, 1992, 1994; Orr, 2001; Mángano and Droser, 2004), or in certain ecosystems through geological time (e.g. Buatois *et al.*, 1998c, 2005). However, the three components of global diversity are not commonly discriminated in ichnological studies and, as a result, the term ichnodiversity has been used in more than one sense. This is illustrated by studies dealing with the colonization of deep-marine ecosystems (e.g. Orr, 1996). Seilacher (1974) recorded the ichnodiversity of individual deep-marine trace-fossil associations in a use analogous to that of alpha diversity (Sepkoski, 1988), while Crimes and Crossley (1991) recorded diversity as the total number of ichnotaxa for that same time interval (global ichnodiversity). In that case, alpha ichnodiversity provides information about the structure of individual deep-marine communities, while global ichnodiversity gives evidence of large-scale diversification patterns in the deep sea (Buatois *et al.*, 2001).

An analog to alpha diversity is the most commonly used in ichnological studies dealing with paleoenvironmental characterization, in which ichnodiversity is assessed for individual facies or environmental zones. In turn, changes in alpha ichnodiversity throughout a succession represented by different facies or at different localities are evaluated to detect environmental changes. Conversely, beta ichnodiversity is commonly overlooked although it may provide information about the degree of similarity between ichnofaunas formed along an environmental gradient. For example, beta ichnodiversity could be useful to assess the degree of differentiation between nearshore and offshore trace-fossil associations, commonly represented by the *Skolithos* and *Cruziana* ichnofacies. Application of the notion of gamma diversity to ichnological studies is less evident because few studies deal with paleobiogeographic implications (e.g. Seilacher, 1992a, 1994; Orr, 1996; Systra and Jensen, 2006). However, gamma ichnodiversity may provide information to detect trace-fossil provincialism.

While diversity reflects taxonomic richness, paleontologists have also introduced the concept of morphological diversity or disparity (Gould, 1989, 1991; Foote, 1997; Erwin, 2007). This concept refers to variability in anatomical design, and has been used in current debates on the evolutionary significance of Cambrian faunas (e.g. Gould, 1989, 1991; Briggs and Fortey, 1989; Briggs *et al.*, 1992; Fortey *et al.*, 1996). Gould (1991) stressed the need for developing quantitative techniques to define morphospaces and map their fillings as a way of assessing disparity, a task subsequently undertook in several studies (e.g. Hickman, 1993; Foote, 1993, 1997).

The concept of disparity may be adapted by ichnology, albeit in a qualitative way. While ichnodiversity simply refers to ichnotaxonomic richness, ichnodisparity provides a measure of the variability of morphological plans in biogenic structures (or trace-fossil bauplan *sensu* Bromley, 1990, 1996). The fact that ichnodiversity and ichnodisparity are not necessarily concordant can be illustrated with a series of examples. The *Mermia* ichnofacies is relatively diverse, but ichnodisparity is remarkably low. Very minor behavioral variants result in relatively high ichnodiversity, but the different ichnotaxa mostly belong to a few basic morphological plans represented by simple grazing trails. On the other hand, the *Cruziana* ichnofacies is characterized by both high ichnodiversity and ichnodisparity because it is taxonomically rich and, at the same time, contains a wide variety of trace-fossil bauplans (e.g. branching feeding systems, galleries, spreiten burrows, concentrically laminated structures, bilobate trails). A special situation is recorded by the *Nereites* ichnofacies. The ichnodisparity is relatively high and represented by different basic designs (e.g. networks, meandering systems, branching meandering systems, radial structures).

However, the most diagnostic feature of this ichnofacies is the remarkably high ichnodiversity, which results from small but multiple variations of these basic patterns (e.g. Seilacher, 1977a). Future work on this topic will be essential to attain more refined definitions of ichnodisparity, if possible, including quantitative techniques.

6.4 POPULATION STRATEGIES

The subdivision between r- and K-selection was introduced by MacArthur and Wilson (1967) to explain two different types of natural selection. Subsequently Pianka (1970) explored the concept in further detail, and noted that both types represent, in fact, end members of an r–K continuum. In particular, r-selection characterizes colonization in an ecological vacuum under little competition, typically following an environmental disturbance. It favors rapid reproductive and growth rates, small body size, short lives, wide environmental range, generalized trophic habits, high density of individuals, and low diversity of species. K-selection characterizes stable, specialized populations at equilibrium that have developed due to keen competition. Organisms are slow to colonize a new habitat, but are adaptively superior in the long term. It favors slow reproductive and growth rates, larger body size, long lives, narrow environmental range, specialized trophic habits, low density of individuals, and high diversity of species.

These concepts on population strategies have been successfully adapted to ichnology by distinguishing r-selected ichnotaxa (opportunistic) and K-selected ichnotaxa (equilibrium) (Miller and Johnson, 1981; Ekdale, 1985, 1988). Bromley (1990, 1996) further discussed the application of these concepts in ichnology, and suggested replacing equilibrium by climax trace fossils to avoid confusion with the ethological category equilibrium traces or equilibrichnia. Opportunistic ichnofaunas commonly display low ichnodiversity, high density of trace fossils, simple morphologies that reflect poorly specialized feeding strategies, and production over a short period of time (Ekdale, 1985). Examples of opportunistic ichnofaunas include monospecific suites of *Skolithos* or *Ophiomorpha* in high-energy shorelines and post-event suites in tempestites and turbidites (see Section 6.5). *Spirophyton* has been suggested as an opportunistic ichnotaxa based on its profuse occurrence in Devonian marginal-marine environments (Miller and Johnson, 1981), while *Fuersichnus* may represent another example but in continental environments (Bromley, 1990, 1996). Other ichnotaxa seem to be more controversial. *Chondrites* and *Zoophycos* have been suggested as opportunistic ichnotaxa by Ekdale (1985), but other authors tend to favor a climax strategy based on the fact that sophisticated feeding strategies seem to be involved (e.g. Bromley, 1990, 1996).

Climax ichnofaunas commonly display high ichnodiversity, low density of trace fossils, complex morphologies that reflect sophisticated feeding strategies, and production over a long period of time commonly revealed by permanent structures (Ekdale, 1985). Individual ethological categories in climax ichnofaunas are represented by numerous ichnotaxa. Graphoglyptids are a typical example of climax ichnofaunas. These complex burrow systems flourish under the stable conditions that characterize the deep sea. Graphoglyptid associations are commonly characterized by large diversity, both at ichnogeneric and ichnospecific level (Seilacher, 1977a; Uchman, 1995, 1998). Although graphoglyptids are shallow-tier structures, Bromley (1990, 1996) noted that most climax biogenic structures (e.g. *Zoophycos*) occupy deep tiers.

Bromley (1990, 1996) noticed that subtle modifications in the environment could result in the two communities (opportunistic and climax) alternating in a stratigraphic succession. Fair-weather associations of the *Cruziana* ichnofacies that alternate with storm-related suites of the *Skolithos* ichnofacies represent a classic example of alternating climax and opportunistic ichnofaunas (Pemberton and Frey, 1984a; Pemberton *et al.*, 1992c; Pemberton and MacEachern, 1997) (see Section 7.1). Interestingly, the established link between population strategies and time spans involved in bioturbation is at odds with observation from modern shallow-marine environments (Gingras *et al.*, 2008b). Measurement of burrowing rates in various suspension and deposit feeders indicates that intensely burrowed examples in the *Skolithos* ichnofacies require longer time spans than in the *Cruziana* ichnofacies!

6.5 RESIDENT AND COLONIZATION ICHNOFAUNAS

The topic of population strategies is directly linked to the notion of resident and colonization ichnofaunas. Recognition of these ichnofaunas is essential in any paleoecological analysis. Resident ichnofaunas record the activity of the indigenous benthic fauna, while colonization ichnofaunas reflect the activity of a pioneer community that becomes established after a major environmental disturbance. In fully marine settings, resident ichnofaunas are commonly highly diverse and tend to be morphologically complex, reflecting the activity of climax communities. As such, they reflect depositional conditions associated with times of stable background sedimentation. In the case of environments affected by episodic sedimentation, resident ichnofaunas are commonly preserved as pre-depositional suites at the base of event sandstones. This is typically illustrated by graphoglyptids on the soles of deep-marine turbidite sandstone (Seilacher, 1962; Leszczyński and Seilacher, 1991). Although these structures are preserved as secondary casts in the turbidite layers, they reflect the activity of the organisms that inhabit the mudstone biotope during interturbidite times (see Section 9.2). Therefore, the *Nereites* ichnofacies, in particular, the *Paleodictyon* subfacies of Seilacher (1974), represents the archetypal resident ichnofauna of the deep sea. In shallow-marine, wave-dominated environments resident ichnofaunas record the activity of fair-weather communities. Resident suites are preserved either at the base of storm deposits or in the intercalated, fair-weather finer-grained deposits (e.g. Mángano and Buatois, 2011). The *Cruziana* ichnofacies typifies the activity of the indigenous biota in this setting.

Colonization ichnofaunas are typically of low diversity and are morphologically simple, reflecting the activity of opportunistic communities. They represent the work of a pioneer community that rapidly invades an ecosystem, and is able to thrive under unstable and stressful conditions. Because colonization ichnofaunas establish immediately after a rapid depositional episode, they are commonly preserved as post-depositional suites in event sandstone. The classic example is the bathymetrically displaced suites of the *Skolithos* ichnofacies (i.e. *Arenicolites* ichnofacies of Bromley and Asgaard, 1991). This ichnofacies occurs in deeper water than that of its archetypal position, colonizing offshore tempestites (Pemberton and Frey, 1984a; Frey, 1990) or deep-marine turbidites (Leszczyński and Seilacher, 1991). Low-diversity suites of simple grazing trails may represent colonization ichnofaunas in lacustrine turbidites (Buatois and Mángano, 1995c).

6.6 ECOSYSTEM ENGINEERING

In the previous sections of this chapter, we have essentially adopted an adaptationist and externalist view of ichnology that is based on the assumption that an ichnofauna is shaped by environmental controls via their influence on the behavior of the tracemakers. However, some organisms modify, maintain, and create habitats, exerting profound changes in the ecosystems. The concept of ecosystem engineering (Jones *et al.*, 1994) helps to explain the active role that some organisms play in modifying their environment. This concept refers to the modification of the physical environment by the action of organisms that directly or indirectly modulate the availability of resources to other species (Jones *et al.*, 1994; Coleman and Williams, 2002; Berkenbusch and Rowden, 2003; Wright and Jones, 2006). Empirical studies have demonstrated that the loss of key bioturbators is critical in ecosystem performance (e.g. primary productivity) and results in a decrease in biodiversity (Lohrer *et al.*, 2004). The impact of burrowing organisms in ecosystem function has been emphasized in studies framed within the perspective of biodiversity and ecosystem function (Solan *et al.*, 2008, 2009).

In particular, Jones *et al.* (1994) classified ecosystem engineers into two types: autogenic, or those who change the environment via their own physical structures (i.e. their living and dead tissues), and allogenic, or those who do so by transforming living or non-living materials from one physical state to another via mechanical or other means. For example, by constructing dams, beavers alter the hydrology of an alluvial plain and create water bodies, representing a typical example of allogenic engineers (Naiman *et al.*, 1988). It is this latter type that has implications in ichnology, because the process of bioturbation itself physically modifies the environment in a significant way (e.g. Reise and Volkenborn, 2004; Wada *et al.*, 2004; Dewitt *et al.*, 2004). Although ichnology certainly has not emphasized this aspect of animal activity, the role of bioturbation in ecosystem engineering has long been recognized. In fact, Darwin (1881) provided one of the earliest studies on the effects of bioturbation in his classic book on soil formation through earthworm activity.

For example, infaunal burrowers influence the chemical properties of the substrate by increasing oxygen circulation through the sediment, which in turn has a positive feedback on the biomass of organisms within the sediment, the rate of organic matter decomposition, and the regeneration of nutrients, which is essential for primary productivity (Solan *et al.*, 2004a, 2008). The depth and abruptness of the redox potential discontinuity depend on the amount of oxidizable organic matter within the sediment and oxygen flow. Subsurface deposit feeders extend the oxic layer of sediment from close to the surface down to their depth of feeding in modern environments (e.g. Rhoads and Germano, 1982; Reise, 1985).

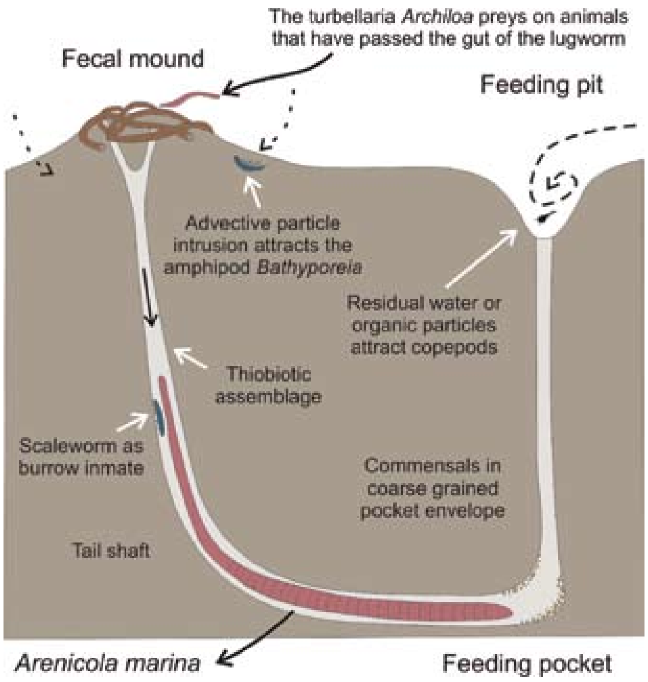


Figure 6.15 The polychaete *Arenicola marina* as an ecosystem engineer. Modified from Reise and Volkenborn (2004).

In addition, burrows may provide habitats for other organisms. Reise and Volkenborn (2004) analyzed the role of the polychaete *Arenicola marina*, which increases diversity on modern sand flats by maintaining a complex burrow in which other animals live (Fig. 6.15). At the surface, feeding pits become water ponds during low tide and serve as refuges for swimming copepods, turbelarians, and juvenile shrimps. Amphipods exploit organic particles that are flushed into the interstitial system associated with the fecal mound, and turbelarians (e.g. *Archiloa*) prey on small animals that have passed through the gut of *A. marina* and can be trapped in the fecal mound itself. Within the coarse-grained sand that envelopes the burrow, several meiofaunal organisms are established, together with small capitellid polychaete, tubificid oligochaetes, nemertines, and amphipods. Up to 173 specimens of the amphipod *Urothoe poseidonis* were counted at a single burrow. Other inhabitants (e.g. copepods, nematodes) live between the bushy gills, the tail shaft, and the sediment enveloping the tail shaft of *A. marina*.

Trace fossils may also provide evidence, albeit indirect, of amensalism (one species is unaffected, and the other one is harmed). Rhoads and Young (1970) proposed that deposit feeders may negatively affect suspension feeders to the point of making life impossible for the affected group. This phenomenon is referred to as trophic-group amensalism and has been subsequently regarded as an example of ecosystem engineering by Jones *et al*. (1994). Mobile, mostly detritus- and deposit-feeder infauna and epifauna, but also some sedentary organisms, whose feeding and defecation activities may provide abundant particles in suspension, destabilize the substrate (Rhoads and Young, 1970; Rhoads, 1974). Physical instability tends to clog the filtering structures of suspension feeders, bury newly settled suspension-feeding larvae or inhibit their settling, and prevent sessile epifauna from attaching to an unstable mud bottom (Rhoads and Young, 1970). In contrast, sedentary organisms that build mucus-lined tubes within the sediment reduce resuspension and erosion, and represent sediment stabilizers. At least in part, this is commonly expressed in the trace-fossil record by the segregation of two distinct associations broadly reflected by the *Skolithos* and *Cruziana* ichnofacies.

Based on observations on an example of the latter in Carboniferous tidal-flat deposits, Mángano *et al*. (2002a) suggested that dense concentrations of mobile detritus-feeding nuculanid bivalves (producers of *Protovirgularia* and *Lockeia*) may have acted as sediment destabilizers, precluding the development of vertical burrows of suspension feeders. The same role may have been played by the worm-like producers of dense associations of *Nereites* that altered the nature of the substrate, encapsulating within the sediment large volumes of defecation products. The intruding up-and-down movements of the *Curvolithus* tracemaker (gastropods or flat worms) may have also played a destabilizing role in some communities.

On a larger scale, bioturbation results in landscape changes. This has been clearly illustrated by ichnological studies documenting pervasive changes in intertidal landscape due to the activity of callianassids (Curran and Martin, 2003) (Box 6.2), and sturgeons (Pearson *et al*., 2007). Bioturbation can also significantly alter continental landscapes. Extensive burrows are dug and excavated by a wide variety of mammals (e.g. rabbits, mole rats, prairie dogs, pocket gophers), creating complex underground gallery systems that are expressed by a complex topography on the surface and provide opportunities for ecological interactions (Whicker and Detling, 1988; Bromley, 1990, 1996; Neal and Roper, 1991; Moloney *et al*., 1992; Whitford, 2002).

Spectacular examples of “ichnolandscapes” are provided by the activity of the South African harvester termite *Microhodotermes viator*, which produces a mounded topography referred to as heuweltjies (Afrikaans for “little hills”) (Lovegrove and Siegfried, 1989; Turner, 2004; Fey, 2010). These mounds are 1–2 m in height above ground level, and 20–30 m in diameter, becoming easily recognizable because they support plant communities that are different from those in surrounding areas (Fig. 6.17a–b). The mounds represent long-term structures that result from successive colonization events by several generations of termites (Milton and Dean, 1990). Mounds produced by the hairy-nosed wombat *Lasiorhinus latifrons* in Australia can cover several hundred square meters and can be seen on LANDSAT images (Löffler and Margules, 1980).

6.7 ORGANISM–ORGANISM INTERACTIONS

Although ichnology is defined as the science of organism–substrate interactions, trace fossils also provide information on organism–organism interactions. As discussed in the previous section, some of these effects result from the impact of ecosystem engineers (see Section 6.6). However, other effects are due to direct interactions between organisms (Abrams, 1987). This commonly occurs when another organism acts as a substrate, suggesting a symbiotic association. Symbiosis refers to relationships between two or more different species, in which at least one of them benefits from the association (Smith and Douglas, 1987; Tapanila and Ekdale, 2007). Three main types of symbiotic relationships can be established: parasitism (one species benefits to the detriment of the other), commensalism (one species benefits and the other one is not affected), and mutualism (both species benefit).

Parasitic infestation may be expressed by bioerosion structures. In order to recognize parasitism, the alternative explanation of post-mortem bioerosion should be ruled out and one should rely on detecting evidence of specific responses by the host organism (e.g. overgrowth, regeneration, or embedment).

Box 6.2 Thalassinidean shrimps as ecosystem engineers in modern tidal flats of San Salvador Island, Bahamas

A spectacular example of ichnolandscapes has been documented in tidal flats of Pigeon Creek, in the Bahamian island of San Salvador (Fig. 6.16a–b). These tidal flats are formed along the margins of a hypersaline lagoon. The tidal flat is characterized by a mounded topography, resulting mostly from the activity of the callianassid shrimp *Glypturus acanthochirus*. This shrimp produces deep, large and complex burrows, with a downward spiraling morphology, generating intense bioturbation. *Glypturus acanthochirus* is an ecosystem engineer that completely transforms the intertidal landscape. Mounds are up to 30 cm high and 1 m wide. The resulting mounds may coalesce forming larger structures that are flattened by tidal action. In addition to the activity of *Glypturus acanthochirus*, microbial mats stabilize the mounds by tending to armor their surfaces. As a result, the mounds are highly resistant to erosion and are long lived. The mounds are also colonized by the shrimp *Upogebia vasquezi* and the fiddler crab *Uca major*. The former produces U-shaped, commonly paired, burrows, while the latter constructs simple vertical burrows with a basal bulbous turnaround.

Reference: Curran and Martin (2003).

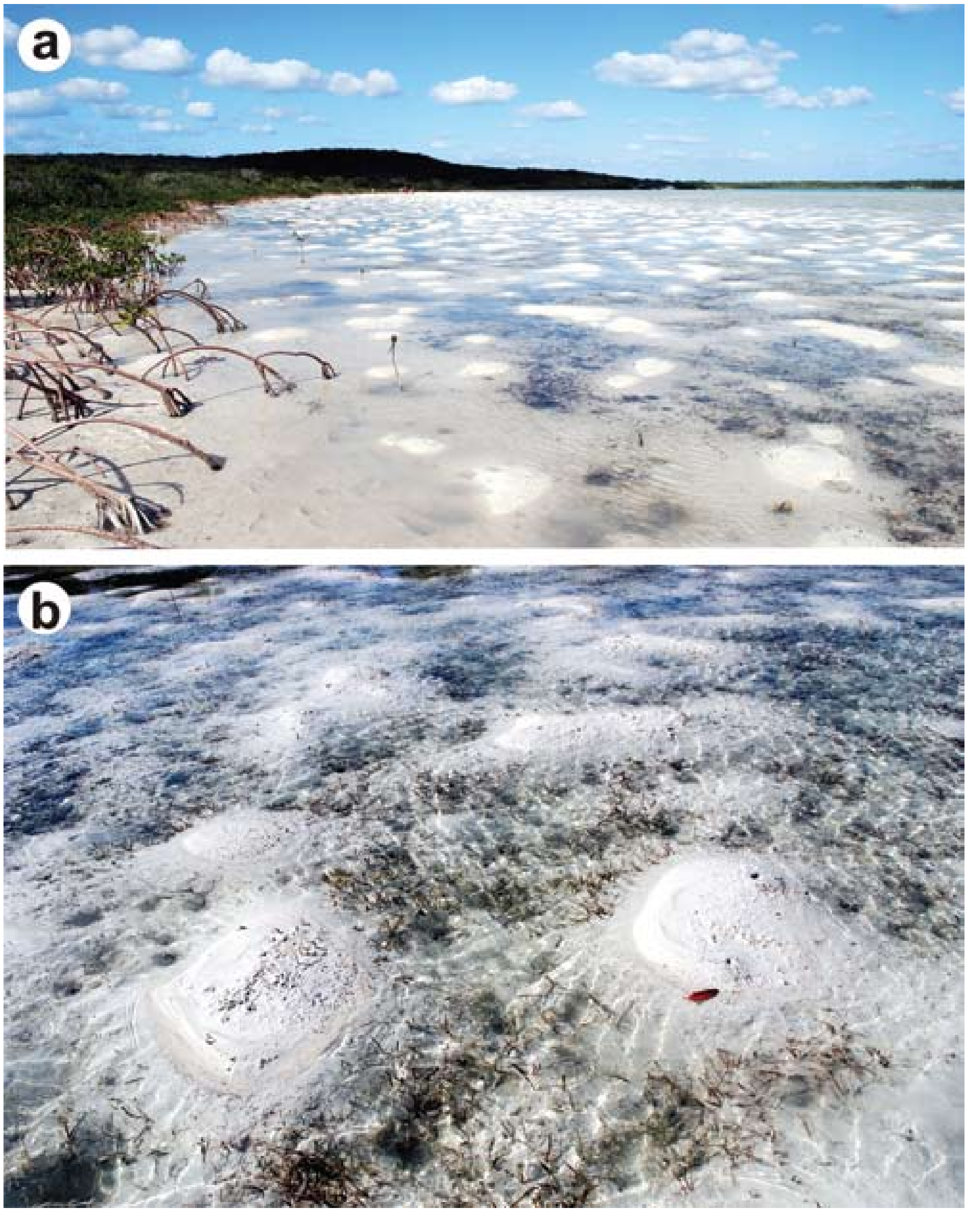


Figure 6.16 Mounded topography resulting from the activity of the thalassinidean shrimp *Glypturus acathochirus*. Pigeon Creek, San Salvador Island, Bahamas. (a) General view. (b) Close-up of mounds. See Curran and Martin (2003).

Neumann and Wisshak (2006) noted that echinoderms favor the recognition of infestation of parasites, because the echinoderm skeleton represents a living tissue capable of reacting to disturbance. These authors documented Late Cretaceous etched attachment scars produced by parasitic foraminifers on the oral surface of a holasteroid echinoid. A specific type of parasitism is revealed by the dual behavior of endosymbionts that is preserved in the ichnological record as bioclaustrations or embedment structures (Bromley, 1970; Tapanila, 2005; Tapanila and Holmer, 2006; Tapanila and Ekdale, 2007). In these cases, a trace-fossil cavity is produced by the growth-interfering behavior of a symbiont living in the growing skeleton of the host. The dual activity of the settler symbiont is revealed by interference of host growth and maintenance of the dwelling structure (Tapanila, 2005). Although less common, parasitism may be expressed by structures that are not strictly due to bioerosion, but preserved in a trace fossil itself. An example is illustrated by beetle nests in paleosols that contain internal galleries formed by cleptoparasites (Mikuláš and Genise, 2003; see Section 1.2.4). Nara *et al*. (2008) documented a Pleistocene bivalve, *Cryptomya busoensis*, with its posterior end attached to the upogebiid burrow *Psilonichnus*, and compared this association with modern examples. They interpreted this as a mild form of parasitism, in which the bivalve used the sediment–water interface on the internal surface of the crustacean burrow, taking food and oxygen, and expelling wastes.

Even less common is ichnological evidence of commensalism in the ichnofossil record, and only very recently have examples been documented. Wisshak and Neumann (2006) documented a commensal association between a spionid polychaete and a

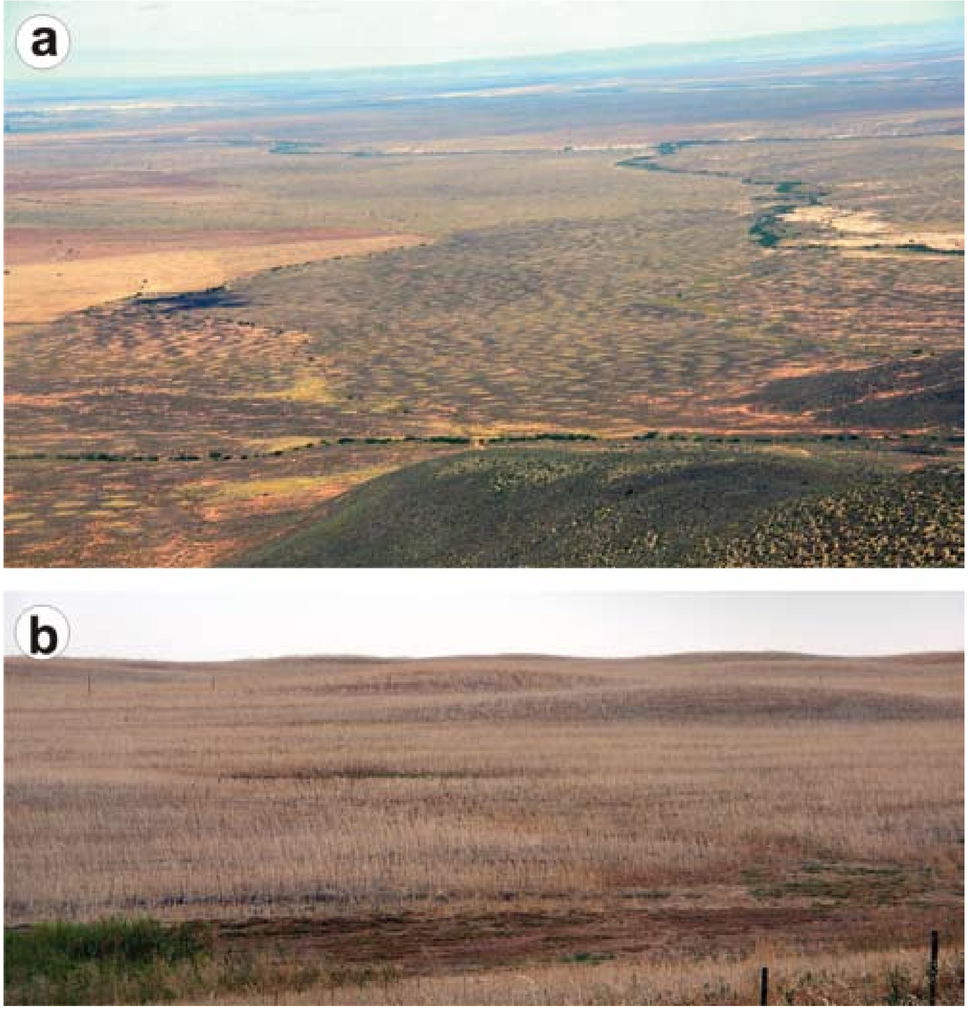


Figure 6.17 Mounded topography (heuweltjies) produced by the harvester termite *Microhodotermes viator*, Matjiesgloof Farm, South Africa. See Fey (2010) (a) General view. (b) Close-up of termite mounds.

holasteroid echinoid from the Late Cretaceous. The interaction is suggested by the presence of abundant specimens of the boring *Caulostrepsis* associated with distinct regeneration textures in the echinoderm. These authors suggested commensalism rather than parasitism, based on the fact that while the polychaete sheltered and fed from organic matter resuspended by the echinoderm, there was no evident harm involved for the latter.

Mutualism is expressed in the ichnological record by farming behavior. For example, some termites (i.e. subfamily Macrotermitinae) build gardens where a symbiotic fungus is cultivated (Sands, 1969). Termites use their own feces to build a structure where the fungus grows (fungus comb). Fossil fungus combs are associated with termite nests in Miocene paleosols, recording the earliest example of symbiotic termite fungiculture (Duringer *et al.*, 2007).

6.8 SPATIAL HETEROGENEITY

Trace fossils commonly display a heterogeneous distribution across an individual sedimentary unit (i.e. they show a deviation from randomness). In fact, any casual observer inspecting an outcrop can find substantial differences in the trace-fossil content along a single bedding plane. However, despite being spatial heterogeneity, a well-known feature in ecological studies (e.g. Schäfer, 1972; Reise, 1985; Gili and Coma, 1998), it has been noted in ichnological analysis relatively recently (Pemberton and Frey, 1984b; Leszczyński, 1991b; Mángano *et al.*, 2002a; Genise *et al.*, 2004b; McIlroy, 2007a; Scott *et al.*, 2007a). In many instances, spatial heterogeneity is produced by the impact of ecosystem engineers (see Section 6.6). Also, computer simulations and experiments seem to indicate that resource patchiness plays a strong control on invertebrate behavior, particularly in foraging organisms (Plotnick and Koy, 2005; Koy and Plotnick, 2010) (see Section 3.4).

Zonation and patchiness of benthic communities is common in modern marine environments, both in shallow-marine (e.g. Schäfer, 1972; Anderson and Meadows, 1978; Newell, 1979; Reise, 1985; Tufail *et al.*, 1989) and deep-marine settings (Gage and Tyler, 1991). Within shallow-marine settings, intertidal areas are particularly heterogeneous as a result of both physical and biotic processes. The tidal cycles, tidal currents, river input, and wind processes lead to a wide variety of salinity changes and hydrodynamic regimes (Meadows *et al*., 1998). For example, different suspension feeders capture particles of variable sizes, leading to patchy species distribution controlled by the flow rate of the surrounding water (Gili and Coma, 1998). In addition, the complex biogenic interactions of the intertidal zone result in further complexity (Reise, 1985; Bertness, 1999; Little, 2000). In fact, the process of bioturbation itself, which involves particle selective feeding, influences spatial heterogeneity (Murray *et al*., 2002). Under these conditions, heterogeneity occurs primarily at two scales. At the larger scale, zonational distribution is expressed along the entire tidal range, as illustrated by different animal communities living in different areas within the tidal flat (i.e. tidal channels and tidal flats; upper, middle, and lower tidal flats); these changes are better understood within the framework of facies analysis (see Section 7.2).

Of more interest here are those changes revealed at a smaller scale. Spatial segregation of species may reflect distinct microhabitats and partitioning of energy resources within each environment. A particular spatial array of organisms permits the exploitation of particular food resources within the limits of their tolerance to environmental conditions. This allows maximum utilization of available food resources and minimum interspecific competition (Newell, 1979). The spatial separation of barnacles and limpets within the lower intertidal zone of rocky shorelines represents an example (Lewis, 1961). In the middle- and, particularly, in the lower-intertidal area, food resources are abundant and varied, but, equally, the organisms are bound by other species whose requirements may overlap with their own. In these settings, patchiness commonly results from niche specialization, thereby significantly reducing interspecific competition. Selection commonly favors those behavioral responses that tend to restrict organisms to particular niches at which they convert energy more efficiently than their neighbors (Wolcott, 1973).

Substrate microtopography across the tidal flat exerts a control on spatial heterogeneity because it strongly influences sediment grain size, sorting, and organic richness (Thum and Griffiths, 1977). These authors noted that water enters through ripple troughs and exits through the crests along a pressure gradient. This circulation pattern results in a re-sorting of sediment with small grains and organic debris being drawn into the troughs. Organics are trapped within the sediment to a depth equal to the height of the ripple crest. The localized distribution of organic matter accounts for the aggregation of meiofauna, and invertebrate grazers in ripple troughs (Jansson, 1967; Harrison, 1977, Newell, 1979). Small patches of nematodes may occur in ripple troughs as a response to preferential accumulation of organic detritus (Hogue and Miller, 1981).

The polychaete *Scolecolepsis squamata* constructs vertical shafts on slight topographic rises, while the spiral traps of the paraonid polychaete *Paraonis fulgens* occur in nearby depressions in intertidal areas (Röder, 1971; Bromley, 1990, 1996). Segregation of associations of the amphipod *Corophium volutator*, the polychaete *Arenicola marina*, and the prosobranch *Hydrobia* has been noted in modern sand flats (Reise, 1985). Mounds are stabilized and inhabited by the tube-dwelling amphipods, the prosobranch tends to concentrate at the fringe of the mounds, and the polychaete causes high sediment turnover in the surrounding areas. In this case, heterogeneity most likely reflects trophic amensalism as a result of the mutual exclusion of sediment stabilizers and destabilizers (see Section 6.6). Evaluation of spatial heterogeneity in modern intertidal areas has been quantitatively assessed through the establishment of three transects in intertidal areas of the Clyde Estuary, Scotland (Meadows *et al*., 1998). The first transect was at right angles to the sand dunes (crest/trough transect), the second and third crossed the crest (crest transect) and trough (trough transect), respectively. Correlation, cluster, and principal component analysis highlighted patterns of spatial patchiness in the microhabitats and the associated macrobenthic community.

Information from marine benthic ecology can be used to understand heterogeneous distribution of biogenic structures in the stratigraphic record. Heterogeneity related to local microtopography, typically bedforms or small positive areas along individual bedding planes, has been detected in Carboniferous tidal flats (Mángano *et al*., 2002a). In particular, patchiness is revealed by the preferential presence of *Psammichnites implexus* in ripple troughs. Small-scale spatial heterogeneity probably documents the effects of bedform topography on the partitioning of food resources. *Psammichnites implexus* commonly displays a guided meandering pattern in ripple troughs, reminiscent of the hyporelief *Helminthorhaphe* of deep-marine settings. Absence of self-overcrossing suggests phobotaxis. This distribution may reflect food searching in ponded areas of ripple troughs during the low tide (Mángano *et al*., 2002a, b).

Patchiness in these Carboniferous tidal flats is also represented by mounds characterized by dense aggregations of U-shaped tubes (*Protovirgularia bidirectionalis*) and small vertical burrows. U-shaped, mucus-lined bivalve burrows most likely stabilized the substrate and trapped the sediment to form the mounds on the tidal-flat surface (see Section 6.7). Similar mounds are produced by *Corophium volutator* (Reise, 1985) and tube-building polychaete worms (Jones and Jago, 1993) in modern tidal flats. The reason why the infaunal burrowers chose this particular spot is more difficult to assess, but it may have been related to some particularly attractive feature of the sediment, as site selection is rarely random. Larval preference for settlement in particular sites has been associated with specific substrate features, either physical properties (e.g. grain roundness) or biological components (e.g. organic film induced by bacteria, type of interstitial organisms, presence/absence of seagrass) (Newell, 1979; Reise, 1985). For example, the presence of a film of microorganisms on the surface of sand grains is instrumental in allowing the settlement of the polychaete *Ophelia bicornis* (Wilson, 1954, 1955). Meadow and Anderson (1968) conducted a survey of microorganisms attached to grains of intertidal sand and found an uneven distribution, with microorganisms tending to concentrate in small pits and grooves on the surface. Microbial stabilization is also a major controlling factor in creating topographic irregularities in tidal flats, such as erosive remnants, mounds, and domal upheavals, and projecting bedding planes in tidal flats (Gerdes *et al.*, 1994, 2000; Noffke *et al.*, 1996; Noffke, 1999, 2010; Schieber *et al.*, 2007).

Patchiness in trace-fossil distribution has been systematically analyzed in wave-dominated shallow-marine successions from an ichnofabric perspective (McIlroy, 2007a). Lateral changes in ichnodiversity, proportions of ichnotaxa, and behavioral types are remarkable over short distances (less than 55 m along a depositional strike). In contrast, the size of trace fossils shows less spatial variation. Accordingly, McIlroy (2007a) suggested caution in the use of ichnofabrics for intra-regional correlations.

Heterogeneity is also very common in deep-marine environments (Gage and Tyler, 1991; Leszczyński, 1991b). Observations from modern deep-sea floors indicate that benthic organisms display a heterogeneous distribution as result of a complex interplay of factors (e.g. local environmental changes, larval settlement). One of the most common cases is the concentration of organisms (e.g. ophiuroids, holothurians) forming patches across the sea floor (e.g. Billett *et al.*, 1983; Gage and Tyler, 1991). Examination of turbidite soles reveals lateral variation in the distribution of complex grazing traces and graphoglyptids at different scales (e.g. Leszczyński and Seilacher, 1991; Leszczyński, 1991b). Trace-fossil patchiness seems to be common in thin-bedded turbidites, including radial patches of *Ophiomorpha* and gregarious occurrences of *Scolicia*.

Patchiness is particularly common in the continental realm, where it has been noted in both terrestrial and freshwater settings. Habitat heterogeneity is also common in lakes, as a result of a wide variety of factors, such as food resources, shelter, and breeding opportunities (Cohen, 2003). In particular, hypersaline-lake environments associated with hot springs display heterogeneous distribution of biogenic structures (Scott *et al.*, 2007a). These lakes are very stressful, but may contain local zones where less extreme environmental conditions allow formation, and preservation of biogenic structures (see Section 10.3.1). These so-called oases are commonly present around freshwater point-sourced springs and contain a concentrated view of the biodiversity within the lake (Scott *et al.*, 2007a).

River floodplains are also extremely variable, being characterized by sharp environmental gradients, leading to strong spatial heterogeneity at different scales (Baker and Barnes, 1998; Ward *et al.*, 1999, 2002). Species-rich areas commonly exist as isolated fragments across the channel and overbank landscape. At a smaller-scale, terrestrial–aquatic gradients linked to overbank flooding create local patches that influence formation and preservation of biogenic structures (e.g. Smith, 1993) (see Section 10.2.2). In this respect, proximity to the river channel is directly linked to water availability, which is one of the main controlling factors in alluvial environments (see Section 6.1.10).

Genise *et al.* (2004b) mentioned variable lateral distribution in coleopteran pupation chambers (*Rebuffoichnus*) from Cretaceous paleosol ichnofabrics. This pattern was in sharp contrast with that of meniscate trace fossils present in the same ichnofacies, which display a more homogeneous lateral distribution. Ecological studies in modern soils suggest that heterogeneity may be linked to patchy distribution of populations in response to several factors, such as soil texture and carbon content (Ettema and Wardle, 2002).

In deserts, heterogeneity is linked to both patterns of plants in relationship to soil and topography, and animal-generated disturbances in soil (Whitford, 2002). Vertebrates (e.g. mammals, reptiles) and even arthropods create patches in arid environments (see Section 6.6). Some holes excavated by mammals serve as collection points for seeds and organic matter, having a strong impact in arid ecosystem dynamics. Animal activity affects soil chemistry and vegetation growth, resulting in heterogeneous distribution of root traces in desert environments. Water availability is also highly variable across desert areas controlling distribution of biogenic structures (e.g. dunes versus interdunes, dry versus wet interdunes).

7 Ichnology of shallow-marine clastic environments

> As discussed in other chapters of this book, traces commonly receive a paleontologic or zoologic connotation. Because of this aspect, traces are often given a short shrift by sedimentologists. This situation is unfortunate, and indeed unfair, to the study of sediments because the contained lebensspuren are sedimentary structures (albeit biologically formed) and should receive attention equal to that devoted to structures developed by physical processes. In fact, these traces often supply evidence of sedimentological conditions that is superior to information gained only by the study of physical structures. If the foregoing is not sufficient reason for sedimentologists to be concerned with the study of ichnology, perhaps they can be prodded into it by virtue of the fact that the nefarious beasts creating the biogenic structures have a nasty habit of destroying their beloved physical structures, and they should at least attempt to identify the enemy!
>
> Jim Howard
>
> "The sedimentological significance of trace fossils" (1975)

Historically, one of the major strengths of ichnology is its utility in facies analysis and paleoenvironmental reconstructions. Undoubtedly, marine ichnology has been the main focus of most trace-fossil research in this respect. However, our knowledge of marine ichnofaunas is still uneven. The vast majority of ichnological studies applied to facies analysis and paleoenvironmental reconstruction deals with ichnofaunas from siliciclastic successions, rather than carbonates, mixed carbonates-clastics, or volcaniclastics. In siliciclastic settings, both shallow- and deep-marine ichnofaunas have received similar attention. However, ichnological studies in shallow-marine environments have attained better integration with sedimentological data than those in deep-marine settings. In turn, the ichnology of wave-dominated shallow-marine environments has been explored in more detail than their tide-dominated counterparts. In connection with this, the ichnological content of sandy shores is much better known than that of muddy coasts. In fact, some specific types of muddy shorelines, such as chenier plains (e.g. Augustinus, 1989), remain essentially unrecognized in the geological record. Also, end members, with respect to wave and tidal dominance, are better understood than mixed systems (e.g. Anthony and Orford, 2002). In this chapter, we will review the ichnology of different shallow-marine clastic environments, covering wave-dominated, tide-dominated, mixed systems, and muddy shorelines.

7.1 WAVE-DOMINATED SHALLOW MARINE

Shallow-marine wave-dominated environments host a large number of benthic organisms that interact with the substrate in many different ways. As a result, trace fossils are diverse and abundant in wave-dominated shallow-marine deposits. Alternating and contrasting hydrodynamic energy levels due to repeated storm events are among the most important limiting factors for trace-fossil distribution and preservation (Pemberton and Frey, 1984a; Vossler and Pemberton, 1989; Frey, 1990; Frey and Goldring, 1992; MacEachern and Pemberton, 1992; Pemberton *et al.*, 1992c; Pemberton and MacEachern, 1997; Buatois *et al.*, 2002b, 2007b; Mángano *et al.*, 2005a). These studies demonstrated that storms involve erosion followed by rapid deposition, which in turn is followed by a waning phase and the re-establishment of fair-weather sedimentation under a lower-energy regime (Fig. 7.1). Storms impose a stress factor on the benthic communities inhabiting these wave-dominated environments (see Section 6.1.1).

Storm-dominated successions contain two contrasting trace-fossil suites revealing the response of the benthic fauna inhabiting two successive and different habitats (Pemberton and Frey, 1984a; Pemberton *et al.*, 1992c, 2001; Pemberton and MacEachern, 1997). The resident, fair-weather suite is produced by a benthic community developed under stable and rather predictable conditions. This suite typically illustrates the *Cruziana* ichnofacies, and reflects the activity of populations displaying K-selected or climax strategies (see Section 6.4). Common components of the fair-weather suite are *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Teichichnus*, *Asteriacites*, *Rhizocorallium*, *Asterosoma*, *Dactyloidites*, *Phycodes*, and *Arthrophycus*, among many others. By contrast, the storm-related trace-fossil suite indicates colonization after the storm event. This suite is produced by an opportunistic community displaying r-selected population strategies in an unstable, physically controlled environment. Opportunistic colonizers commonly, though not always, belong to the *Skolithos* ichnofacies (or *Arenicolites* ichnofacies of Bromley and Asgaard, 1991). *Skolithos*, *Ophiomorpha*, and *Arenicolites* are typical components of the storm-related assemblage. Escape trace fossils do not belong to any of these suites, but are produced during the sedimentation event in an attempt to avoid rapid burial (Bromley, 1990, 1996). Extremely dense concentrations of *Chondrites* at the top of tempestites may suggest the burial of high quantities of organic matter during storms (Vossler and Pemberton, 1988a). Also, fair-weather *Chondrites* may rework burrow-fills of the storm-related suite, representing the only evidence of the resident fauna (Fig. 7.2a–b).

Integration of ichnological and sedimentological information has resulted in a detailed paleoenvironmental model that

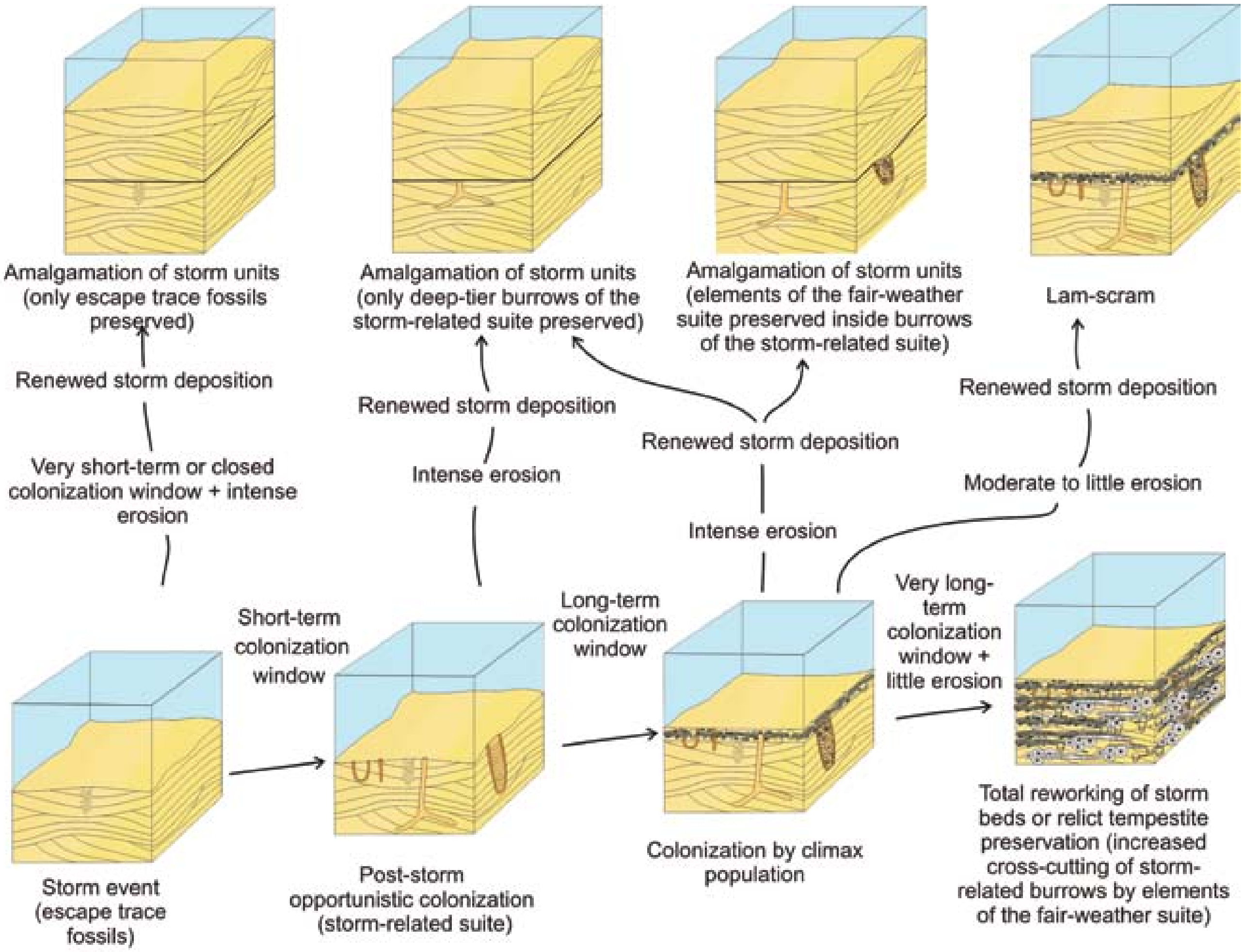


Figure 7.1 Taphonomic pathways of shallow-marine environments affected by storm erosion and deposition. A high frequency of storms results in very short-term to negligible colonization windows. Under these conditions, amalgamated storm deposits are formed. These tempestites are either non-bioturbated, or contain only escape burrows. Under slightly lower frequency of storms, short-term colonization windows allows the establishment of elements of the storm-related trace-fossil suite. Strong erosion due to intense storms results in removal of shallow-tier trace fossils and burrow truncation, allowing preservation of only deep-tier burrows (e.g. *Ophiomorpha*, *Diplocraterion*). Long-term colonization windows allow development not only of the storm-related suite but also establishment of the fair-weather suite. If erosion by a subsequent storm is intense, the latter is removed and only deep-tier burrows of the former are preserved. Alternatively, elements of the fair-weather suite (e.g. *Chondrites*) may be preserved inside burrows of the storm-related suite. Under moderate to little erosion, the fair-weather suite is preserved, resulting in the alternation of intervals preserving the storm primary fabric (plus burrows of the storm-related suite) and bioturbated intervals due to the activity of the fair-weather suite (lam-scram). Very long-term colonization windows accompanied by little erosion results in total obliteration of storm deposits or relict tempestite preservation.

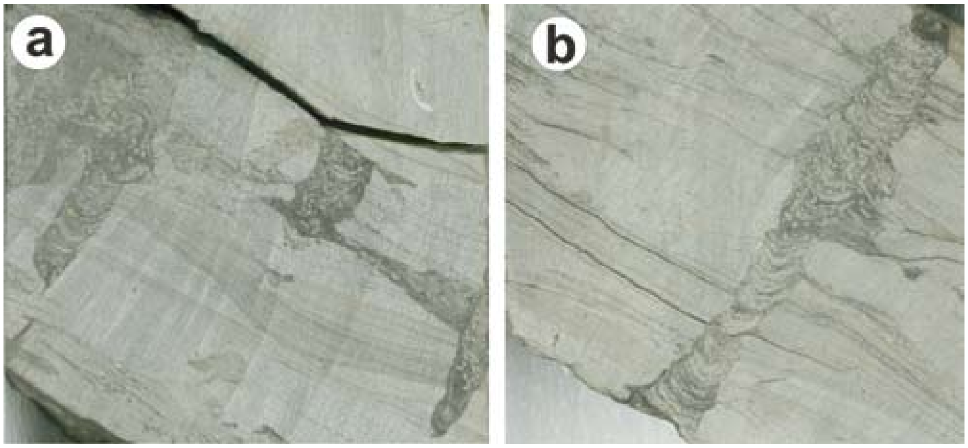


Figure 7.2 Fair-weather *Chondrites* isp. reworking storm-related *Diplocraterion parallelum*. Middle Eocene, Pauji Formation, Motatán Field, Maracaibo Basin, western Venezuela. Core width is 6 cm. (a) General view. (b) Close-up. See Delgado *et al.* (2001).

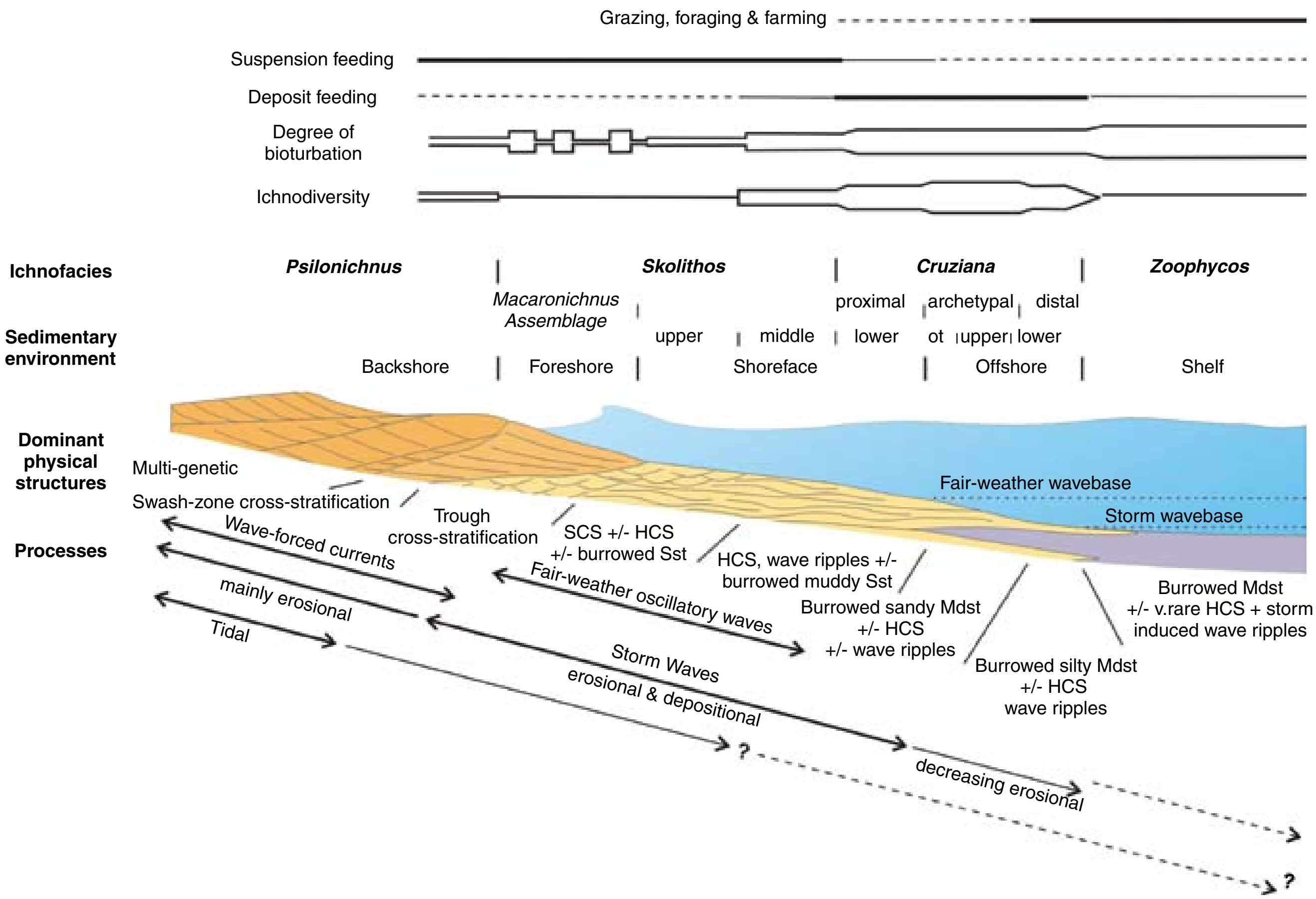


Figure 7.3 Ichnological and sedimentological aspects along a wave-dominated depositional profile. Alternating low and high intensity of bioturbation in the foreshore is due to local patches displaying intense reworking by *Macaronichnus*. HCS, hummocky cross-stratification; SCS, swaley cross-stratification. Distribution of ichnofacies and depositional processes based on MacEachern *et al.* (1999a).

allows delineation of proximal–distal trends along a backshore-nearshore-offshore-shelf transect, referred to as the "shoreface model" (MacEachern and Pemberton, 1992; MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001) (Figs. 7.3 and 7.4). In this model the term "shelf" is used in a more restricted way and separated from the offshore. Observations were originally based on outcrops and cores from the Mesozoic foreland basin of western North America (e.g. Pemberton *et al.*, 1992d), but the database has been subsequently expanded to include information from elsewhere (e.g. Buatois *et al.*, 2002b; Mángano *et al.*, 2005a; Angulo and Buatois, 2009) (Box 7.1).

The proximal–distal energy gradient in open-marine wave-dominated systems is rather straightforward, with a seaward decrease in wave energy (Yoshida *et al.*, 2007). In connection to the energy gradient, other environmental factors change in a predictable way. The energy gradient determines the type of substrate available for benthic colonization. Sand–mud rate decreases seaward and, therefore, wave-dominated environments are represented by sandy shores (Brown and McLachlan, 1990). The distribution of biogenic structures is also controlled by the available food supply (the food resources paradigm of Pemberton *et al.*, 2001). Proximal settings typically contain food particles kept in suspension in the water column by currents and waves, while distal environments are characterized by organic detritus within the sea bed (see Section 6.1.6). Oxygen content usually is not a limiting factor in agitated shallow waters, but dysaerobic and even anoxic conditions may occur in low-energy distal settings, significantly affecting ichnodiversity (see Section 6.1.3).

Analysis of selected case studies documenting shallow-marine clastic ichnofaunas shows that few ichnotaxa are restricted to particular subenvironments of the nearshore to offshore transect. The available information reveals, therefore, the pitfalls of the checklist approach, as previously noted by Howard and Frey (1975). An integrated approach, taking into account several characteristics, such as degree of bioturbation, abundance of individual ichnotaxa, ethological, and ecological significance of the biogenic structures, ichnofabrics, and tiering structure, is more useful to delineate environmental subdivisions of shallow-marine clastic successions (e.g. Buatois *et al.*, 2002b; Mángano *et al.*, 2005a).

7.1.1 BACKSHORE

Backshore environments are characterized by stressful conditions, resulting from a combination of subaerial exposure and rapid variations in substrate types and energy levels, mostly reflecting torrential rains and storm surges (Frey and

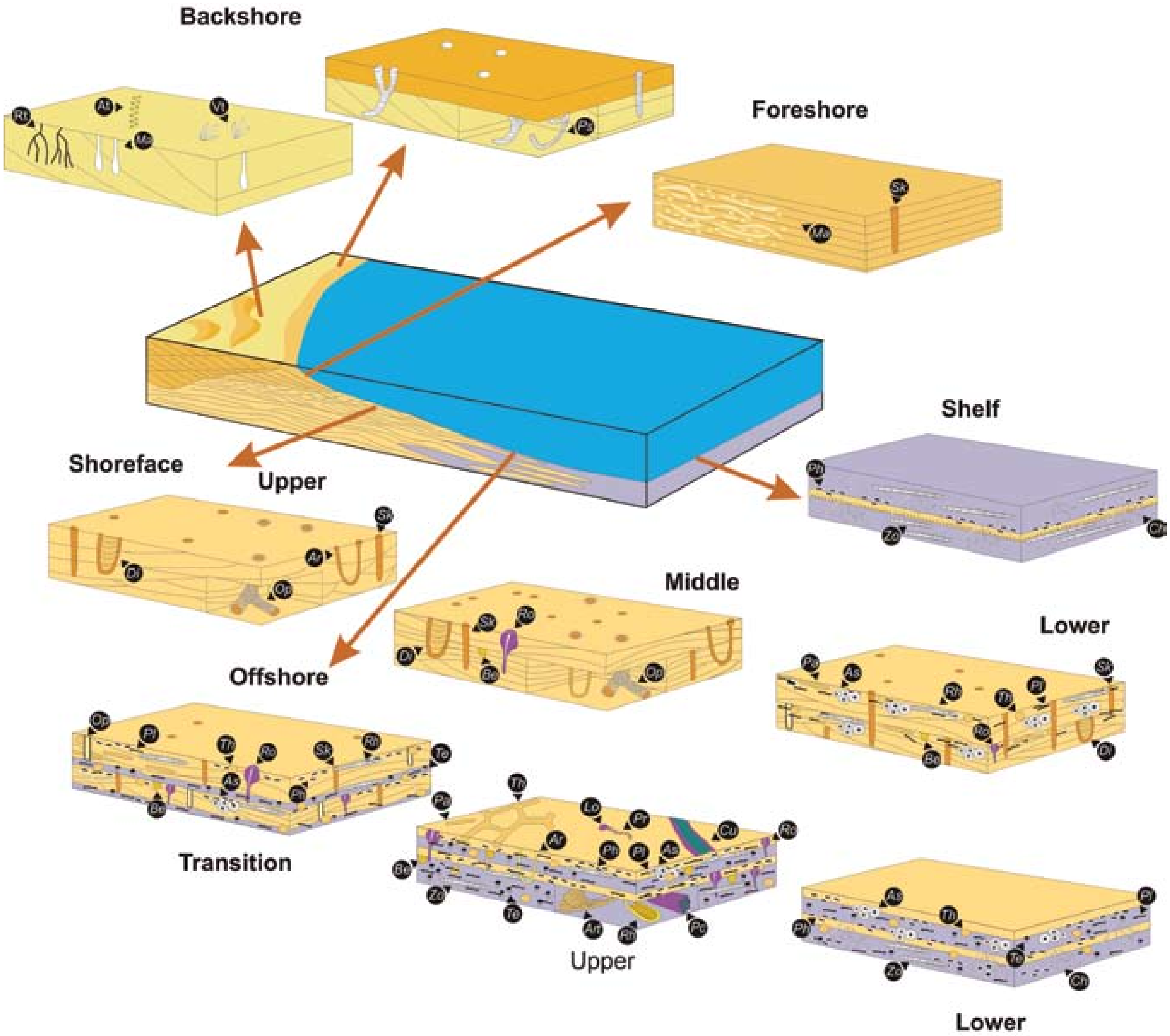


Figure 7.4 Schematic reconstruction of trace-fossil distribution in wave-dominated shallow-marine environments. The proximal zone of the backshore is characterized by vertical dwelling structures with a bulbous basal cell, which are assigned to *Macanopsis* (*Ma*) together with arthropod trackways (At), vertebrate trackways (Vt), and root traces (Rt). The seaward zone of the backshore is dominated by *Psilonichnus* (*Ps*). The foreshore is unbioturbated for the most part, but it may contain *Skolithos* (*Sk*) and high-density occurrences of *Macaronichnus* (*Ma*). The upper shoreface is sparsely bioturbated and may contain vertical burrows, such as *Skolithos* (*Sk*), *Diplocraterion* (*Di*), and *Arenicolites* (*Ar*), as well as crustacean galleries, such as *Ophiomorpha* (*Op*), dominated by vertical components. The middle shoreface is similar to the lower shoreface, but tends to be more bioturbated and other ichnotaxa, such as *Bergaueria* (*Be*) and *Rosselia* (*Ro*), may be added. The lower shoreface is extremely variable with respect to intensity and frequency of storms. *Asterosoma* (*As*), *Bergaueria* (*Be*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Thalassinoides* (*Th*), *Rhizocorallium* (*Rh*), *Rosselia* (*Ro*), *Skolithos* (*Sk*), and *Diplocraterion* (*Di*) are typical components. The offshore transition is similar in taxonomic composition to the lower shoreface, but tends to display higher ichnodiversity and intensity of bioturbation. Ichnogenera, such as *Teichichnus* (*Te*) and *Phycosiphon* (*Ph*), may become abundant. The upper offshore is highly diverse, and may include *Asterosoma* (*As*), *Arenicolites* (*Ar*), *Bergaueria* (*Be*), *Planolites* (*Pl*), *Curvolithus* (*Cu*), *Protovirgularia* (*Pr*), *Lockeia* (*Lo*), *Palaeophycus* (*Pa*), *Arthrophycus* (*Art*), *Phycodes* (*Pc*), *Thalassinoides* (*Th*), *Rhizocorallium* (*Rh*), *Rosselia* (*Ro*), *Teichichnus* (*Te*), *Zoophycos* (*Zo*), and *Phycosiphon* (*Ph*). The lower offshore is less diverse, and tends to be dominated by *Asterosoma* (*As*), *Planolites* (*Pl*), *Thalassinoides* (*Th*), *Chondrites* (*Ch*), *Teichichnus* (*Te*), *Zoophycos* (*Zo*), and *Phycosiphon* (*Ph*). Shelf deposits are intensely bioturbated, but trace-fossil diversity is low. *Chondrites* (*Ch*), *Zoophycos* (*Zo*), and *Phycosiphon* (*Ph*) are typical components.

Pemberton, 1987). Beach-backshore deposits are extremely diverse, including wave and current-rippled cross-laminated sand in ponded areas, and a wide variety of wind-generated structures (e.g. wind ripples and small-scale blowouts) in sand exposed to eolian action. The landward edge of the beach is characterized by eolian dunes, which in the rock record are commonly preserved as planar cross-stratified sandstone commonly displaying steeply dipping foresets.

Box 7.1 Ichnology of lower Paleozoic wave-dominated shallow-marine deposits of northwest Argentina

The Alfarcito Member of the Upper Cambrian–Tremadocian Santa Rosita Formation in northwestern Argentina contains well-preserved and laterally continuous outcrops, recording deposition in a wave-dominated, low-gradient open-marine system. The lower interval of the Alfarcito Member represents a transgressive-regressive cycle, encompassing lower offshore to lower-middle shoreface environments (Fig. 7.5). Benthic fauna and trace-fossil distribution were essentially controlled by alternating and contrasting energy conditions due to repeated storm events superimposed on fair-weather deposition. The fair-weather suite is the most diverse and includes a wide variety of behaviors, such as locomotion (*Archaeonassa fossulata*, *Cruziana semiplicata*, *C. problematica*, *Cruziana* isp., and *Diplichnites* isp.), resting (*Rusophycus moyensis*, *R. carbonarius*, *Rusophycus* isp., and *Bergaueria* aff. *B. hemispherica*), pascichnia (*Dimorphichnus* aff. *D. quadrifidus*), feeding (*Arthrophycus minimus*, ?*Gyrolithes* isp., *Gyrophyllites* isp., ?*Phycodes* isp., and *Planolites reinecki*), and dwelling (*Palaeophycus tubularis* and *P. striatus*). The storm-related suite is monospecific and consists of *Skolithos linearis*, preserved as relatively deep, endichnial structures that penetrate into sandstone tempestites. While the fair-weather suite is represented by the *Cruziana* ichnofacies, the storm-related suite illustrates the *Skolithos* ichnofacies. Integration of ichnological and sedimentological data allows ichnological proximal–distal trends along a nearshore-offshore transect to be established (Fig. 7.5). High energy prevailed in lower-and middle-shoreface environments, and bioturbation is restricted to vertical burrows (*Skolithos linearis*), recording colonization after storm events. Environmental conditions in the offshore transition and the upper offshore are more variable as a result of the alternation of high-energy storm events and low-energy fair-weather mudstone deposition. The storm-related *Skolithos* ichnofacies is present, but alternates with the fair-weather suite (*Cruziana* ichnofacies) which reaches a diversity maximum in the upper offshore. Trace fossils are scarce in lower-offshore deposits, mostly being restricted to *Palaeophycus tubularis*. Shoreface deposits are of the strongly storm-dominated type.

Reference: Mángano *et al.* (2005a).

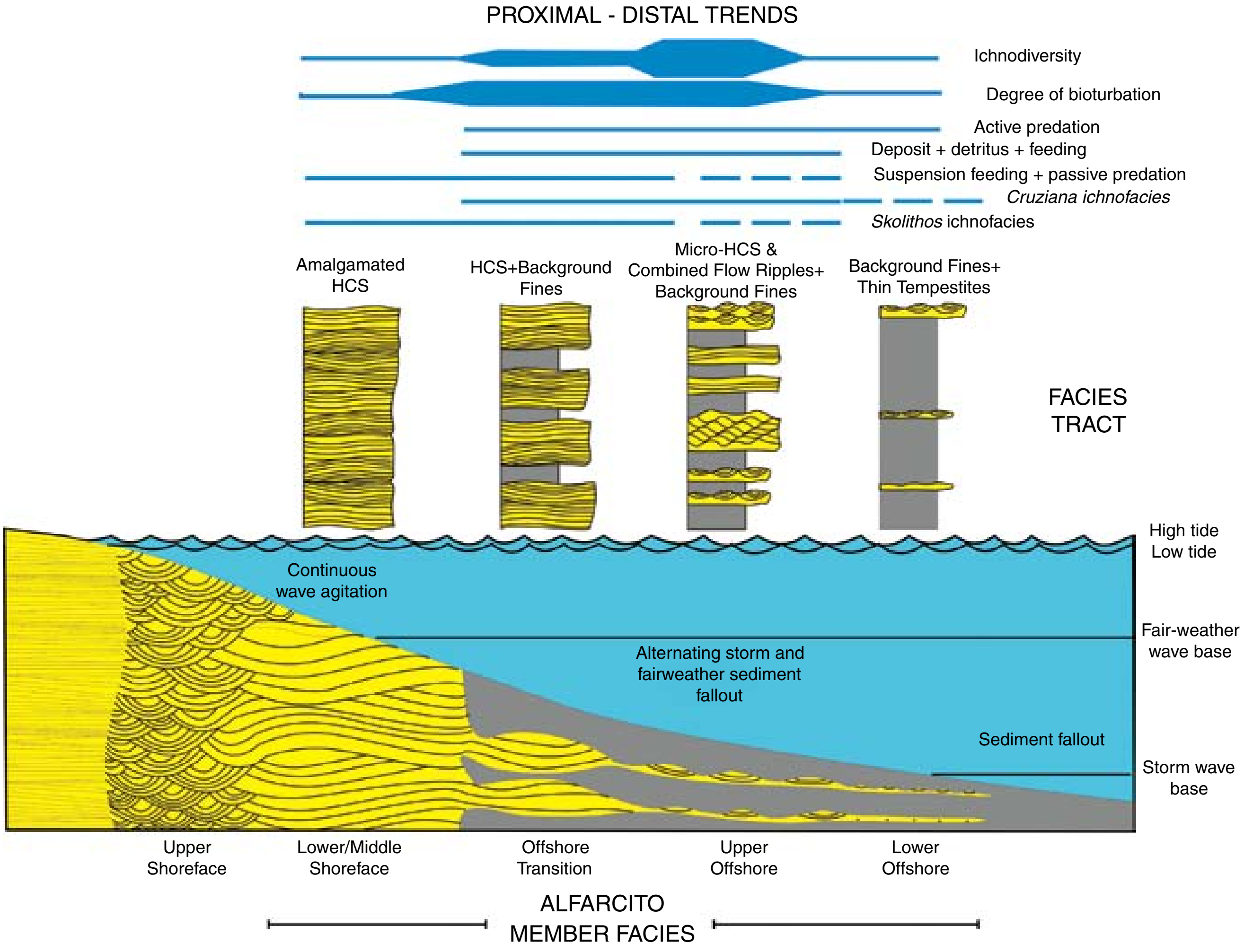


Figure 7.5 Ichnological and sedimentological model of the Alfarcito Member of the Upper Cambrian–Tremadocian Santa Rosita Formation of northwest Argentina (after Mángano *et al.*, 2005a). HCS, hummocky cross-stratification.

As a result of harsh conditions, few animals are able to survive in supralittoral areas and, therefore, ichnofaunas are characterized by low ichnodiversity and abundance. Backshore areas contain a mix of structures produced by terrestrial and marine animals, as well as plant-generated structures (Frey and Pemberton, 1987). Terrestrial elements occur in dune areas, while the marine components are present in the beach. A link between both settings occurs, mostly represented by exchange of sand, groundwater, salt spray, and living and dead organic material (Brown and McLachlan, 1990).

The terrestrial component is represented by invertebrate, vertebrate, and plant traces. Terrestrial invertebrate structures include vertical domiciles of insects and spiders, commonly with a bulbous basal cell, and horizontal locomotion and grazing tracks and trails of insects. However, these horizontal traces have minimum preservation potential. The vertebrate ichnofauna consists of different trackways produced by amphibians, reptiles, birds, and mammals (Frey and Pemberton, 1986). Coprolites may also be abundant. Plant traces are represented by root structures mostly generated by halophytic vegetation (adapted to conditions of high salinity) in seaward areas and by other types of plants landward. In particular, foredunes, relict foredunes, and parabolic dunes are extensively vegetated by aggressive pioneer plants and relatively robust plants (Brown and McLachlan, 1990).

Marine organisms are mainly represented by ghost crabs of the family Ocypodidae (e.g. *Uca pugilator* and *Ocypode quadrata*), including both detritus feeders and scavengers. Ghost crabs construct vertical J-, Y-, and U-shaped dwelling structures assigned to the ichnogenus *Psilonichnus* (Radwański, 1977; Fürsich, 1981; Curran, 1984; Frey *et al.*, 1984a; Nesbitt Campbell, 2006). In siliciclastic settings, ghost crabs extend from the beach to the eolian dune area (Frey *et al.*, 1984a; Curran and White, 1991). Crawling traces of crabs, although extremely common in modern shorelines, have a very low preservation potential (Curran, 1984; Frey *et al.*, 1984a). Other locomotion and grazing horizontal traces are produced by limulids, amphipods, bivalves, and gastropods in modern examples, but remain virtually unknown in fossil examples of backshore environments.

Collectively these structures are included in the *Psilonichnus* ichnofacies (Frey and Pemberton, 1987). Backshore areas grade landwards into a wide variety of terrestrial environments characterized by different trace-fossil assemblages that mostly belong to the *Scoyenia* and *Coprinisphaera* ichnofacies, as well as other potential terrestrial ichnofacies (Buatois and Mángano, 1995b; Genise *et al.*, 2000).

7.1.2 FORESHORE

The foreshore is characterized by high-energy conditions due to intense swash and backwash processes in the intertidal area. Foreshore deposits mostly consist of well-sorted, coarse- to medium-grained sandstone with subparallel to low-angle cross stratification, known as swash-zone stratification. Parting lineation is common. In some cases, foreshore deposits consist of clast-supported pebble to cobble conglomerate displaying clast imbrication (Buscombe and Masselink, 2006).

Because of high energy, foreshore deposits tend to be sparsely bioturbated and of low ichnodiversity (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001). Locally, zones intensely bioturbated by *Macaronichnus* are common (see Section 6.1.1), representing the *Macaronichnus* assemblage of Pemberton *et al.* (2001) (see also Seike, 2008, 2009) (Fig. 7.6a–b). Deep-tier vertical dwelling structures of suspension feeders, such as *Skolithos* (Fig. 7.6c) and *Ophiomorpha*, are typical elements, reflecting abundant organic particles kept in suspension by energetic wave-forced currents. Middle-tier horizontal to inclined dwelling traces (e.g. *Palaeophycus* and *Schaubcylindrichnus*) involving other trophic groups, such as passive predators and deposit feeders, have lower preservation potential (Pemberton *et al.*, 2001). The foreshore ichnofauna is ascribed to the *Skolithos* ichnofacies. In any case, most foreshore deposits are unburrowed.

7.1.3 UPPER SHOREFACE

The upper shoreface occurs below the low-tide line, and is subjected to multidirectional current flows in the build up and surf zones (Clifton *et al.*, 1971; Komar, 1976; Walker and Plint, 1992). As in the foreshore, high-energy conditions are predominant. Upper-shoreface deposits typically consist of trough and planar cross-stratified well-sorted, coarse- to medium-grained sandstone. Locally, pebble conglomerate and pebbly sandstone beds may occur.

Continuous migration of large bedforms results in sparse colonization by the benthic fauna. Accordingly, it is not uncommon to find upper-shoreface deposits that are unburrowed. As a result of overall high-energy conditions, upper-shoreface ichnofaunas resemble those from the foreshore in their sparse distribution, low diversity, dominance of vertical domiciles of the *Skolithos* ichnofacies (e.g. *Skolithos*, *Ophiomorpha*, and *Diplocraterion*), and local abundance of *Macaronichnus* (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001). Although *Macaronichnus* is more common in the upper shoreface–foreshore transition, in reflective shorelines it may occur down in the upper shoreface (Pemberton *et al.*, 2001). In addition, *Conichnus* may occur locally. Although shallow-tier biogenic structures may be emplaced, deep-tier elements have much higher preservation potential. As a result, upper-shoreface ichnofabrics are overwhelmingly dominated by deeply penetrating vertical burrows (Fig. 7.7a).

7.1.4 MIDDLE SHOREFACE

The middle shoreface is located in the area of shoaling and initial breaking of waves (Reinson, 1984; Clifton, 2006). High energy due to migration of longshore bars is predominant. Middle-shoreface deposits consist of swaley cross-stratified, well-sorted, medium- to fine-grained sandstone. Locally, trough cross-stratification, combined-flow ripples and, more rarely, hummocky cross-stratification may occur. Storm-induced

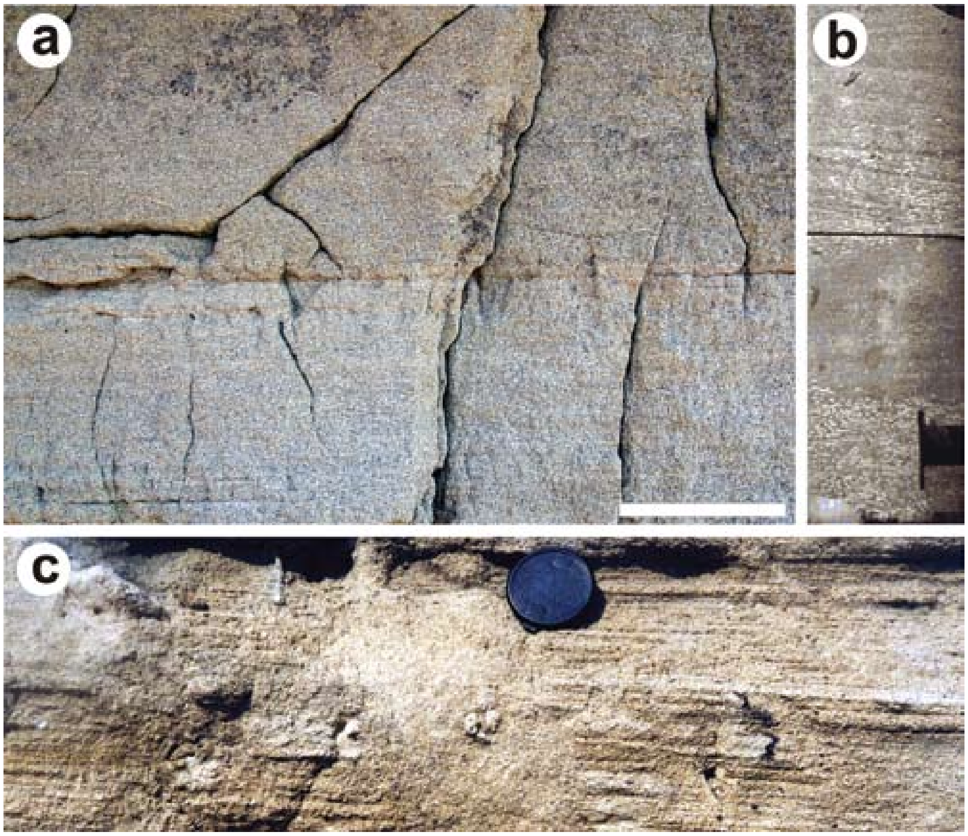


Figure 7.6 Ichnofaunas from foreshore deposits. (a) Low-angle cross-stratified sandstone with a monospecific dense assemblage of *Macaronichnus segregatis*. Upper Cretaceous, Horseshoe Canyon Formation, Drumheller, Alberta, western Canada. Scale bar is 10 cm. See Pemberton *et al.* (2001). (b) Core expression of similar deposits containing *Macaronichnus segregatis*. Upper Oligocene-Lower Miocene, Naricual Formation, El Furrial Field, Eastern Venezuela Basin. Core width is 8 cm. See Quiroz *et al.* (2010). (c) Sparsely bioturbated parallel-laminated sandstone showing low density of *Skolithos linearis*. Pleistocene, Tablazo Formation, Ballenita, Pacific coast, Ecuador. Lens cap is 5.5 cm.

scouring is particularly intense in the middle shoreface (Aigner and Reineck, 1982).

Because of overall high-energy conditions, middle-shoreface deposits are typified by the *Skolithos* ichnofacies (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001). However, in contrast to the foreshore and upper shoreface, ichnodiversity and intensity of bioturbation is somewhat higher. *Ophiomorpha* (Fig. 7.7b), *Skolithos* (Fig. 7.7e), *Diplocraterion*, *Arenicolites*, *Conichnus*, and *Bergaueria* are common components. *Thalassinoides* with dominantly vertical components may occur (Fig. 7.7c). Escape trace fossils may also be present. The frequency and intensity of storms play a major role on patterns of substrate colonization by the benthic fauna (see Section 7.1.5). Under weak and infrequent storms, some elements of the *Cruziana* ichnofacies, such as *Rosselia* (Fig. 7.7d and f) and *Asterosoma* (Fig. 7.7g), may be present. Under increased storm influence nearly all the components are vertical burrows of suspension feeders and passive predators (Pemberton *et al.*, 2001). If the intensity and frequency of storms is high, deposits are unburrowed or only dominated by a few deep-tier forms, resembling upper-shoreface ichnofabrics.

7.1.5 LOWER SHOREFACE

The lower shoreface occurs immediately above the fair-weather wave base (Reinson, 1984; Walker and Plint, 1992). Wave action is the most important process in this zone. Lower-shoreface deposits consist of thick hummocky cross-stratified fine- to very fine-grained sandstone. Wave and combined-flow ripples are locally common at the top of hummocky beds. Individual sandstone beds generally pinch out, but bedsets are commonly laterally persistent (Brenchley *et al.*, 1993). Millimetric partings may occur locally between some hummocky cross-stratified units.

MacEachern and Pemberton (1992) noted that lower-shoreface deposits display strong ichnological variability as a result of contrasting regimes in terms of intensity and frequency of storm events. The weakly storm-affected lower shorefaces (low energy) are characterized by relatively minor amounts of tempestites. These deposits are dominated by fair-weather trace-fossil assemblages, and thin storm beds are commonly obliterated by biogenic reworking or thoroughly bioturbated (e.g. Buatois *et al.*, 2002b, 2003; Carmona *et al.*, 2008). In addition, ichnodiversity is high, and assemblages tend to be dominated by feeding traces of infaunal deposit feeders, such as *Phycosiphon* (Fig. 7.8a), *Teichichnus* (Fig. 7.8e), *Phycodes*, *Asterosoma* (Fig. 7.8a–b), *Schaubcylindrichnus* (Fig. 7.8a–b and f), *Taenidium* (Fig. 7.8d and f), *Helicodromites*, and *Rhizocorallium* (Fig. 7.8h). Grazing trails of deposit feeders, including *Planolites*, *Nereites* (Fig. 7.8b–c) and *Scolicia* (Fig. 7.8a–b,e–g), feeding traces of chemosymbionts (*Chondrites*) and dwelling traces of suspension feeders (e.g. *Palaeophycus*) and deposit or detritus feeders (e.g. *Cylindrichnus* and *Rosselia*) are also present. Crustacean burrow networks, such as *Thalassinoides* (Fig. 7.8f) and *Ophiomorpha* may be abundant. Equilibrium structures, mostly *Diplocraterion* (Fig. 7.8h), may occur locally. *Asterosoma*, *Diplocraterion*, and

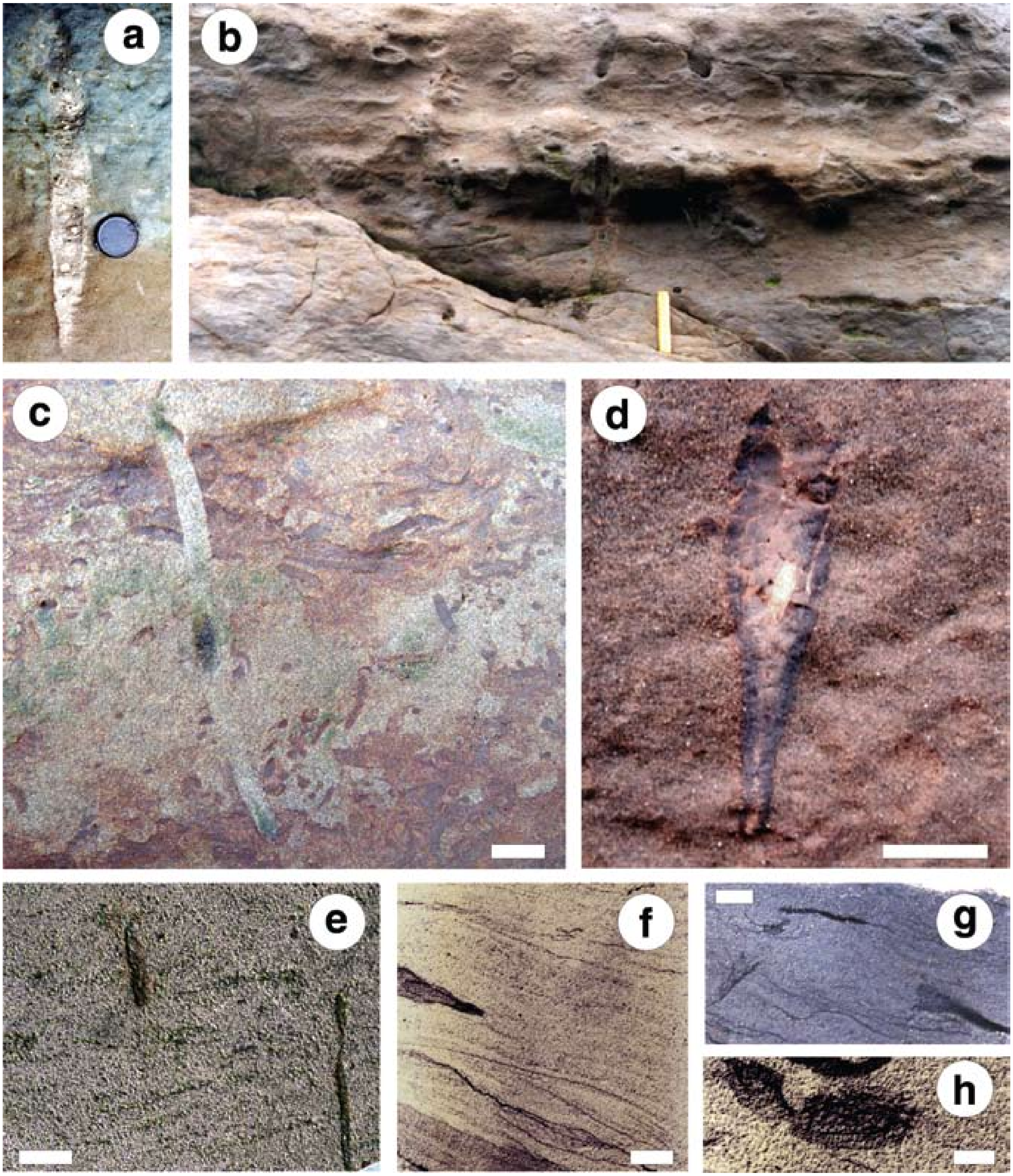


Figure 7.7 Ichnofaunas from upper- to middle-shoreface deposits. (a) Vertical *Ophiomorpha nodosa* in upper-shoreface deposits. Lower Miocene, Chenque Formation, Playa Alsina, near Comodoro Rivadavia, Patagonia, Argentina. Lens cap is 5.5 cm. See Carmona *et al*. (2008). (b) Several vertical specimens of *Ophiomorpha* isp. in middle-shoreface deposits. Lower Miocene, Chenque Formation, Punta Delgada, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 20 cm. See Carmona *et al*. (2008). (c) Vertical *Thalassinoides* isp. cross-cutting variably oriented *Planolites beverleyensis* in middle-shoreface deposits. Pliocene, Lacui Formation, Cucao, Chiloé Island, southern Chile. Scale bar is 1 cm. (d) Sideritized *Rosselia socialis* in middle-shoreface deposits. Pliocene, Lacui Formation, Cucao, Chiloé Island, southern Chile. Scale bar is 1 cm. (e) Core expression of *Skolithos linearis* in middle-shoreface, planar cross-bedded medium-grained sandstone. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b). (f) Core expression of middle-shoreface, planar cross-bedded medium-grained sandstone with reworked *Rosselia* isp. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b). (g) Core expression of *Cylindrichnus concentricus* in middle-shoreface deposits. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b). (g) Core expression of *Asterosoma* isp. in middle-shoreface sandstone. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b).

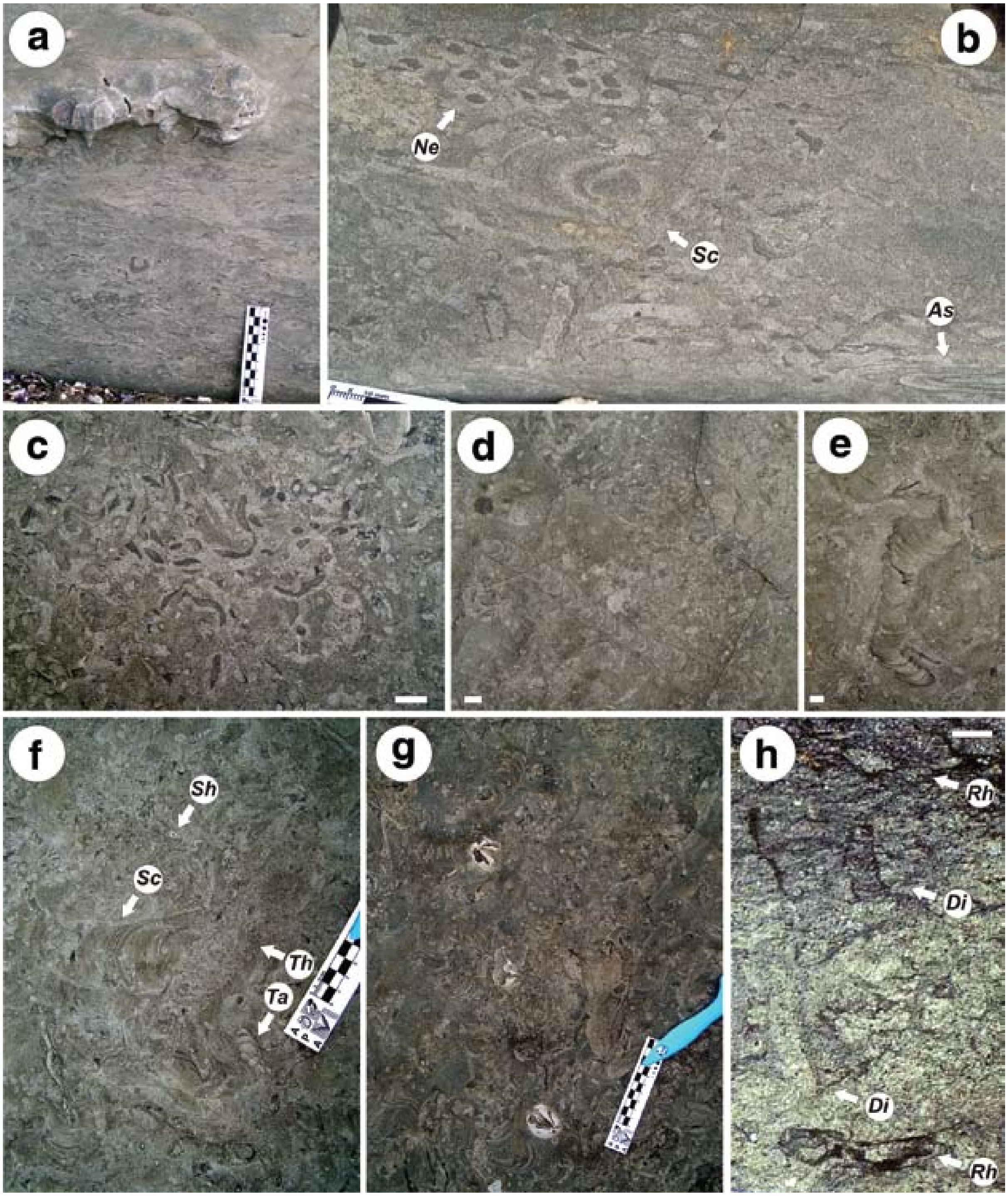


Figure 7.8 Ichnofaunas from weakly storm-affected lower-shoreface deposits (low energy). (a) Cross-section view of intensely bioturbated very fine-grained sandstone below a horizon with *in situ* specimens of *Pinna* sp. containing *Nereites missouriensis*, *Schaubcylindrichnus freyi*, *Asterosoma* isp., *Scolicia* isp., and *Phycosiphon incertum*. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 10 cm. See Carmona *et al*. (2008). (b) Close-up showing of *Nereites missouriensis* (*Ne*), *Asterosoma* isp. (*As*), and *Scolicia* isp. (*Sc*). Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale shows 1 cm division. See Carmona *et al*. (2008). (c) Bedding-plane view of *Nereites missouriensis*. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 1 cm. See Carmona *et al*. (2008). (d) Bedding-plane view of *Taenidium* isp. cross-cutting a background ichnofabric. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 1 cm. See Carmona *et al*. (2008). (e) Oblique view of *Teichichnus zigzag* cross-cutting *Scolicia* isp. and overprinted on a background ichnofabric. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 1 cm. See Carmona *et al*. (2008). (f) Bedding-plane close-up view of intensely bioturbated very fine-grained sandstone containing *Taenidium* isp. (*Ta*), *Schaubcylindrichnus freyi* (*Sh*), *Thalassinoides* isp. (*Th*), and *Scolicia* isp. (*Sc*). Note complex cross-cutting relationships. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale shows 1 cm divisions. See Carmona *et al*. (2008). (g) Bedding-plane view of abundant *Scolicia* isp. (and their echinoid producers) overprinted on a background ichnofabric. Lower Miocene, Chenque Formation, Playa Las Cuevas, near Comodoro Rivadavia, Patagonia, Argentina. Scale bar is 10 cm. See Carmona *et al*. (2008). (h) Core expression of intensely bioturbated fine-grained sandstone containing *Rhizocorallium* isp. (*Rh*) and *Diplocraterion* isp. (*Di*) overprinted on a background mottling ichnofabric. Upper Carboniferous, Lower Morrow Sandstone, Gentzler Field, southwest Kansas, United States. Scale bar is 1 cm. See Buatois *et al*. (2002b).

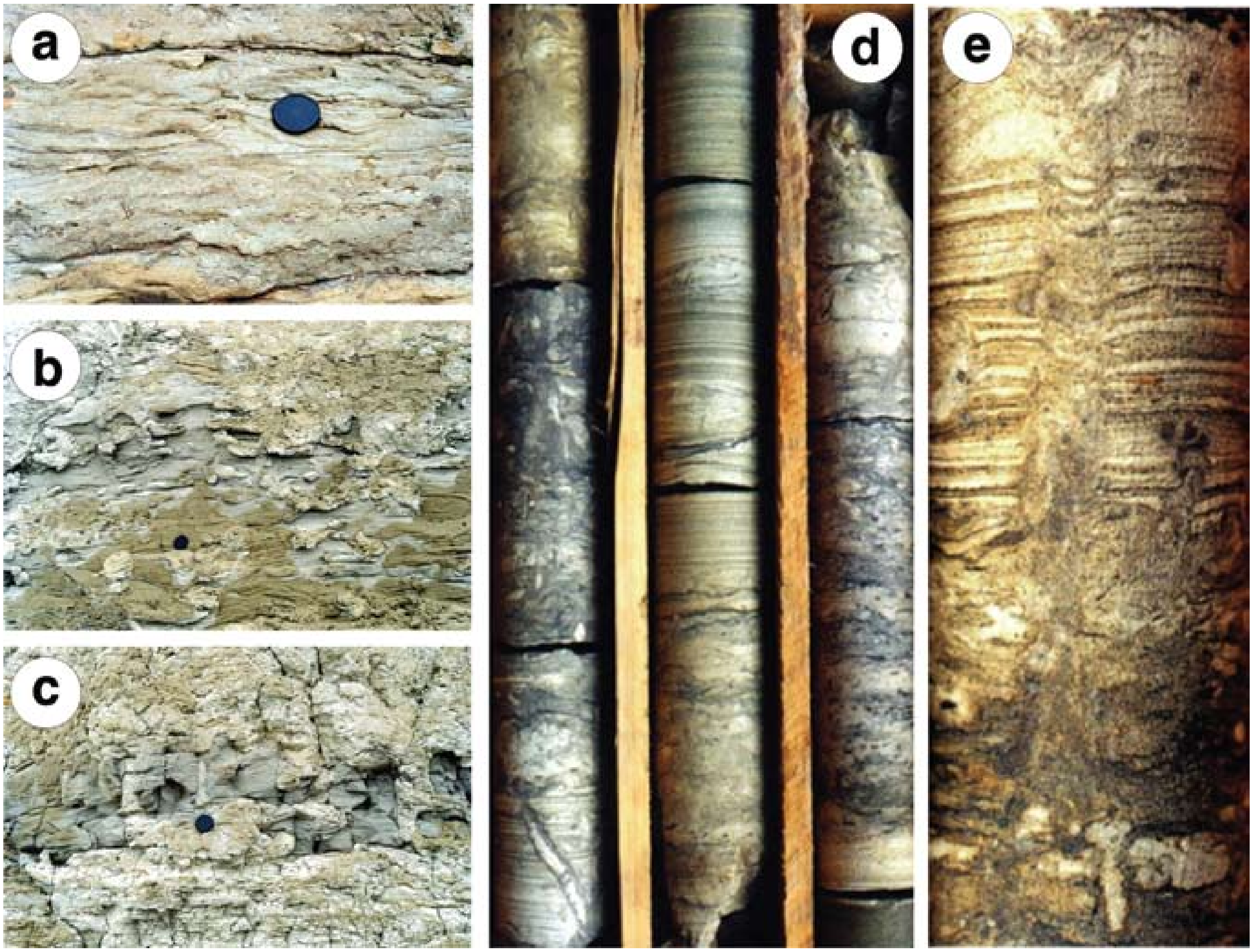


Figure 7.9 Ichnofaunas from moderately storm-affected lower-shoreface deposits (intermediate energy), displaying the typical "lam-scram" pattern. (a) Sparsely bioturbated to non-bioturbated hummocky cross-stratified sandstone zone interbedded with intensely bioturbated sandstone. Note deeply penetrating *Diplocraterion* into hummocky sandstone. Lower Jurassic, Staithes Sandstone Formation, Hartle Loup, North Yorkshire Coast, England. Lens cap is 5.5 cm. See Taylor and Pollard (1999). (b) Alternating hummocky cross-stratified and burrowed zones. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Scasso and Bellosi (2004). (c) Intensely burrowed sandstone with hummocky zones preserved as relict lenses. Lower to Middle Miocene, Gaiman Formation, Bryn Gwyn Paleontological Park, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Scasso and Bellosi (2004). (d) Alternating hummocky cross-stratified and burrowed zones. Base is on the lower left and top on the upper right. Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al*. (2007b). (e) Close-up showing deep *Diplocraterion* penetrating throughout the whole hummocky sandstone into the underlying bioturbated zone. Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al*. (2007b).

Ophiomorpha tend to be more abundant towards the proximal edge of the lower shoreface. Ichnofabrics from weakly affected lower shorefaces typically display complex tiering structures, revealing finely tuned, climax communities displaying vertical niche partitioning (Buatois *et al*., 2003). A transition from the *Cruziana* to the *Skolithos* ichnofacies is coincident with the lower to middle shoreface transition in this type of shoreface. An archetypal *Cruziana* ichnofacies characterizes weakly affected lower-shoreface deposits.

The moderately storm-affected shorefaces (intermediate energy) show an alternation of laminated storm beds and bioturbated fair-weather deposits, resulting in the so-called "lam-scram" pattern (Howard, 1978; MacEachern and Pemberton, 1992) (see Section 6.1.5). These deposits commonly display the alternation of elements of the *Skolithos* ichnofacies as opportunistic pioneers colonizing sandstone tempestites and the *Cruziana* ichnofacies recording the activity of the fair-weather resident community (e.g. MacEachern and Pemberton, 1992; Buatois *et al*., 2007b) (Fig. 7.9a–e). The laminated storm beds either are totally unburrowed or contain a few deeply penetrating burrows (e.g. *Ophiomorpha*, *Diplocraterion*, and *Skolithos*). The fair-weather deposits are moderately to strongly bioturbated, and contain *Asterosoma*, *Helminthopsis*, *Planolites*, *Palaeophycus*, *Rhizocorallium*, and *Thalassinoides*, among other ichnotaxa. Escape trace fossils are locally present. Tiering structure is less developed than in the weakly affected lower shorefaces. Moderately storm-affected lower-shoreface deposits display an alternation of the *Skolithos* and proximal *Cruziana* ichnofacies.

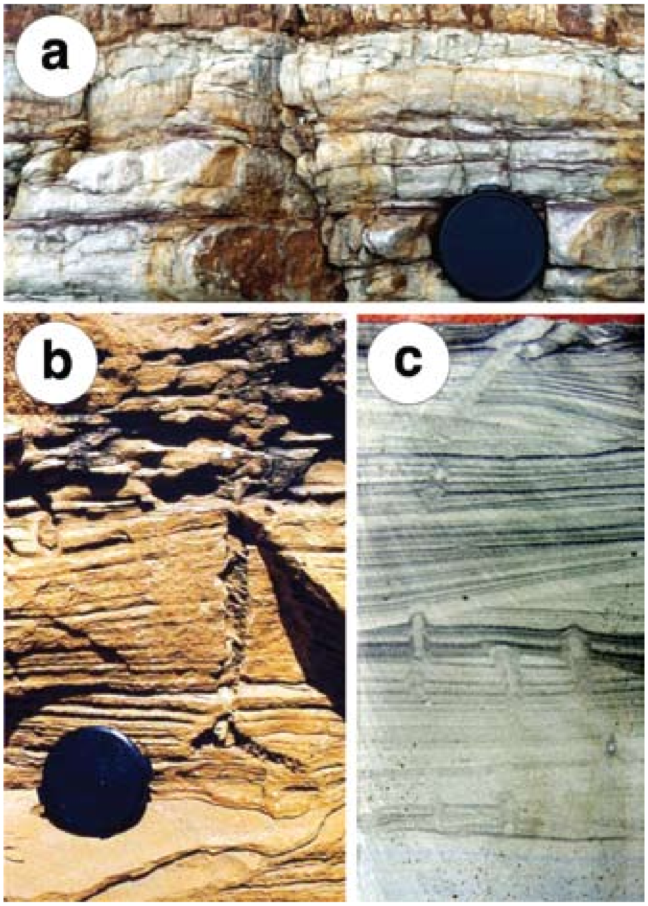


Figure 7.10 Ichnofaunas from strongly storm-dominated lower/middle shoreface deposits (high energy). (a) *Skolithos linearis* forming a pipe rock. Upper Cambrian-Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada Casa Colorada, Alfarcito Range, northwest Argentina. Lens cap is 5.5 cm. See Mángano *et al.* (2005a). (b) *Ophiomorpha nodosa* in hummocky cross-stratified sandstone. Lower Miocene, Capiricual Formation, El Anfiteatro, Serranía del Interior, Eastern Venezuela. Lens cap is 5.5 cm. (c) Escape trace fossils in amalgamated hummocky cross-stratified sandstone. Lower Permian, San Miguel Formation, Mallorquín #1 well, Paraguay. Core width is 8 cm.

The strongly storm-dominated shorefaces (high energy) commonly consist of amalgamated hummocky sandstone showing little or no bioturbation (Fig. 7.10a–c). High-energy conditions prevailed, commonly precluding the preservation of biogenic structures. Only the deepest components of the post-storm *Skolithos* ichnofacies (e.g. *Skolithos* and *Ophiomorpha*) are present. Shallow- to mid-tier biogenic structures were most likely removed by erosion due to deep scouring. Repeated storm-wave erosion either precluded the establishment of fair-weather suites, or limited their preservation in these high-energy settings (MacEachern and Pemberton 1992; Pemberton and MacEachern 1997; Buatois *et al.*, 2007b; Mángano *et al.*, 2005a). The absence of fair-weather suites in strongly storm-dominated shorefaces precludes distinction between the middle and the lower shoreface based on ichnological aspects (MacEachern and Pemberton 1992).

7.1.6 OFFSHORE TRANSITION

The offshore transition occurs immediately below the fair-weather wave base (Pemberton *et al.*, 2001). Environmental conditions in the offshore transition are more variable, and reflect the alternation of high-energy storm events and low-energy fair-weather mudstone deposition. Accordingly, offshore-transition deposits consist of regularly interbedded, parallel-laminated to burrowed mudstone, and thin to thick erosive-based, fine- to very fine-grained sandstone with hummocky cross-stratification, and combined-flow and wave ripples at the top (Fig. 7.11a). Gutter casts, flute casts, tool marks, and load casts may occur at the base of sandstone beds (e.g. Myrow, 1992; Mángano *et al.*, 2005a). Sandstone beds are laterally extensive, but commonly display important thickness variation.

The storm-related *Skolithos* trace-fossil suite is present in the offshore transition, but alternates with the fair-weather suite illustrating an archetypal *Cruziana* ichnofacies (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001). Although the degree of bioturbation is somewhat lower than in offshore deposits, some hummocky sandstone may have intensely bioturbated tops (e.g. Mángano *et al.*, 2005a) (Fig. 7.11b–c). These sandstone tops are palimpsest surfaces, recording a storm-related assemblage overprinted by the subsequent fair-weather assemblage. If the frequency and intensity of storms is low to moderate, the mudstone intervals will be thoroughly bioturbated. The resident biota is represented by a wide variety of ichnotaxa, such as *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Diplichnites* (Fig. 7.11d), *Gyrophyllites* (Fig. 7.11b), *Arthrophycus*, *Scolicia* (Fig. 7.11e), *Cylindrichnus*, *Rosselia* (Fig. 7.11f–g), *Phycosiphon* (Fig. 7.11a), *Lockeia*, *Protovirgularia*, *Siphonichnus*, *Teichichnus* (Fig. 7.11f), *Phycodes*, *Asterosoma*, *Schaubcylindrichnus*, *Taenidium*, *Helicodromites*, *Rhizocorallium*, *Thalassinoides* (Fig. 7.11h), *Chondrites* (Fig. 7.11h), *Palaeophycus* (Fig. 7.11f–g), *Planolites* (Fig. 7.11f), and *Nereites* (Fig. 7.11i). The colonizers are recorded by a few ichnotaxa, mostly *Skolithos*, *Ophiomorpha*, and *Arenicolites* (Fig. 7.11f). Escape trace fossils are also present.

7.1.7 UPPER OFFSHORE

The upper offshore occurs between the offshore transition and the lower offshore. As in the offshore transition, the upper offshore is subjected to the alternation of high-energy, short-term storm events and longer periods of suspension fallout during fair-weather. Compared with the lower offshore and offshore transition, upper-offshore deposits are commonly the most variable. Due to its bathymetric position, the upper offshore experiences a lesser degree of storm-wave influence than the offshore transition. Upper-offshore deposits consist of bioturbated mudstone intervals interbedded with thin, laterally extensive, erosionally based, very fine-grained silty sandstone layers with parallel lamination, combined-flow ripples, and wave ripples (Fig. 7.12a). Thin beds with micro-hummocky cross-stratification, hummocky cross-stratification, and planar lamination may occur.

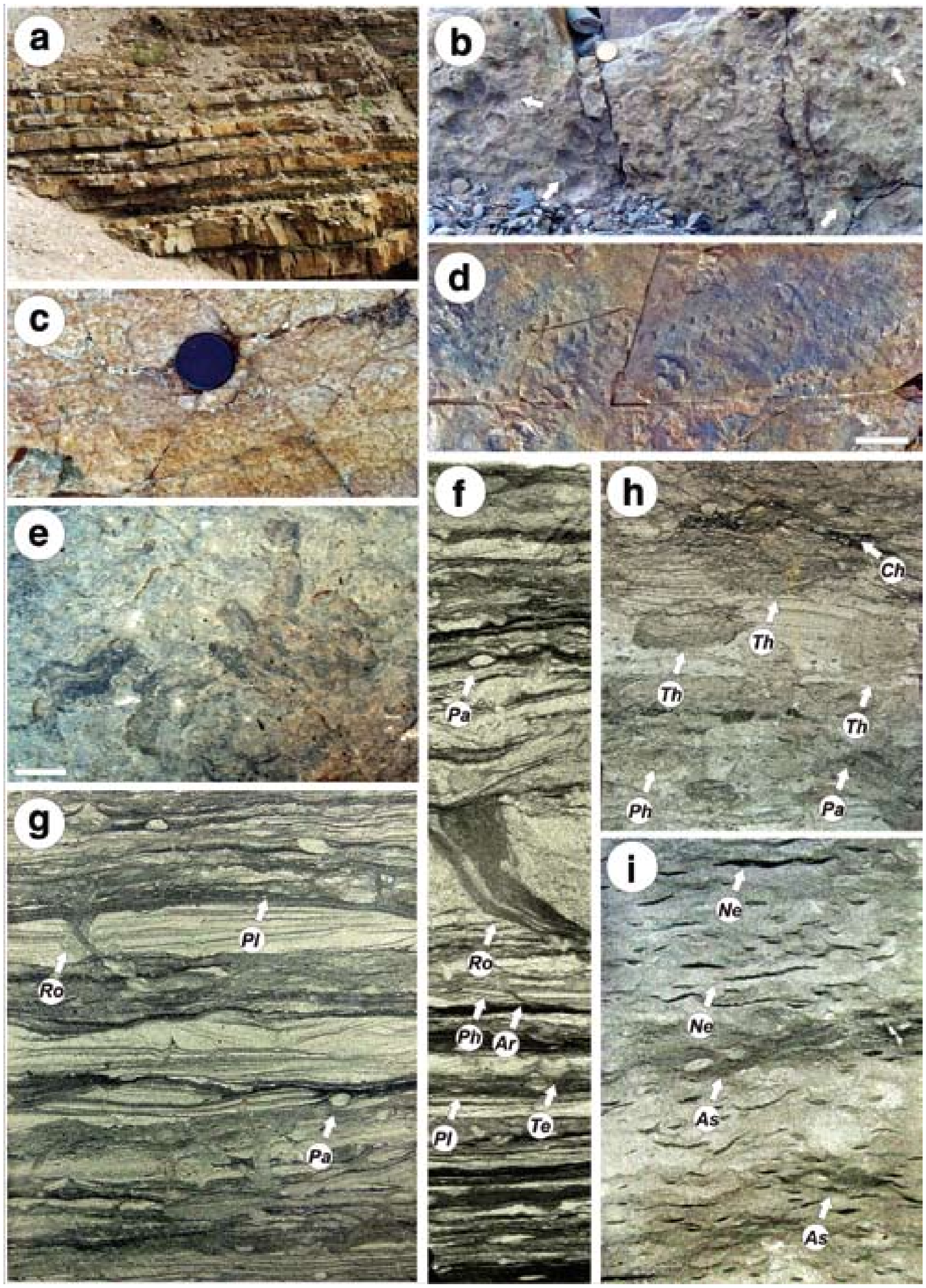


Figure 7.11 Ichnofaunas from offshore–transition deposits. (a) General outcrop view of offshore–transition deposits showing regular intercalation of very fine-grained hummocky cross-stratified sandstone and mudstone. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada de Moya, northwest Argentina. Length of hammer is 33.5 cm. See Mángano *et al.* (2005a). (b) Close-up of the top of a hummocky cross-stratified sandstone, displaying high density of the radial feeding trace fossil *Gyrophyllites* isp. (arrows). Upper Cambrian–Lower Ordovician, Humacha Member, Santa Rosita Formation, Quebrada de Humacha, near Huacalera, northwest Argentina. Coin (upper center) is 1.8 cm. See Mángano *et al.* (2005a). (c) Bedding-plane view of intensely bioturbated very fine-grained sandstone tempestite with high-density circular cross-sections of *Skolithos linearis*. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Arroyo Pintado, northwest Argentina. Lens cap is 5.5 cm. See Mángano *et al.* (2005a). (d) *Diplichnites* isp. at the top of a hummocky cross-stratified sandstone. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Arroyo Pintado, northwest Argentina. Scale bar is 2 cm. See Mángano *et al.* (2005a). (e) Fair-weather deposits containing *Scolicia* isp. Upper Cretaceous, Panther Tongue Member, Star Point Formation, Kennilworth Wash, Book Cliffs, Utah, United States. Scale bar is 2 cm. See Bhattacharya *et al.* (2007). (f) Offshore–transition deposits showing alternation of fair-weather mudstone and thin- to moderately thick-bedded very fine-grained sandstone tempestites. Ichnofauna represented by *Rosselia* isp. (*Ro*), *Arenicolites* isp. (*Ar*), *Teichichnus rectus* (*Te*), *Palaeophycus* isp. (*Pa*), *Planolites* isp. (*Pl*), and *Phycosiphon incertum* (*Ph*). Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al.* (2007b). (g) Interbedded fair-weather mudstones and discrete layers of very fine-grained sandstone tempestites. Note small *Rosselia* isp. (*Ro*) in sandstone layer, and abundant *Palaeophycus* isp. (*Pa*) and *Planolites montanus* (*Pl*) in fair-weather deposits. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (h) Partially preserved storm sandstone layer interbedded with intensely bioturbated deposits with *Thalassinoides* isp. (*Th*), *Chondrites* isp. (*Ch*), *Phycosiphon incertum* (*Ph*) and *Palaeophycus* isp. (*Pa*). In some cases, *Chondrites* is reworking *Thalassinoides* burrow fills. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (i) Intensely bioturbated offshore-transition deposits showing diffuse layers of very fine-grained sandstone emplaced by storms interbedded with fair-weather mudstone. Sandstone is dominated by *Nereites missouriensis* (*Ne*). *Asterosoma* isp. (*As*) tends to be more common in fair-weather deposits. Upper Devonian–Lower Mississippian Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2009, 2010).

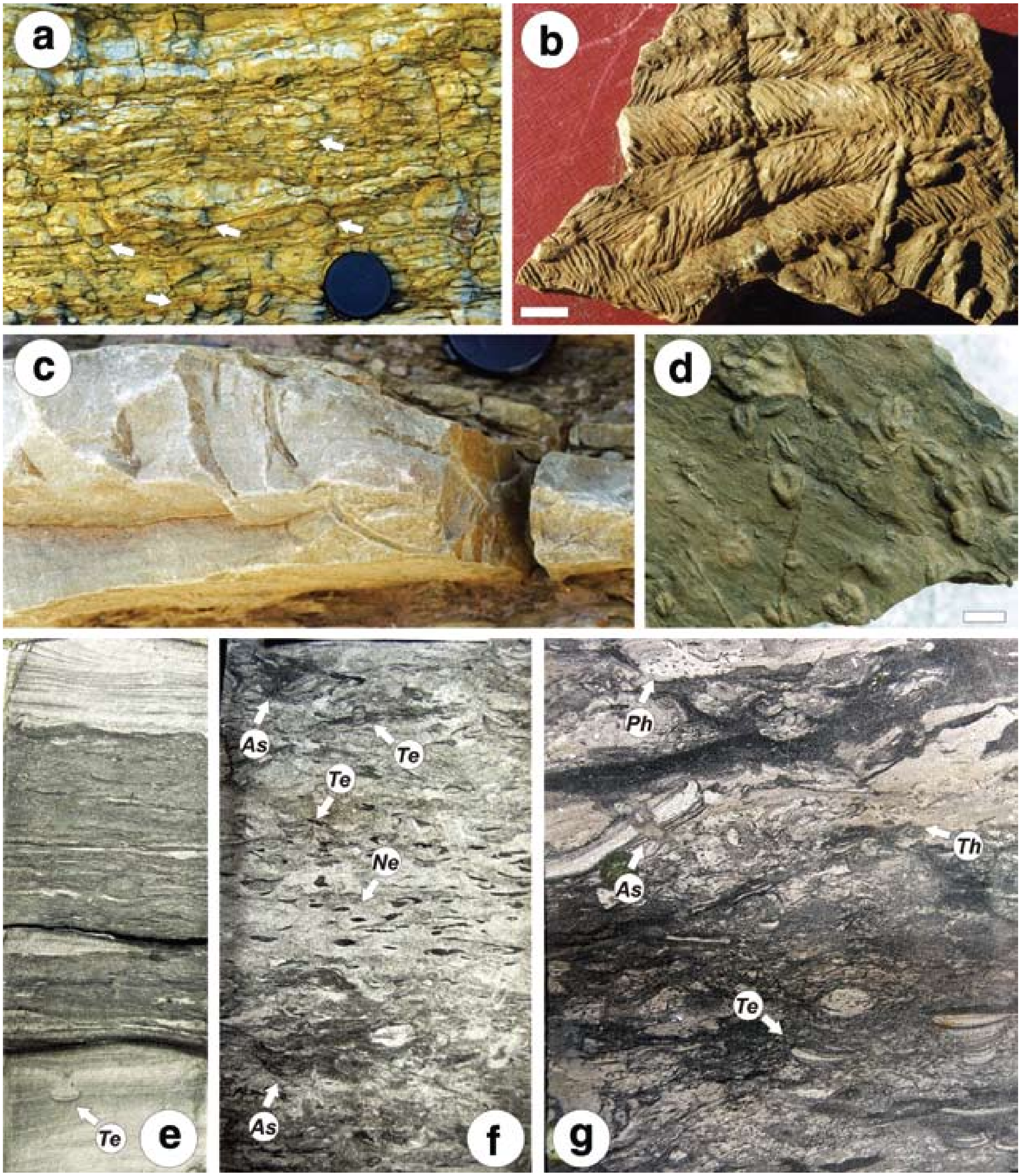


Figure 7.12 Ichnofaunas from upper-offshore deposits. (a) General outcrop view of upper-offshore deposits showing thinly bedded mudstone and very fine-grained sandstone with combined-flow and oscillatory ripples. The ichnofabric is dominated by *Trichophycus venosus* (arrows). Lower Ordovician, Rupasca Member, Santa Rosita Formation, Angosto del Ferrocarril, Chucalezna, northwest Argentina. Lens cap is 5.5 cm. See Mángano and Buatois (2011). (b) Close-up of base of a sandstone tempestite, displaying high density of *Cruziana semiplicata* cross-cut by *Palaeophycus tubularis*. Upper Cambrian, Lampazar Formation, Angosto del Moreno, northwest Argentina. Scale bar is 1 cm. See Mángano and Buatois (2003a). (c) *Arenicolites* isp. colonizing a very-fine grained sandstone tempestite. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada del Arenal, near Huacalera, northwest Argentina. Lens cap is 5.5 cm. See Mángano and Buatois (2003a). (d) Base of a sandstone tempestite, displaying abundant *Rusophycus moyensis*. Upper Cambrian–Lower Ordovician, Alfarcito Member, Santa Rosita Formation, Quebrada de Moya, northwest Argentina. Scale bar is 1 cm. See Mángano *et al.* (2002c). (e) Moderately bioturbated fair-weather offshore-transition deposits intercalated with discrete very fine-grained sandstone layers emplaced by storms displaying sparse bioturbation by *Teichichnus rectus* (*Te*). Overall moderate bioturbation degree and presence of discrete storm layers suggest relatively high frequency and intensity of storms. Upper Devonian–Lower Mississippian, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (f) Intensely bioturbated fair-weather deposits showing diffuse layers of very fine-grained storm sandstone. Sandstone is dominated by *Nereites missouriensis* (*Ne*). *Asterosoma* (*As*) isp. tends to be more common in fair-weather deposits, while *Teichichnus rectus* (*Te*) occurs in both fair-weather and storm deposits. Overall high bioturbation degree and presence of diffuse storm layers suggest relatively low frequency and intensity of storms. Upper Devonian–Lower Mississipian, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2009, 2010). (g) Partially preserved storm sandstone layer interbedded with intensely bioturbated deposits having *Asterosoma* isp. (*As*), *Phycosiphon incertum* (*Ph*) and *Teichichnus rectus* (*Te*). Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm.

Upper-offshore deposits display the alternation of the resident fair-weather and storm-related colonization trace-fossil suites. The fair-weather suite commonly reaches a diversity maximum in the upper offshore, and represents the archetypal *Cruziana* ichnofacies (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001) (Fig. 7.12b,d,f–g). This ichnofacies is represented by a wide variety of morphological patterns and ethological groups. Its composition tends to be similar to that of the offshore transition. The fair-weather mudstone is commonly completely bioturbated, and the sandstone tempestites may be moderately to intensely bioturbated. In the case of weakly storm-affected settings, bioturbation is intense, and thin storm layers may be completely homogenized or only recorded by remnant lamination (MacEachern and Pemberton, 1992; Pemberton *et al.*, 2001) (Fig. 7.12f–g). Under greater intensity and frequency of storms, the degree of bioturbation in both fair-weather and event deposits may be lower (Fig. 7.12e). The less-erosive nature of these more distally emplaced tempestites coupled with the overall lower energy of the upper offshore favor development and preservation of the fair-weather suite (Mángano *et al.*, 2005a). The storm-related suite is less distinctive, with some sandstone beds recording small and dispersed vertical burrows, most commonly *Skolithos*, *Arenicolites* (Fig. 7.12e), and *Ophiomorpha.*

7.1.8 LOWER OFFSHORE

The lower offshore occurs immediately above the storm wave base (MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001). Suspension fallout is the dominant process and, therefore, lower-offshore deposits are mudstone-dominated. However, because sedimentation occurs above the storm wave base, bioturbated mudstone background deposits are locally punctuated by laterally extensive, sharp-based, erosive storm-emplaced, very fine-grained silty sandstone with combined-flow ripples and parallel lamination.

Bioturbation is commonly very intense in lower-offshore deposits (Fig. 7.13). Background mudstone is thoroughly bioturbated, while bioturbation patterns in the associated distal tempestites are more variable. Thin tempestites are commonly represented by remnant lamination, while thick sandstone beds show better preservation of the primary fabric, and trace fossils are commonly restricted to the top (Pemberton *et al.*, 2001). The storm-related trace-fossil assemblage is commonly poorly developed and the fair-weather assemblage represents the distal *Cruziana* ichnofacies (MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001). Typical components are *Phycosiphon* (Fig. 7.13a–f), *Helminthopsis*, *Nereites* (commonly *N. missouriensis*), *Chondrites* (Fig. 7.13e, and f), *Zoophycos* (Fig. 7.13g), *Planolites* (Fig. 7.13f), *Teichichnus* (Fig. 7.13e), *Palaeophycus*, *Asterosoma* (Fig. 7.13f), *Scolicia*, *Schaubcylindrichnus* (Fig. 7.13a–b and d) and *Thalassinoides* (Fig. 7.13c). The tiering structure is commonly complex, displaying multiple ichnoguilds. Although the degree of bioturbation and ichnodiversity are typically high, more impoverished suites may be present under oxygen-depleted conditions (Mángano *et al.*, 2005a). In addition, the scarcity of sandstone interbeds may have inhibited preservation and visibility of biogenic structures in the field.

7.1.9 SHELF

The shelf extends from the storm wave base to the slope break. Therefore, suspension-fallout sedimentation is the dominant process and bioturbated mudstone is the typical facies. Locally, thin normally graded siltstone layers, representing storm-induced turbidites, may occur.

Shelf deposits are typically pervasively bioturbated, and feeding and grazing traces of deposit feeders dominate, illustrating the *Zoophycos* ichnofacies (MacEachern *et al.*, 1999a; Pemberton *et al.*, 2001). Typical components are *Zoophycos*, *Chondrites*, and *Phycosiphon*. *Trichichnus* and *Planolites* may also be present. Ichnofabrics tend to be dominated by deep-tier structures that commonly obliterate shallowly emplaced biogenic structures. However, under certain conditions, the shelf may lie within the oxygen minimum zone and, therefore, deposits may be scarcely bioturbated or even totally unburrowed. In the latter case, parallel laminated black shales represent the typical facies (e.g. Buatois *et al.*, 2006a; Angulo and Buatois, 2009).

7.2 TIDE-DOMINATED SHALLOW MARINE

Our present knowledge of the ichnology of tidal depositional systems lags behind that of wave-dominated environments. However, a number of contributions have outlined some of the most relevant characteristics of ichnofaunas from tidal-flat, subtidal-sandbar complexes and tidal dunes (e.g. Mángano and Buatois, 1999b; Mángano *et al.*, 2002a; Desjardins *et al.*, 2010a). While wave-dominated systems display a clear onshore–offshore trend in energy conditions (see Section 7.1), the energy gradient in tide-dominated shallow-marine environments is not straightforward (Yoshida *et al.*, 2007).

Despite all these complexities, Klein (1971, 1977) proposed a facies model for tide-dominated shorelines based on the integration of observations from modern and ancient deposits. In this model, tide-dominated shorelines are subdivided into a supratidal region, the upper-, middle-, and lower intertidal zones, and the subtidal area (see summary in Dalrymple, 1992). Within this setting, tidal energy increases seaward reaching a maximum in the proximal-subtidal zone and then decreases towards the distal shelf. Accordingly, tidal flats in general coarsen seaward, in contrast to wave-dominated shorelines that coarsen landward. Therefore, a typical tidal-flat profile in a landward direction comprises a lower-intertidal sand flat, a middle-intertidal mixed (sand and mud) flat, and an upper-intertidal mud flat. As a result, many tide-dominated shorelines are represented by muddy coasts (Wang *et al.*, 2002). Landward of the mud flat, supratidal salt marshes are typically present under temperate conditions, while mangroves may occur in tropical to subtropical settings (see Section 8.1.2). The subtidal zone is present seaward of the sand flat.

The intertidal zone represents a harsh ecosystem where marine organisms often approach the survival boundaries of

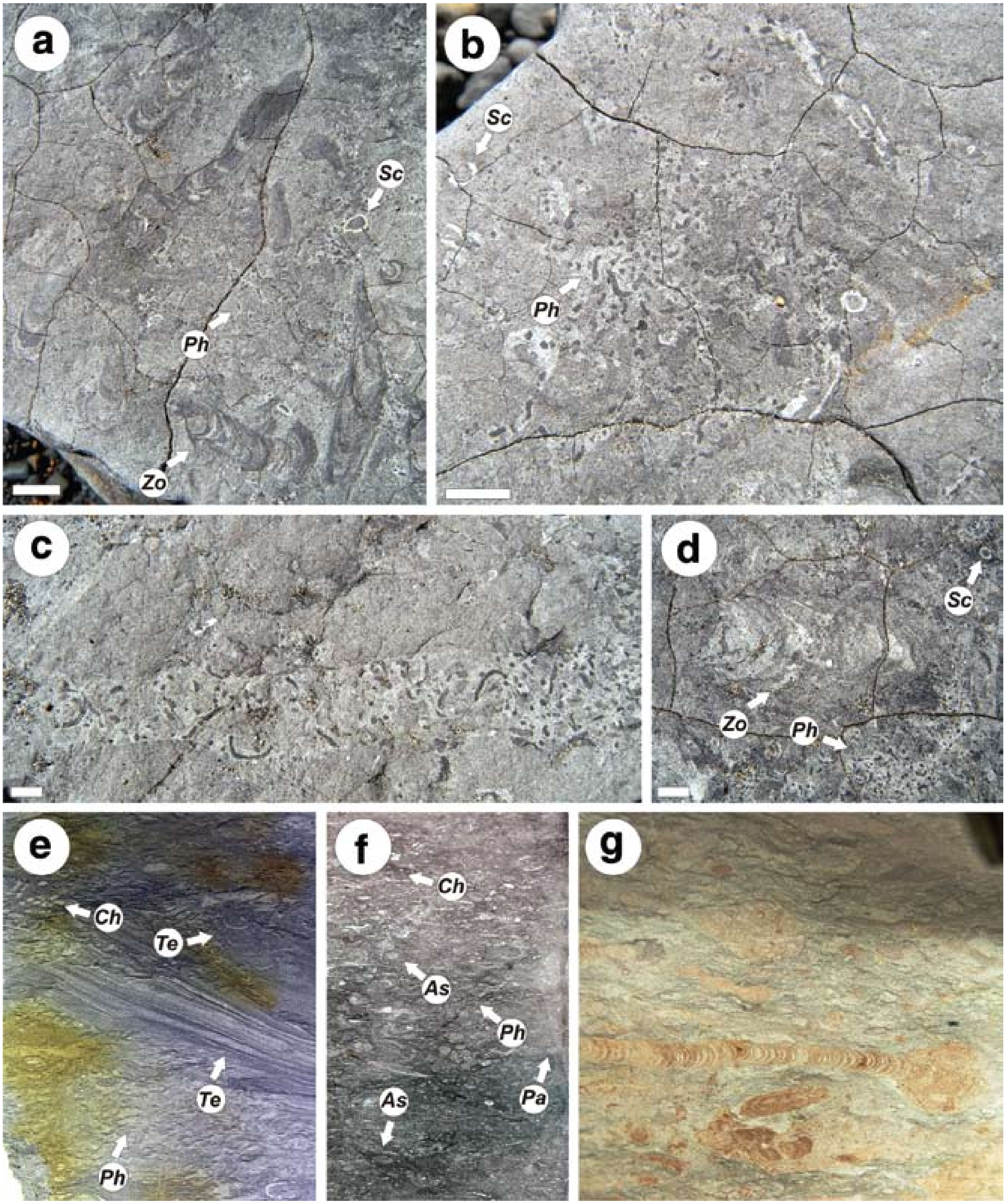


Figure 7.13 Ichnofaunas from lower-offshore deposits. (a) Bedding-plane surface view of intensely bioturbated deposits containing *Phycosiphon incertum* (*Ph*), *Zoophycos* isp. (*Zo*), and *Schaubcylindrichnus freyi* (*Sc*). Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (b) Close-up showing *Phycosiphon incertum* (*Ph*) and *Schaubcylindrichnus freyi* (*Sc*). Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (c) *Thalassinoides* isp. reworked by *Phycosiphon incertum*. Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (d) Close-up of intensely bioturbated deposits with *Phycosiphon incertum* (*Ph*), *Zoophycos* isp. (*Zo*), and *Schaubcylindrichnus freyi* (*Sc*). Lower Pliocene, Lacui Formation, Punta Pirulil, Chiloe Island, southern Chile. Scale bar is 1 cm. (e) Evenly distributed *Phycosiphon* (*Ph*) cross-cut by *Chondrites* (*Ch*) and *Teichichnus* (*Te*). Note longitudinal view of *Teichichnus* spreiten that may be confused with primary sedimentary lamination. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (f) Intensely bioturbated deposits dominated by distinctive deep-tier *Chondrites* isp. (*Ch*). Shallow-tier *Asterosoma* isp. (*As*), *Phycosiphon incertum* (*Ph*), and *Planolites* isp. (*Pl*) form the background ichnofabric. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (g) Deep-tier *Zoophycos* isp. overprinted on a background ichnofabric. Lower Cretaceous, Muderong Shale Formation, Pluto Field, Carnavon Basin, offshore northwestern Australia. Core width is 10 cm.

their tolerance range to environmental extremes. Only a very few species are able to inhabit the entire tidal range (Reise, 1985). Zonational distribution of organisms is, therefore, the rule. Accordingly, different animal communities live in different areas within the tidal flat, where various environmental parameters differ substantially. Although tidal flats are primarily a marine habitat, they are subject to the extremes of terrestrial climate, heating, frost, desiccation, and rain (Reise, 1985). Temperature, time of exposure to subaerial conditions, salinity, hydrodynamic energy, and substrate are effective limiting factors. In the upper-intertidal zone, environmental conditions are not only more extreme; high temporal instability and unpredictability resulting in a decrease in species diversity are the norm. Physical factors, such as heating, frost, and water loss, play a crucial role in benthic communities. In general, biological diversity and biomass decrease toward the level of high tide (Newell, 1979; Reise, 1985). Although primary production by benthic microalgae increases in a landward direction, benthic consumers do not show a corresponding increase, most likely due to the difficulties for marine organisms to adapt to prolonged low-tide emersion (Reise, 1985).

Periodic emersions and submersions of the intertidal zone are matched by periodic fluctuations in salinity. In addition, seasonal rains and drainage from the continent strongly control the salinity and position of the water table. Changes in salinity, together with subaerial exposure and temperature, are more drastic in the upper-intertidal area, diminishing towards the lower-intertidal zone (Newell, 1979; Reise, 1985). In general, euryhaline species tend to be more abundant in the upper-intertidal zone (Newell, 1979). Complex hydrological conditions of the tidal flat promote particular behavioral strategies for protection, such as infaunalization. Inhabiting a burrow or temporary refuge in the sediment is an effective strategy in avoiding salinity variations (see Section 6.1.4). In low-energy settings, close to the low-water mark, surface salinity changes have little effect on the salinity of interstitial water below a depth of about 2 cm (Sanders *et al.*, 1965; Johnson, 1967).

Many organisms of the intertidal zone have developed biological rhythms (e.g. circa-tidal and circa-semilunar rhythms) of vertical or horizontal migration controlled by tide cyclicity (Palmer, 1995). Many species (e.g. the modern crab *Sesarma reticulatum*) hide in their burrows during low tide and are active during high tide (Palmer, 1967, 1995; Seiple, 1981). Horizontal migration is another strategy to minimize the dramatic salinity shifts in the upper-intertidal zone. For example, the modern predator isopod *Eurydice pulchra* lives buried in the sand flat during emersion, but rises into the water column with flood tides to swim at the water's edge and feed on epifauna, infauna, and debris. Subsequently, it retreats seaward with ebb tide and reburies itself for protection (Warman *et al.*, 1991). Marine invertebrate surface activity on the tidal flat tends to be more intense during high tide (Vader, 1964; Pieńkowski, 1983). In contrast, many semi-terrestrial and terrestrial animals (e.g. terrestrial crabs and the modern intertidal beetle *Thalassotrechus barbarae*) typically display a peak of activity during low-tide emersions (Palmer, 1995). Other adaptations to stressful salinity conditions involve protection by organic substances (e.g. mucus) and osmoregulation (Kinne, 1964). Some animals combine several strategies for better protection. For example, the modern *Corophium* is a good osmoregulator and a well-known burrower that can tolerate salinities between 2‰ and 47‰.

In contrast to the more stressful conditions of the upper-intertidal zone, lower-intertidal invertebrate communities resemble contiguous communities that inhabit environments below the fair-weather wave base (Schäfer, 1972; Reise, 1985; Swinbanks and Murray, 1981). The higher predictability of the middle- to lower-intertidal zones results in high species diversity containing species that are particularly adapted to utilize the resources of specific microhabitats (Sanders, 1968, 1969; Slobodkin and Sanders, 1969).

An integrated ichnological and sedimentological model has been proposed for tidal flats and related settings (Mángano and Buatois, 2004a) (Figs. 7.14 and 7.15) (Box 7.2). This model attempts to address patterns of distribution of biogenic structures in tide-dominated shorelines which, albeit sheltered, developed under fully or near-fully marine salinity conditions. Therefore, the model does not address ichnofaunas from tidal flats formed in more restricted, marginal-marine settings, such as estuaries or interdistributary bays, which are typically of lower diversity in brackish-water environments or contain freshwater trace fossils in the case of fluvio-estuarine transitions (see Chapter 8). Although the early observations were based on Paleozoic outcrops (Mángano and Buatois, 1999b; Mángano *et al.*, 2002a), the model was subsequently expanded to encompass the rest of the Phanerozoic (Mángano and Buatois, 2004a).

The ichnofacies gradient in tide-dominated shorelines is opposite to that in wave-dominated shoreface environments. As overall tidal energy increases from supratidal to subtidal settings, the *Skolithos* ichnofacies tends to occur seaward of the *Cruziana* ichnofacies (Mángano *et al.*, 2002a). This shoreward decrease of energy parallels a decrease in oxygenation, sand content, amount of organic particles in suspension, and mobility of the substrate. This gradient is consistent with information from modern tide-dominated environments, where the highest faunal diversity is present around mid-tide level (Beukema, 1976). In fact, similar ichnological trends have been detected in modern tidal flats (Bajard, 1966; Howard and Dorjes, 1972; Swinbanks and Murray, 1981; Ghare and Badve, 1984; Gerdes *et al.*, 1985; Frey *et al.*, 1987a, b; Aitken *et al.*, 1988; Larsonneur, 1994). For example, Swinbanks and Murray (1981) recognized five zones in the tidal flats of British Columbia, each characterized by different associations of biogenic structures. Similar zonations have been established in tidal flats of South Korea (Frey *et al.*, 1987a, b) (Box 7.3).

7.2.1 SUPRATIDAL MARSH AND MANGROVES

The supratidal area may be vegetated forming salt marshes or mangroves, depending on the predominant climatic conditions (see Section 8.1.2). Sporadically the supratidal zone may be affected by storm surges (Wang *et al.*, 2002). In supratidal

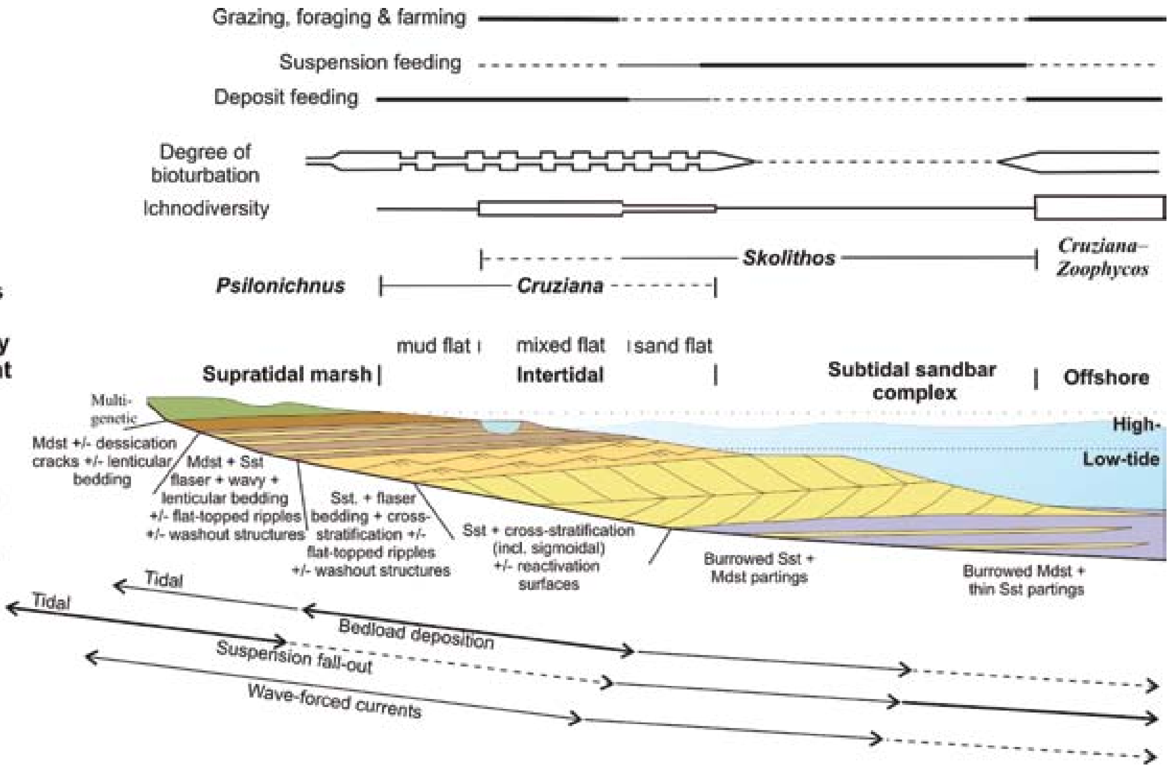


Figure 7.14 Ichnological and sedimentological aspects along a tide-dominated depositional profile. High intensity of bioturbation in supratidal areas is due to plant root traces. Irregular pattern of intensity of bioturbation in the tidal flat reflects spatial heterogeneity. Distribution of ichnofacies and depositional processes based on Mángano and Buatois (1999b, 2004a).

Box 7.3 Ichnology of modern tidal flats in South Korea

Extensive macrotidal flats near the mouth of the Yellow River, in South Korea, span from the shore to approximately 4 km seaward. Analysis of biogenic structures across these low-energy tidal flats allows recognition of ichnofaunal gradients across a tide-dominated depositional profile. Three different ichnocoenosis (brachyuran, molluscan, and holothurian assemblages) have been distinguished. The brachyuran ichnocoenose occurs from 0 to 900 m from the shore, in the muddiest, most landward reaches of the tidal flat. It is dominated by dwelling, locomotion, and grazing traces of crabs, with secondary presence of gastropod locomotion traces and polychaete dwelling traces. The molluscan ichnocoenose is present from 900 to 2100 m from the shore, in mid-flat deposits consisting of sandy and clayey silt. It is dominated by dwelling traces of bivalves and locomotion traces of gastropods, with subordinate occurrences of dwelling traces of polychaetes and grazing and locomotion traces of crabs. The holothurian ichnocoenose is present from 2100 to more than 3900 m from the shore, corresponding to the sandiest, most seaward end of the tidal flat. This ichnocoenose is dominated by feeding and grazing traces of synaptid holothurians; gastropod locomotion traces and bivalve dwelling structures are also present. All the ichnocoenoses belong to the *Cruziana* ichnofacies, demonstrating the presence of this archetypal association in tidal flats.

Reference: Frey *et al*. (1987a, b).

deposits, the sedimentary fabric is commonly obliterated by root traces. The cordgrass *Spartina* is by far the most widespread plant in many supratidal marsh settings, and its root traces are pervasive (e.g. Edwards and Frey, 1977; Basan and Frey, 1977; Pomeroy *et al*., 1981; Montague *et al*., 1981). In mangroves, root networks of *Avicennia*, *Rhizopora*, and *Sonneratia* are extremely widespread (Cadée, 1998). Animal traces include elements of the *Psilonichnus* ichnofacies (Frey and Pemberton, 1987). Gastropods and crustaceans (mainly crabs) are among the most important marine representatives. The supratidal zone grades landwards into a wide variety of terrestrial environments characterized by different trace-fossil assemblages that are mostly included in the *Scoyenia* and *Coprinisphaera* ichnofacies, being insects the most important tracemakers (Buatois and Mángano, 1995b; Genise *et al*., 2000) (see Section 7.1.1). Vertebrates, mostly mammals, reptiles and birds, also produce a wide variety of structures (Frey and Pemberton, 1986).

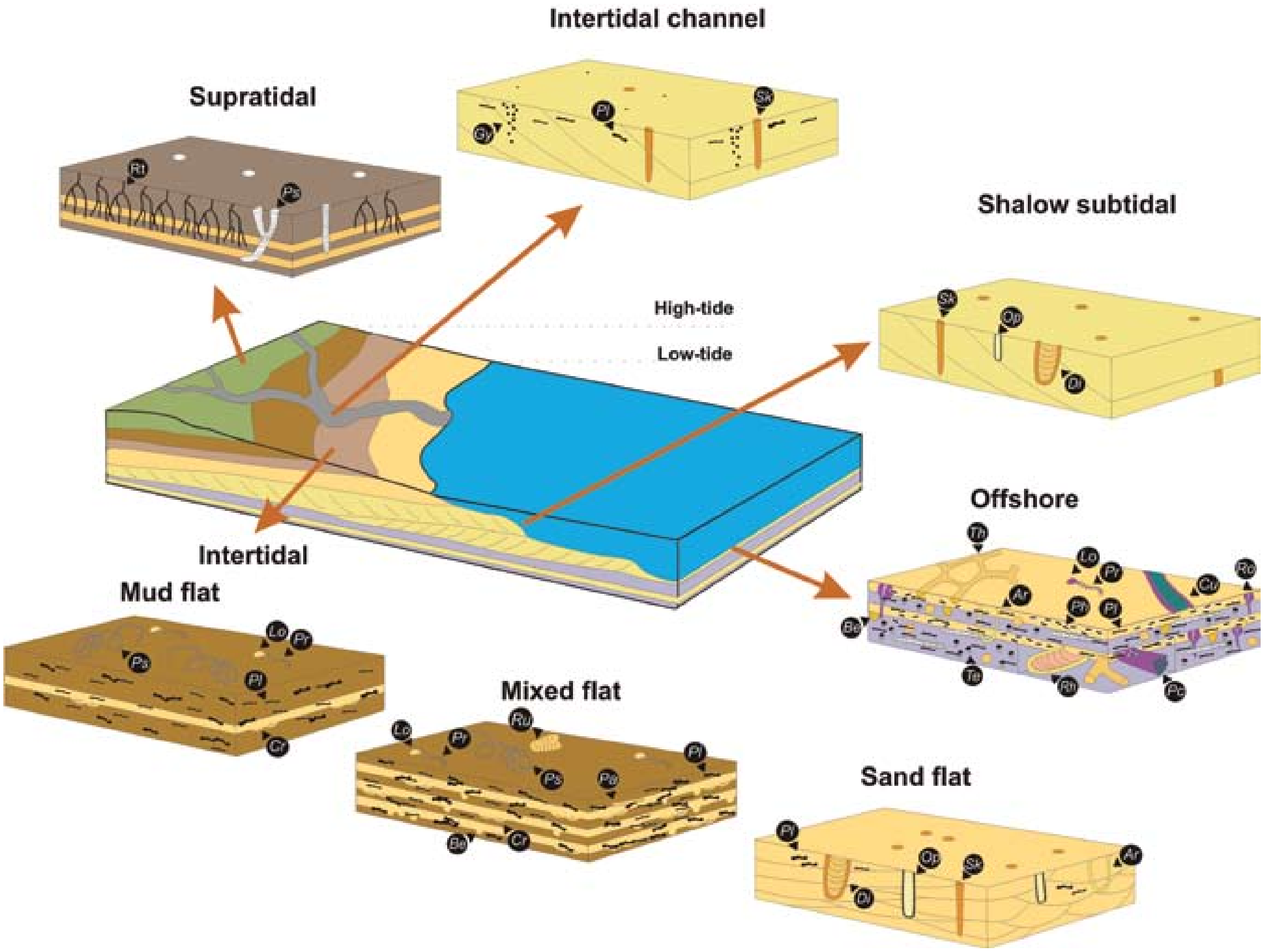


Figure 7.15 Schematic reconstruction of trace-fossil distribution in tide-dominated shallow-marine environments. The supratidal marsh may be intensely bioturbated by root traces (Rt). *Psilonichnus* (*Ps*) may be present also. Deposit-feeder traces, such as *Planolites* (*Pl*), *Psammichnites* (*Ps*), *Cruziana* (*Cr*), *Protovirgularia* (*Pr*), and *Lockeia* (*Lo*) tend to dominate in the mud flat. The mixed flat is similar to the mud flat, but other ichnotaxa may be added mostly along mudstone–sandstone interfaces, including *Rusophycus* (*Ru*), *Palaeophycus* (*Pa*), and *Bergaueria* (*Be*). The sand flat is highly variable depending on the tidal regime. *Ophiomorpha* (*Op*), *Arenicolites* (*Ar*), *Diplocraterion* (*Di*), *Skolithos* (*Sk*), and *Planolites* (*Pl*) are common. Associated intertidal channel deposits are less bioturbated and display less ichnodiversity, *Planolites* (*Pl*), *Gyrolithes* (*Gy*), and *Skolithos* (*Sk*) being common forms. Shallow-subtidal sandbodies typically contain vertical burrows, such as *Ophiomorpha* (*Op*), *Diplocraterion* (*Di*), and *Arenicolites* (*Ar*). These sandbodies tend to grade seaward into fine-grained offshore deposits containing diverse ichnofaunas. Typical components are *Arenicolites* (*Ar*), *Bergaueria* (*Be*), *Planolites* (*Pl*), *Curvolithus* (*Cu*), *Protovirgularia* (*Pr*), *Lockeia* (*Lo*), *Phycodes* (*Pc*), *Thalassinoides* (*Th*), *Rhizocorallium* (*Rh*), *Rosselia* (*Ro*), *Teichichnus* (*Te*), and *Phycosiphon* (*Ph*).

7.2.2 MUD FLAT

The upper zones of the tidal flat, referred to as the mud flat, are dominated by deposition of fine-grained suspended sediment. Mud deposition is also promoted by clay flocculation and biodeposition in the form of the production of fecal pellets and pseudofeces (de Boer, 1998; Augustinus, 2002; Potter *et al.*, 2005). Mud-flat deposits consist of laminated or massive mudstone with rare siltstone and very fine-grained sandstone interbeds and interlaminae. Lenticular bedding is the dominant bedding style. Scarcity of sandstone layers commonly precludes preservation of biogenic structures. Discrete trace fossils are relatively rare, and an indistinct mottled texture (most likely *Planolites*) is common instead. However, interface trace fossils of the *Cruziana* ichnofacies, such as *Cruziana*, *Rusophycus*, *Psammichnites*, *Lockeia*, and *Protovirgularia*, can be preserved in the sporadic sandstone intercalations (e.g. Mángano *et al.*, 2002a). These occurrences may record either a wide environmental range of the producers, or short-term incursions into this zone. High-density trace-fossil assemblages produced by vagile organisms most likely reflect landward migrations from the lower-intertidal zone, rather than upper-intertidal inhabitants (Mángano *et al.*, 2002a). These migrations are probably regulated by tidal cyclicity in connection with the search for food. Also, simple grazing trails, such as *Helminthopsis* and *Helminthoidichnites*, may occur in connection with microbial mats. Vertebrate trackways are also common in tide-dominated shorelines, particularly in supratidal to upper-intertidal zones. Vertebrate trackway assemblages in tidal flats typically illustrate some of the ichnocoenoses of the *Brontopodus* and *Batrachichnus* ichnofacies (Hunt and Lucas, 2007).

Box 7.2 Ichnology of Lower to Middle Cambrian tide-dominated shallow-marine deposits of northwest Argentina

The Campanario Formation of the upper Lower to Middle Cambrian Mesón Group of northwest Argentina records deposition in tide-dominated shallow-marine environments characterized by extensive tidal-flat areas flanked seawards by subtidal-sandbar complexes. Shallow-subtidal and intertidal sand-flat deposits are dominated by vertical domiciles of suspension feeders and passive predators, such as *Skolithos linearis*, *Arenicolites* isp., and *Diplocraterion parallelum*, illustrating the *Skolithos* ichnofacies. Sand-flat deposits also contain high-density occurrences of the ichnogenus *Syringomorpha*, commonly forming monospecific assemblages. Clusters of *Rusophycus leifeirikssoni* are locally present. Although vertical burrows (*Skolithos linearis*, *Syringomorpha nilssoni*) are present in the mixed-flat facies, the dominant form is *Rusophycus leifeirikssoni*. Other ichnotaxa include *Cruziana problematica*, *Rusophycus carbonarius*, large *Rusophycus* isp., *Diplichnites* isp., *Planolites* isp., *Palaeophycus tubularis*, *Helminthoidichnites tenuis*, and *Bergaueria* cf. *B. perata*. In contrast to the sand flat, the mixed flat is dominated by horizontal feeding, locomotion and resting trace fossils, recording a relatively low-diversity *Cruziana* ichnofacies. Trace fossils are rare in the mud-flat deposits, mostly represented by *Planolites* isp. and indistinct mottling. The six ichnoguilds (*Cruziana problematica*, *Palaeophycus*, *Bergaueria*, *Rusophycus leifeirikssoni*, *Syringomorpha*, and *Skolithos*) defined show a preferential palaeoenvironmental distribution following proximal–distal trends (Fig. 7.16). Although there is some superimposition, deep-tier ichnoguilds tend to occur in the higher-energy, seaward distal portions (i.e. shallow-subtidal to intertidal transition and sand flat). Middle- and shallow-tier ichnoguilds are dominant in the moderate- to low-energy, proximal regions (i.e. mixed flat). This resultant pattern of distribution of biogenic structures is shaped by the interplay of key environmental parameters (hydrodynamic energy, substrate and food supply) overprinted by a strong taphonomic control.

Reference: Mángano and Buatois (2004b).

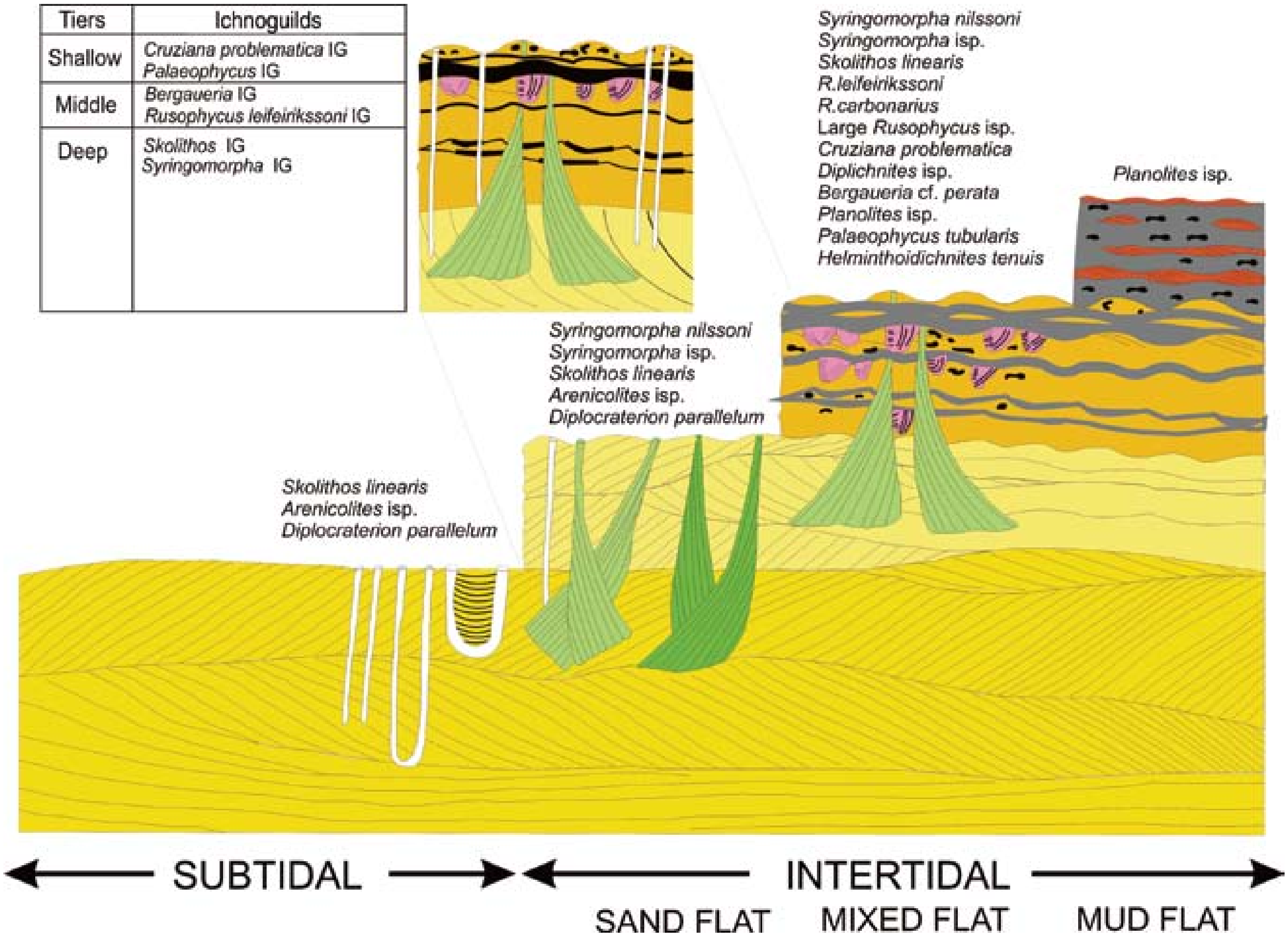


Figure 7.16 Ichnological and sedimentological model of the Campanario Formation of the Lower to Middle Cambrian Mesón Group of northwest Argentina (after Mángano and Buatois, 2004b).

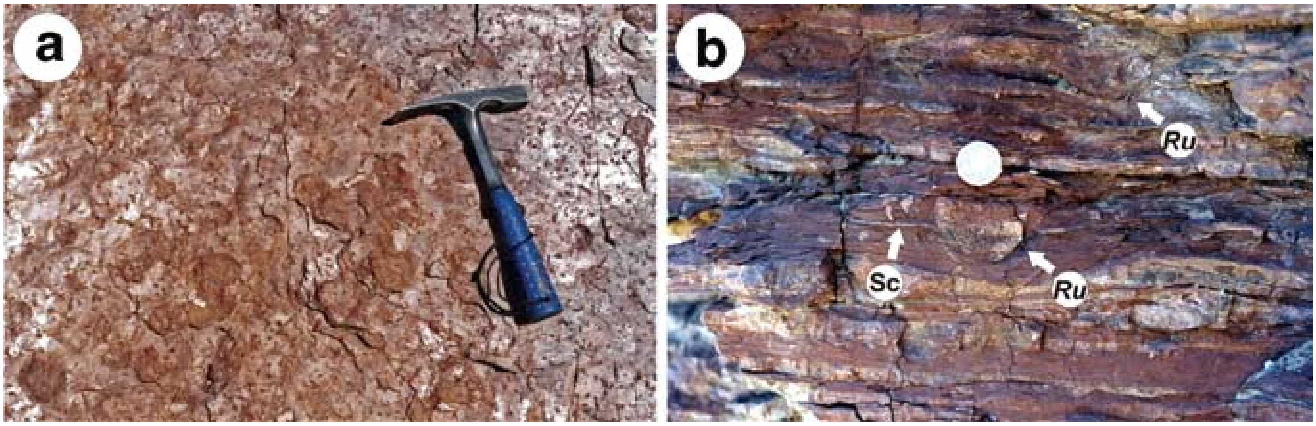


Figure 7.17 Invertebrate ichnofaunas from mixed-flat deposits from the Lower to Middle Cambrian Campanario Formation of the Mesón Group. See Mángano and Buatois (2004b). (a) Bedding plane view (top) of a cluster of *Rusophycus leifeirikssoni* in mixed-flat deposits. Angosto del Morro de Chucalezna, Quebrada de Huamahuaca, northwest Argentina. Length of hammer is 33.5 cm. (b) Cross-section view of *Rusophycus leifeirikssoni* (*Ru*) in mixed-flat deposits. Note associated synaeresis cracks (*Sc*). Angosto del Morro de Chucalezna, Quebrada de Huamahuaca, northwest Argentina. Coin is 2.3 cm.

7.2.3 MIXED FLAT

Middle-intertidal areas (mixed flat) are typified by sedimentation from traction alternating with fallout from suspension. Deposits consist of thinly interbedded wave- and current-ripple cross-laminated very fine-grained sandstone and massive or parallel-laminated mudstone. Heterolithic bedding is typical, mostly represented by flaser and wavy bedding. Wrinkle marks associated with relict troughs are locally common (e.g. Mángano *et al.*, 2002a). Flat-topped ripples and washout structures may occur. Elements of the *Cruziana* ichnofacies are characteristic of the mixed flat (Fig. 7.17a–b). Alternation of sandstone and mudstone layers enhances preservation of horizontal interface traces, such as those that typify the *Cruziana* ichnofacies. Common components are *Cruziana*, *Rusophycus*, *Psammichnites*, *Protovirgularia*, *Lockeia*, *Palaeophycus*, *Planolites*, *Helminthopsis*, *Helminthoidichnites*, and *Bergaueria*. Clusters of *Rusophycus* are common in lower Paleozoic tidal-flat deposits (Mángano and Buatois, 2004b) (Fig. 7.17a). Vertebrate trackways are commonly preserved in sandy layers of the middle-intertidal zone. Mesozoic examples include spectacular dinosaur tracks, commonly forming megatracksites (e.g. Lockley *et al.*, 1992; Avanzini *et al.*, 2006) (Fig. 7.18a–d).

7.2.4 SAND FLAT

Sedimentation in the lower zones of the tidal flat, referred to as the sand flat, is dominated by bedload traction of sand-sized sediment. As is the case of the lower shoreface in wave-dominated shorelines (MacEachern and Pemberton, 1992), the sand flat is the most variable intertidal zone in terms of both sedimentary facies and trace-fossil content. Whereas the character of deposits in the lower shoreface mostly depends on the intensity and frequency of storms (see Section 7.1.5), those of the lower tidal flat are essentially controlled by the intensity of tidal currents (Mángano and Buatois, 2004a). Macrotidal and megatidal regimes are characterized by high current speeds and, therefore, migration of large-scale bedforms (i.e. two-dimensional and three-dimensional dunes) is the dominant process (Dalrymple, 1992; Dalrymple and Rhodes, 1995; Boyd *et al.*, 2006). Deposits consist of thick-bedded, through and planar cross-bedded coarse- to fine-grained sandstone. Medium- to very fine-grained sandstone with upper-flow regime horizontal planar parallel lamination and rare current ripples also occurs in macrotidal and megatidal regimes (Dalrymple *et al.*, 1990; Dalrymple, 1992; Dalrymple and Choi, 2007). Under macrotidal and megatidal conditions, the lower-intertidal zone is very difficult to distinguish from subtidal areas. High energy and rapidly migrating bedforms generally preclude the establishment of a mobile epifauna and shallow infauna, inhibiting development of the *Cruziana* ichnofacies. Bioturbation typically consists of vertical burrows of suspension feeders or passive predators, such as *Skolithos* (Fig. 7.19a), *Ophiomorpha*, *Arenicolites* (Fig. 7.19b), and *Diplocraterion* (Fig. 7.19c), representing the *Skolithos* ichnofacies. In Cambrian examples, the ichnogenus *Syringomorpha* may occur in high densities (Fig. 7.19d). Assemblages reflect short-term colonization windows along reactivation surfaces (Pollard *et al.*, 1993; Mángano *et al.*, 1996b; Mángano and Buatois, 2004b). If mud drapes formed during slack water are preserved, they may contain *Planolites*.

Under tidal currents of lower intensity, the migrating bedforms are small current ripples. Deposits consist of current-ripple cross-laminated fine- to very-fine grained sandstone. Flat-topped ripples, washout structures, and wrinkle marks are common. Low energy coupled with short periods of subaerial exposure allows development of a diverse resident fauna. As a result, these tidal flats contain high-diversity assemblages of the *Cruziana* ichnofacies (Mángano et al., 2002a; Mángano and Buatois, 2004a). A wide variety of ethological groups and trophic types are represented. Common elements are *Cruziana* (Fig. 7.20a), *Rusophycus*, *Asteriacites* (Fig. 7.20a), *Pentichnus*, *Psammichnites*, *Curvolithus* (Fig. 7.20b), *Nereites*

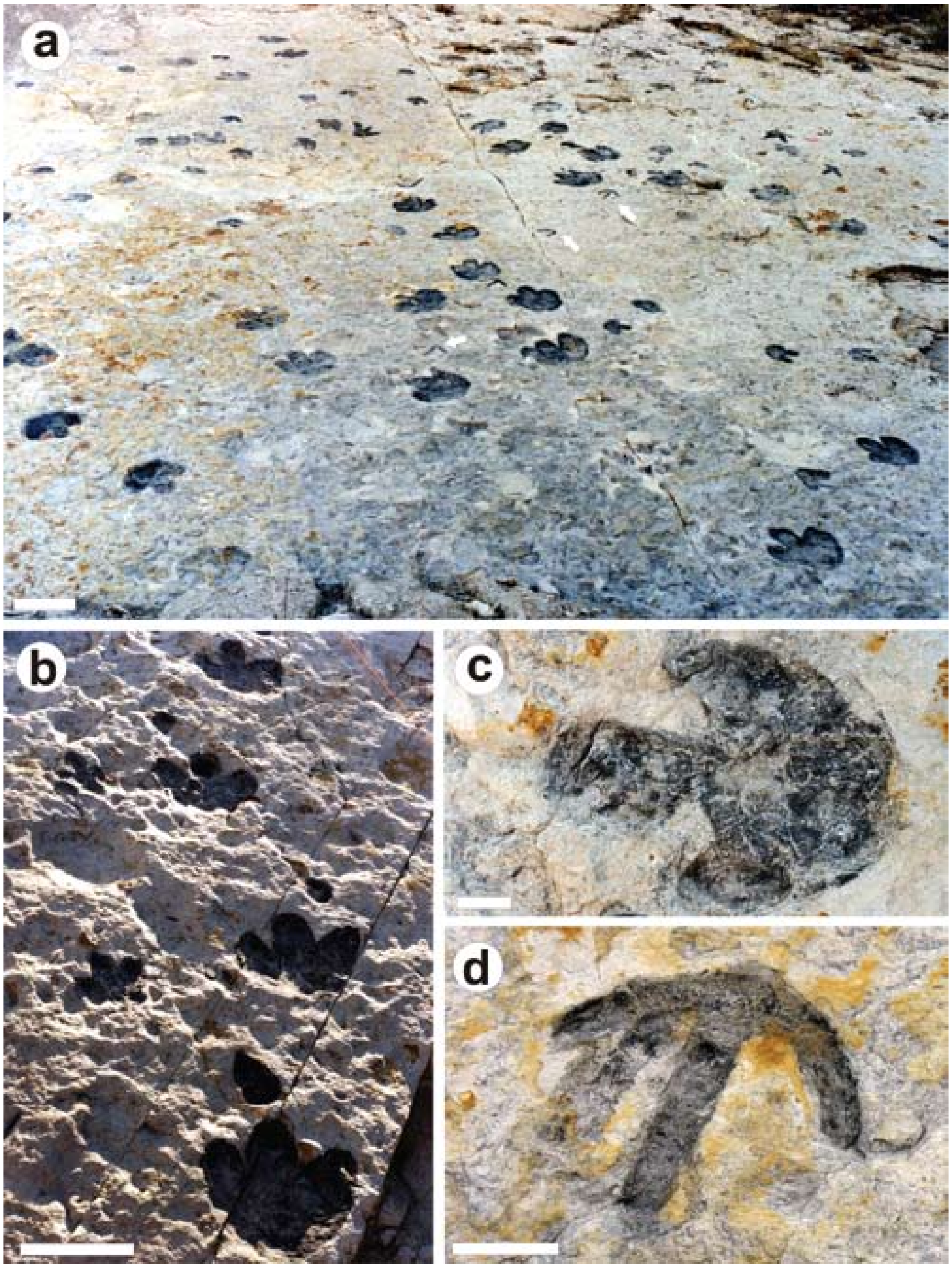


Figure 7.18 Dinosaur tracks in tidal-flat deposits. Lower Cretaceous, Dakota Group, Alameda Avenue, west of Denver, Colorado, United States. (a) General view of a sandstone top with large ornithopod trackways (*Caririchnium leonardii*) and small theropod trackways (*Magnoavipes loewi*, arrowed). Scale bar is 50 cm. (b) The ornithopod trackway *Caririchnium leonardii*. Scale bar is 50 cm. (c) Close up of an ornithopod track (*Caririchnium leonardii*). Scale bar is 5 cm. (d) Close up of a theropod track (*Magnoavipes loewi*). Scale bar is 5 cm. See Lockley (1987, 2001, 2003) and Lockley *et al*. (2001).

(Fig. 7.20c), *Lockeia* (Fig. 7.20d), *Protovirgularia* (Fig. 7.20e–f), *Palaeophycus*, and *Planolites*.

7.2.5 TIDAL CHANNELS AND CREEKS

Tidal-flat deposits are commonly dissected by a network of meandering tidal channels and creeks that migrate across the intertidal zone, producing lateral accretion in point bars (Reineck, 1958; Bridges and Leeder, 1976; Weimer *et al*., 1981; de Mowbray, 1983; Thomas *et al*., 1987; Dalrymple, 1992; Gingras *et al*., 1999b). This process results in the formation of inclined heterolithic stratification (Thomas *et al*., 1987). In the muddy upper-intertidal zones, channels are small to medium size, but in the lower sandy areas, they tend to coalesce forming wider and deeper channels (Dalrymple, 1992). The degree of bioturbation is lower in the point bars than in tidal flats, most likely reflecting higher rates of sedimentation along unstable channel margins (cf. Gingras *et al*. 1999b; Mángano *et al*. 2002a) (see Section 8.1.2).

7.2.6 SUBTIDAL SANDBARS AND TIDAL DUNES

The subtidal zone of tide-dominated shallow-marine environments is characterized by maximum energy with high-current velocities (Dalrymple, 1992). Large-scale bedforms, such as dunes and compound dunes, migrate across the subtidal areas, forming sandbars in the form of sheets and ridges. Deposits

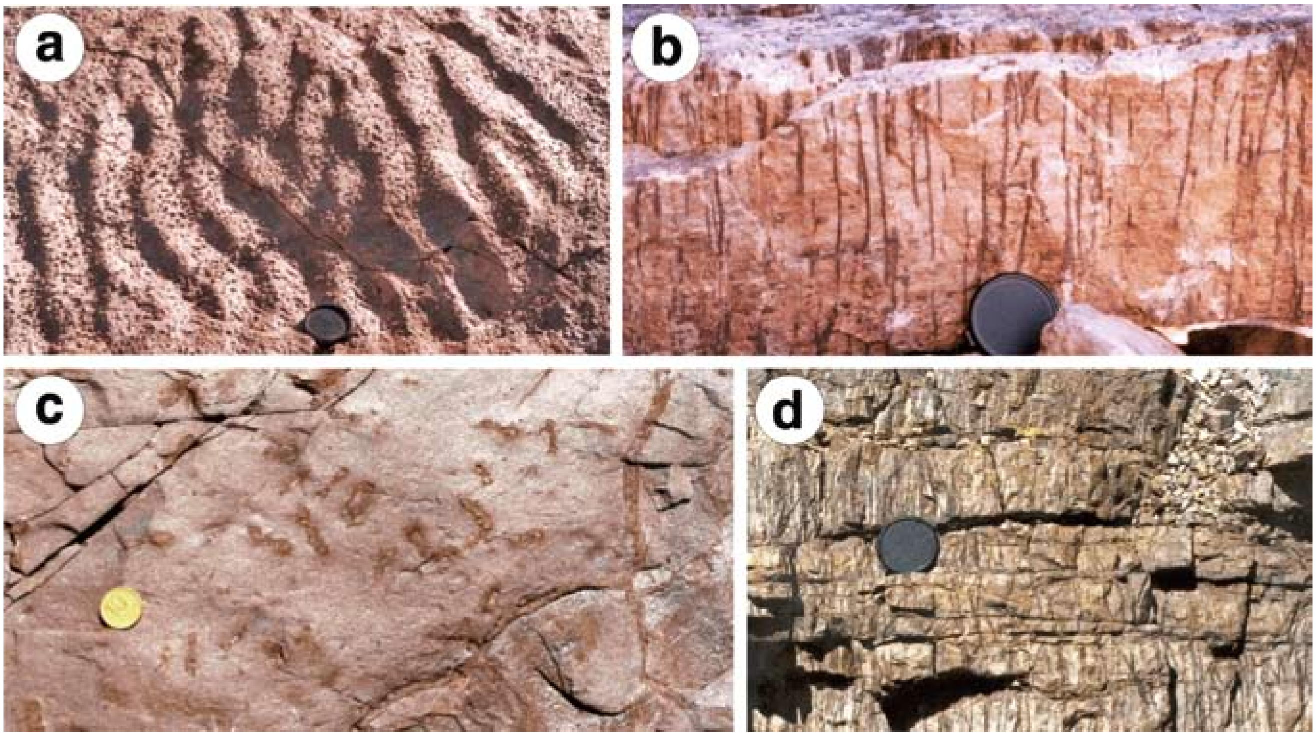


Figure 7.19 Ichnofaunas from high-energy sand-flat deposits from the Lower to Middle Cambrian Campanario Formation of the Mesón Group. See Mángano and Buatois (2004b). (a) Bedding-plane view of a high-density assemblage of *Skolithos linearis* (pipe rock) at a rippled sandstone surface. Angosto de Perchel, Quebrada de Huamahuaca, northwest Argentina. Lens cap is 5.5 cm. (b) Deep *Arenicolites* isp. Angosto de Perchel, Quebrada de Huamahuaca, northwest Argentina. Lens cap is 5.5 cm. (c) General view of the top of a rippled sandstone showing high density of *Diplocraterion parallelum*. Note associated cracks. Quebrada de Moya, northwest Argentina. Coin is 1.8 cm. (d) *Syringomorpha* isp. pipe rock. Angosto del Morro de Chucalezna, Quebrada de Huamahuaca, northwest Argentina. Lens cap is 5.5 cm.

consist of erosionally based, laterally extensive, well-sorted, planar to trough cross-stratified coarse- to fine-grained sandstone. Reactivation surfaces are common, while herringbone cross-stratification and mud drapes may be locally present. In modern subtidal areas, few benthic species are able to survive in zones of actively migrating bedforms (Wilson, 1982, 1986). Accordingly, faunal diversity increases toward areas with smaller bedforms, and in the outer regions where dunes are replaced by small ripples and increasing amounts of mud. Studies of marine benthic ecology also show that suspension feeding is the dominant trophic type in high-energy subtidal environments (Wilson, 1982).

As in the case of high-energy sand flats, vertical trace fossils of the *Skolithos* ichnofacies, such as *Arenicolites* (Fig. 7.21a and d), *Skolithos* (Fig. 7.21b–d) and *Diplocraterion*, are dominant, commonly extending down into the sediment from reactivation surfaces (e.g. Pollard *et al.*, 1993; Desjardins *et al.*, 2010a). The ichnogenus *Rosselia* (Fig. 7.21d) may occur as a response to prolonged periods of sandbar inactivity and suspended mud in the water column (Desjardins *et al.*, 2010a). Vertical burrows are preferentially preserved in high-energy subenvironments, while shallow-tier horizontal traces have low preservation potential, providing a biased picture of the ecology of subtidal sandbars and dunes (Desjardins *et al.*, 2010a). Feeding and locomotion traces of deposit feeders, such as *Teichichnus*, *Planolites*, and *Rusophycus*, tend to be preserved in those deposits formed at the toe of the subtidal sandbar complex (Desjardins *et al.*, 2010a). Subtidal sandbars and tidal dunes grade seaward into lower-offshore or shelf muds, commonly characterized by the *Cruziana* or the *Zoophycos* ichnofacies.

7.3 MIXED TIDE- AND WAVE-INFLUENCED SHORELINES

While integrated sedimentological and ichnological models have been established for wave- and tide-dominated shorelines, our knowledge of intermediate cases in which both tides and waves influence deposition is much more limited. However, a growing literature on sedimentological aspects of modern mixed tide- and wave-influenced shorelines is beginning to accumulate (e.g. Short, 1991; Masselink and Short, 1993; Masselink and Hegge, 1995; Anthony and Orford, 2002; Yang *et al.*, 2005, 2006, 2008a, b; Dashtgard *et al.*, 2009, 2011). Still, no detailed ichnological accounts of these deposits have been produced and their recognition in the stratigraphic record remains a challenge. In addition, the distinction between tide- and wave-dominated systems gets further complicated because many systems show seasonal alternations of wave and tidal dominance. For example,

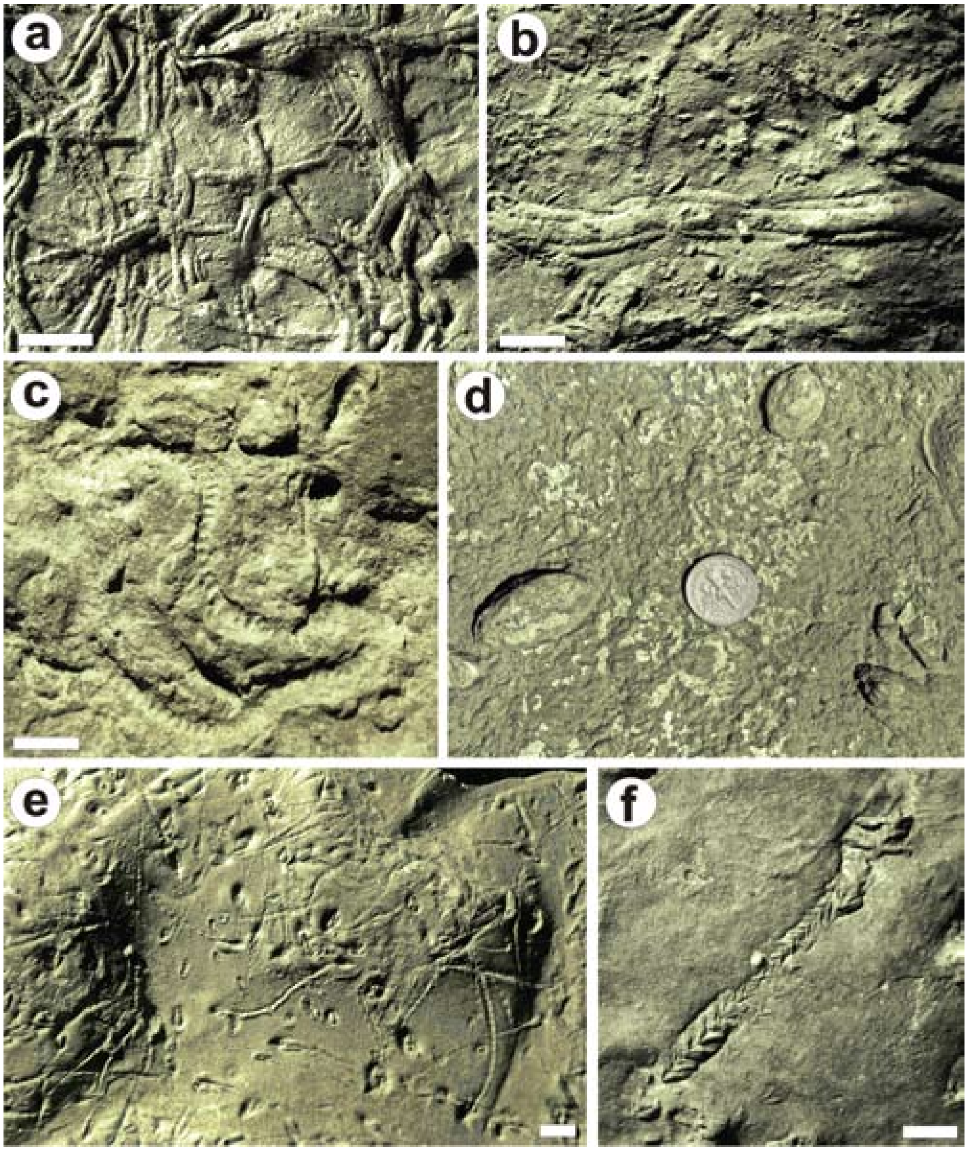


Figure 7.20 Ichnofaunas from low-energy sand-flat deposits in the Upper Carboniferous, Stull Shale of the Kanwaka Formation, Waverly fossil site, Kansas, central United States. See Mángano *et al.* (2002a). (a) Sandstone base showing *Asteriacites lumbricalis* displaying lateral repetition and high density of *Cruziana problematica*. (b) Sandstone top with *Curvolithus simplex*. (c) Sandstone top with *Nereites missouriensis*. (d) Base of sandstone bed containing *Lockeia siliquaria*. Coin is 1.8 cm. (e) Dense assemblage of *Protovirgularia rugosa* and associated resting traces (*Lockeia* isp.) on the upper surface of a sandstone bed. Note preservation as negative epireliefs in *Chevronichnus*-like fashion. (f) Base of sandstone layer containing *Protovirgularia bidirectionalis* display V-shaped markings with opposite directions meeting at a central point. Note that the direction of movement is from the center to the ends. All scale bars are 1 cm.

Yang *et al.* (2005) documented modern coastlines that alternate between tide dominated during summer and wave dominated during winter. Mixed tide- and wave-influenced shorelines can be subdivided into wave-dominated tidal flats (i.e. open-coast tidal flats) and tidal beaches (i.e. tidally modulated shorefaces), with the latter showing increased influence of wave processes (Boyd *et al.*, 1992; Yang *et al.*, 2005; Dashtgard *et al.*, 2009). In these mixed systems, storm sedimentation is tidally modulated (Yang *et al.*, 2008a).

7.3.1 WAVE-DOMINATED TIDAL FLATS

Wave-dominated tidal flats have been mostly described from the central west coast of Korea, which is relatively straight and macrotidal (Yang *et al.*, 2005, 2006, 2008a), in contrast to the typical tidal flats of the north and south west coast which occur in embayed coasts (Frey *et al.*, 1987a, b). In contrast to classic, more sheltered tidal flats (see Section 7.2), wave-dominated tidal flats only locally display mud flats and salt marshes, and typically fine seaward. The central west coast is tide dominated during summer and wave dominated during winter, with wind seasonality controlled by a monsoonal regime (Yang *et al.*, 2005).

In the locally developed inner mud flat, thin storm sand units form during winter and early spring, while mud accumulates during summer and fall. Bioturbation during the summer and fall intensely affects mud-flat deposits, including the winter and spring sandy layer, displaying a lam-scram pattern, but ichnodiversity levels are low (Yang *et al.*, 2008a). The shallower part of the sand flat is dominated by ripple-cross lamination and low-angle inclined lamination during the winter. Mud drapes may form during slack water in the spring. Vertical burrows, such as *Skolithos*, *Lingulichnus*, and *Siphonichnus*, are dominant, locally displaying moderate bioturbation intensities;

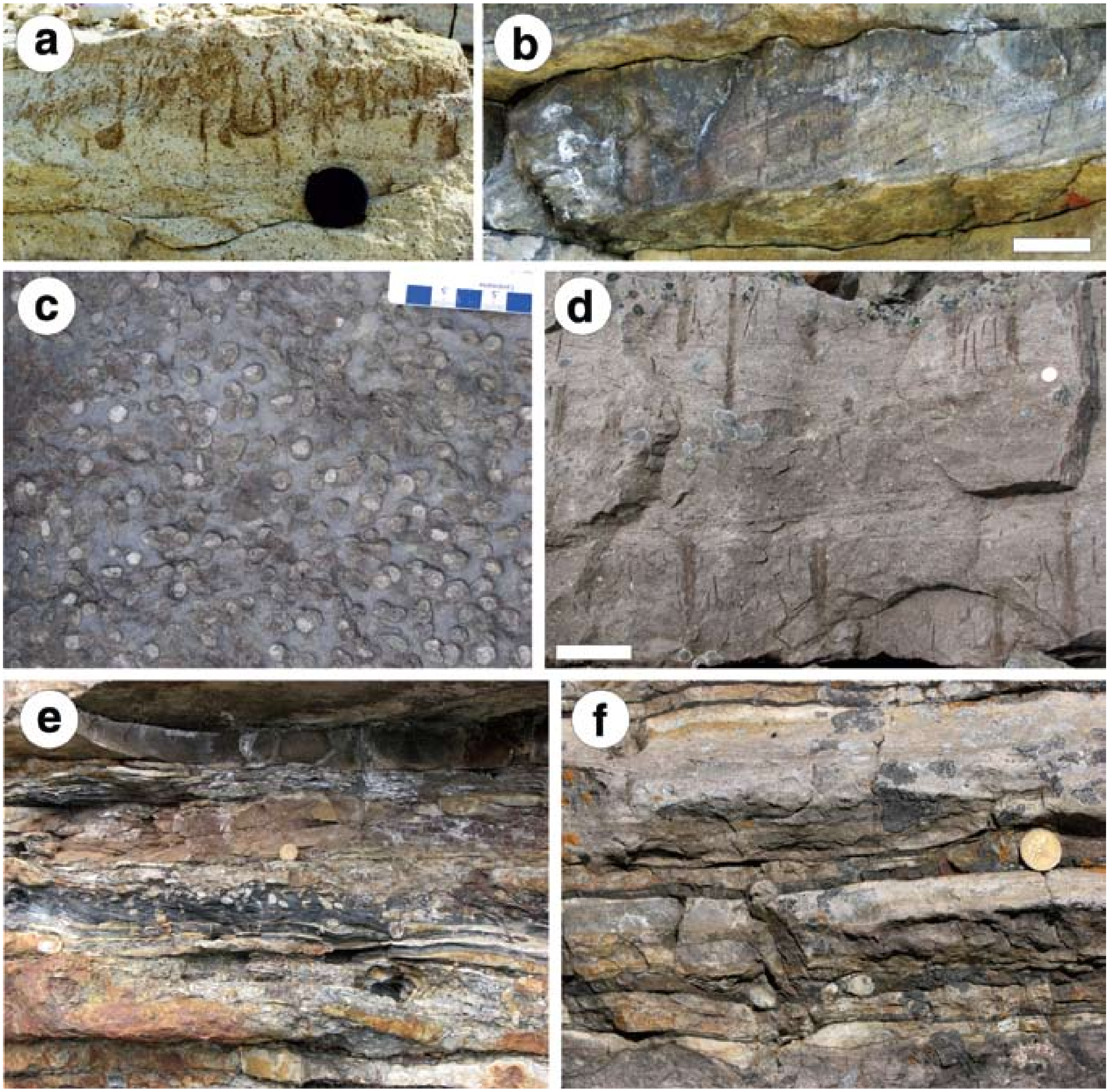


Figure 7.21 Ichnofaunas from subtidal-sandbar deposits. (a) *Arenicolites* isp. penetrating a medium-grained sandstone interpreted as a subtidal-sandbar deposit. Middle Cambrian, Flathead Formation, Absaroka Range, northwest Wyoming, north-central United States. Lens cap is 5.5 cm. (b) *Skolithos linearis* penetrating from a colonization surface at the foreset of a sandbar. Lower Cambrian, Fort Mountain Formation, Gog Group, Mount Assiniboine, Canadian Rockies, western Canada. Scale bar is 10 cm. See Desjardins *et al.* (2010a). (c) Bedding surface view of a high-density association of *Skolithos linearis* at the front of a subtidal sandbar. Lower Cambrian, Fort Mountain Formation, Gog Group, Mount Assiniboine, Canadian Rockies, western Canada. See Desjardins *et al.* (2010a). (d) *Rosselia* isp., *Skolithos linearis*, and *Arenicolites* isp. associated with various colonization surfaces in a subtidal sandbar. Lower Cambrian, Wiwaxi Peaks Member, St. Piran Formation, Gog Group, Larch Valley, Canadian Rockies, western Canada. Scale bar is 5 cm. See Desjardins *et al.* (2010a). (e) Moderately bioturbated subtidal sandbar-toe heterolithic deposits with *Planolites* and synaeresis cracks. Lower Cambrian, St. Piran Formation, Gog Group, Lake O'Hara, Canadian Rockies, western Canada. Coin is 2.6 cm. See Desjardins *et al.* (2010a). (f) Close up of subtidal sandbar-toe heterolithic deposits showing sparse *Planolites*. Lower Cambrian, St. Piran Formation, Gog Group, Lake O'Hara, Canadian Rockies, western Canada. Coin is 2.6 cm. See Desjardins *et al.* (2010a).

Macaronichnus may be present locally, as well as *Ophiomorpha* and *Thalassinoides*. Hummocky cross-stratification and parallel lamination are the dominant structures in the winter sandy beds of the middle and outer part of the sand flat. Bioturbation is extremely rare in the winter beds and typically restricted to sparse polychaete vertical burrows and escape traces. Landward migrating climbing ripples tend to characterize the spring interval, while summer layers are typified by wave-ripple cross-laminated sands and muds. Summer deposits are sparsely bioturbated, containing *Conichnus*, *Palaeophycus*, *Siphonichnus*, *Asterosoma*, and local high densities of *Macaronichnus*.

The overall intensity of bioturbation increases in a landward direction because of decreasing wave energy (Yang *et al*., 2005). However, bioturbation levels across the whole tidal flat are generally low as a result of high rates of sedimentation and episodic high-energy conditions (Yang *et al*., 2008a). On the other hand, a landward decrease in ichnodiversity, most likely as a result of increased duration of exposure, has been proposed. Also, the alternation of storms and fair-weather periods is conducive to a bimodal style of bioturbation characterized by unburrowed intra-storm mud drapes and more bioturbated fair-weather deposits. These authors noted that the bioturbation style in the lower sand flat is similar to that of the upper shoreface of wave-dominated shorelines. In addition, they suggested that the inner sand flat contains a mixed *Skolithos*–*Cruziana* ichnofacies, but of lower diversity than that of offshore environments.

The absence of further case studies prevents any attempt at generalization. However, it seems that ichnologically wave-dominated tidal flats share aspects of both wave-dominated shorefaces and tide-dominated tidal flats. The alternation of unburrowed or sparsely bioturbated intervals with intensely bioturbated units is typical of the former due to the effects of storms (Pemberton and Frey, 1984a). On the other hand, the intense bioturbation in the inner mud zone and the presence of a *Skolithos* ichnofacies seaward of an assemblage containing elements of the *Cruziana* ichnofacies is characteristic of typical tidal flats (Mángano and Buatois, 2004a). As a result of intense wave erosion on the high-tide beach face, the *Glossifungites* ichnofacies may occur, cross-cutting previously emplaced softground trace-fossil suites (Yang *et al*., 2009). Additional studies are necessary to delineate a set of criteria that allow recognition of wave-dominated tidal flats in the fossil record.

7.3.2 TIDAL BEACHES

Tidal beaches have been mostly documented from the central Queensland coast of Australia (Short, 1991; Masselink and Hegge, 1995), and more recently from Waterside Beach in the Bay of Fundy of Eastern Canada (Dashtgard *et al*., 2009). In contrast to wave-dominated shorefaces, sediments of tidal beaches deposited in water depths equivalent to the upper, middle, and lower shoreface are regularly subjected by different wave processes and, in the case of macrotidal and megatidal regimes, the shoreface may be exposed during low tides (Dashtgard *et al*., 2009). In contrast to tide-dominated tidal flats, tidal beaches show a seaward decrease in grain size.

Backshore deposits consist of eolian sand dunes and washover fan sands and gravels, and are characterized by elements of the *Psilonichnus* ichnofacies (Dashtgard *et al*., 2009). Foreshore deposits of tidal beaches are typically unburrowed and dominated by gravels and sands with subparallel to low-angle cross stratification formed due to swash and backwash processes in the upper-intertidal area; eolian processes may also play a role (Masselink and Hegge, 1995; Dashtgard *et al*., 2009). The upper shoreface corresponds to the middle-intertidal zone, and may contain both sand and gravel with through and planar cross-bedding as the dominant structures, as a result of swash and surf processes. Bioturbation is moderate and dominated by elements of the *Skolithos* ichnofacies (Dashtgard *et al*., 2009). The lower shoreface of tidal beaches corresponds to the lower-intertidal to shallow-subtidal zone, and is extremely variable with respect to grain size and physical sedimentary structures. It is essentially dominated by surf zone and shoaling wave processes (Masselink and Hegge, 1995). Fine-grained deposits consist of fine- and very fine-grained sand and silt with abundant oscillatory structures (e.g. hummocky cross-stratification, wave ripples). Coarse-grained deposits consist of medium-grained sand to gravel in which evidence of oscillation alternates with current-generated structures (e.g. trough and planar cross-bedding). Although the *Cruziana* ichnofacies dominates the lower shoreface of tidal beaches, its diversity is reduced and no elaborate grazing or feeding structures occur, illustrating the proximal subdivision of this ichnofacies (Dashtgard *et al*., 2009). The offshore in this type of system falls within the subtidal zone, and is controlled by shoaling wave processes (Masselink and Hegge, 1995). Deposits are fine-grained, mostly consisting of parallel-laminated silt and sand, being characterized by a proximal *Cruziana* ichnofacies (Dashtgard *et al*., 2009).

As in the case of the wave-dominated tidal flats, the scarcity of case studies prevents generalizations. In addition, the more detailed ichnological and sedimentological analysis of a tidal beach corresponds to Waterside Beach in the Bay of Fundy of Eastern Canada (Dashtgard *et al*., 2009) and, therefore, factors other than those typical of open-marine coasts may have influenced the benthic fauna (e.g. salinity dilution), further complicating the proposal of a more general model. While wave-dominated tidal flats share aspects of both wave-dominated shorefaces and tide-dominated tidal flats from an ichnological perspective, tidal beaches seem to have little in common with the latter and mostly resemble wave-dominated shorefaces. The proximal–distal ichnofacies gradient in tidal beaches follows that of wave-dominated shorefaces rather than tide-dominated tidal flats (Mángano and Buatois, 2004a). However, and in contrast to wave-dominated shoreface, no archetypal *Cruziana* is present in tidal beaches, and diversity levels and degree of bioturbation are reduced (Dashtgard *et al*., 2009).

7.4 MUDDY SHORELINES

Muddy shorelines typically form in protected regions, such as bays and lagoons (see Section 8.2). Also, they occur along the open coast forming extensive mud flats in tide-dominated shallow-marine environments (see Section 7.2.2). However, they may also form along open coasts if the supply of suspended sediment is enough to dampen inshore wave power and tidal currents (Potter *et al*., 2005). These muddy coasts are particularly common downcurrent from fine-grained delta systems. However, because muddy shorelines may extend far away from the delta mouth (e.g. 1600 km northwest of the Amazon mouth), they will be addressed herein in the context of shallow-marine open environments rather than in the delta section.

Open-coast mudbelts are relatively well documented in modern environments, such as Surinam (Augustinus, 1978; Rine and Ginsburg, 1985; Allison and Nittrouer, 1998) and western Lousiana (Beall, 1968; Penland and Suter, 1989). Most of the muddy shoreline fauna most likely derived from offshore softground biotopes (Fortes, 2002). Biotic interactions, particularly competition among species, may be quite severe along muddy coasts, although this is not necessarily conducive to reduced diversity, which is essentially a function of physical stress (Fortes, 2002). Information from modern environments indicates that organisms living on muddy shorelines are typically calm-water species, and are affected by a number of stress factors, such as soupy substrates and rapid deposition of mud (Potter *et al.*, 2005). As a result, the diversity of biogenic structures is rather low and bioturbation tends to be sparse. Interestingly, muddy shorelines seem to display significant spatial heterogeneity. On the Surinam muddy coast, rapidly migrating mudbanks oriented obliquely to the shore are formed by fluid mud whose low strength essentially precludes bioturbation (Potter *et al.*, 2005). Between these banks, more consolidated mud is formed and more intense bioturbation occurs.

Although relatively widespread in modern environments, muddy shorelines have remained almost unnoticed in the fossil record and, therefore, palichnological information is virtually absent. A notable exception is that of Hovikoski *et al.* (2008), who documented ichnological and sedimentological aspects of Cretaceous deposits interpreted as being formed in a muddy shoreline based on core data. These authors set up a number of preliminary criteria that may help in the recognition of ancient muddy coasts, including (1) high content of terrestrially derived organic matter; (2) soupy substrates and fluid-mud intervals, which are unburrowed or contain highly deformed trace fossils; (3) high and/or variable depositional rates, resulting in low and/or fluctuating intensity of bioturbation; (4) reduced ichnodiversity and trace-fossil size; (5) dominance of monospecific suites; (7) morphologically simple trace fossils; (8) micro-laminated shale; and (9) abundant erosional features, such as shale-on-shale erosional contacts and scour-and-fill structures.

8 Ichnology of marginal-marine environments

> "Is there any other point to which you would wish to draw my attention?"
> "To the curious incident of the dog in the night-time."
> "The dog did nothing in the night-time."
> "That was the curious incident," remarked Sherlock Holmes.
>
> Sir Arthur Conan Doyle
> "Silver Blaze" (1892)

Marginal-marine environments represent one of the most successful areas of ichnological research. These environments comprise a wide variety of coastal settings characterized by rapid environmental perturbations, typically salinity changes, but also increased sediment discharge and extreme clay flocculation, among many other controls. These different factors generate stressful conditions that strongly affect benthic biotas, imparting clearly detectable signals in the ichnological record (e.g. Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Buatois *et al.*, 1997b; Mángano and Buatois, 2004a; MacEachern and Gingras, 2007). Ichnology is a powerful tool to differentiate deposits formed under marginal-marine conditions from those that accumulated in fully marine settings. In this chapter we review the ichnology of different marginal-marine environments, visiting estuaries, bays, deltas, and fjords.

8.1 ESTUARIES

Dalrymple *et al.* (1992) defined an estuary as "the seaward portion of a drowned valley system which receives sediment from both fluvial and marine sources and which contains facies influenced by tide, wave, and fluvial processes. The estuary is considered to extend from the landward limit of tidal facies at its head to the seaward limit of coastal facies at its mouth". In this definition, the term estuary is restricted to incised valley systems (see Section 12.5.2). However, in subsequent work a wider definition was adopted, allowing consideration of abandoned areas of the delta plain (destructive phase of deltas during transgression) as estuaries (Dalrymple, 2006).

The distinction between open-marine deposits of regional scale and marginal-marine deposits occupying estuarine systems is one of the areas of applied ichnology in which trace fossils have been most extensively used. Integrating ichnological information, and sedimentological and stratigraphic evidence is critical in discriminating between both types of environments. Several recent studies have led to reinterpretation of a great number of successions that were previously regarded as open-marine successions but are now considered to be estuarine in nature (e.g. Buatois *et al.*, 1999). Ichnological data have proved decisive for new interpretations as the key to the identification of these environments lies in recognizing particular ichnofossil assemblages developed under stress conditions resulting from the dilution of seawater, resulting in the brackish-water model, extensively applied in the oil industry. These characteristics allow identification of anomalous ichnofaunas (typical of marginal-marine brackish environments), which, in contrast to open-sea associations, usually exhibit a lower variety and abundance of forms (see Section 6.1.4). Also, the presence of typical marine ichnotaxa (e.g. *Teichichnus*, *Asteriacites*, *Psammichnites*) has been successfully used to detect marine influence in coastal-plain successions (e.g. Hakes, 1976, 1985; Miller and Knox, 1985; Ranger and Pemberton, 1988; Miller and Woodrow, 1991; Mángano *et al.*, 1999).

It should be noted, however, that brackish-water conditions are not exclusive of estuarine systems, being also present in other depositional settings (e.g. delta plains, distributary mouth bars) (Dalrymple and Choi, 2007). On the other hand, the inner zone of estuarine systems is commonly characterized by freshwater conditions (Buatois *et al.*, 1997b). Trace-fossil analysis aids not only in the recognition of estuarine deposits, but also delineation of different clastic facies within the estuarine valley. Estuaries have been classified into two main groups, wave-dominated and tide-dominated estuaries (Dalrymple *et al.*, 1992); the latter is a partial equivalent to the riverine estuarine valleys of MacEachern and Gingras (2007). Here, we address the ichnology of wave- and tide-dominated estuaries.

8.1.1 WAVE-DOMINATED ESTUARIES

Wave-dominated estuaries are characterized by a well-defined tripartite style of sand-to-mud-to-sand fill due to a pronounced spatial distribution of total energy (e.g. Zaitlin and Shultz, 1990). Therefore, wave-dominated estuaries comprise three main zones: (1) an outer zone dominated by marine processes; (2) a central zone where marine energy is dissipated by fluvial currents; and (3) an inner, river-dominated zone (Rahmani, 1988; Dalrymple *et al.*, 1992). As a result of energy distribution, these systems consist of: (1) a high-energy inner zone dominated by the discharge of fluvial tributaries (bay-head delta); (2) a low-energy middle zone, characterized by fine-grained deposition (central basin); and (3) a

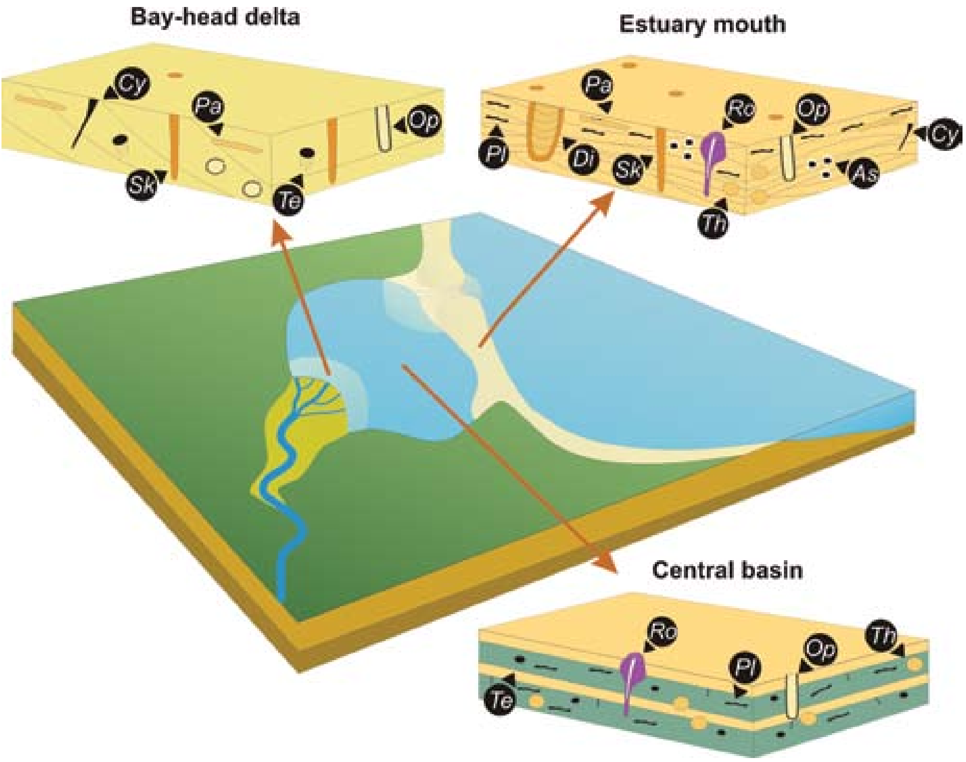


Figure 8.1 Schematic reconstruction of trace-fossil distribution in wave-dominated estuaries. Bay-head delta deposits are sparsely bioturbated and may contain a few ichnotaxa, typically *Cylindrichnus* (*Cy*), *Palaeophycus* (*Pa*), *Ophiomorpha* (*Op*), *Teichichnus* (*Te*), and *Skolithos* (*Sk*). Central-basin deposits also are sparsely bioturbated, and contain low-diversity suites, *Planolites* (*Pl*), *Teichichnus* (*Te*), and *Thalassinoides* (*Th*) being common components. *Ophiomorpha* (*OP*) *and Rosselia* (*Ro*) may be present. Estuary-mouth deposits tend to display more ichnodiversity and intensity of bioturbation, including *Cylindrichnus* (*Cy*), *Palaeophycus* (*Pa*), *Ophiomorpha* (*Op*), *Thalassinoides* (*Th*), *Diplocraterion* (*Di*), *Rosselia* (*Ro*), *Asterosoma* (*As*), *Planolites* (*Pl*), and *Skolithos* (*Sk*).

Box 8.1 Ichnology of a Lower Cretaceous wave-dominated estuary, the Viking Formation of subsurface Alberta, Canada

Recognition of estuarine deposits in the Lower Cretaceous Viking Formation of the Western Canada Sedimentary Basin had profound implications in petroleum exploration and reservoir characterization. The Viking has been previously interpreted as deposited in shoreface environments. However, the discovery of a number of fields (e.g. Crystal) running perpendicular to the paleoshoreline proved to be a challenge to the shoreface model. These fields were then interpreted as estuarine valley fills, and ichnology played a major role in the shaping of this new model. Detailed sedimentological and ichnological studies of cores from the Viking Formation indicated that these fields were actually wave-dominated estuaries. Deposits lateral and underlying Viking valley deposits are characterized by highly diverse ichnofaunas, which contrast with the more impoverished assemblage that typified the estuarine deposits. In addition, the estuarine ichnofauna is characterized by the dominance of opportunistic suites, and variable and sporadic distribution of bioturbation. The typical tripartite facies distribution of wave-dominated estuaries is well illustrated in these Viking fields. Bay-head delta deposits contain sporadic bioturbation as a result of extreme stress conditions. Central-basin deposits, although displaying sporadic bioturbation, reduced size and low ichnodiversities, may contain locally more elaborate and specialized feeding and grazing trace-fossils indicative of periods of less stressful salinity conditions. Estuarine-mouth deposits show a clear increase in ichnodiversity. Opportunistic strategies are dominant on the estuary side of the mouth, while climax ichnofaunas dominate on the seaward side of the estuary mouth. Reincision of channel facies at the top of the Viking valleys has been documented suggesting renewed sea-level fall. These deposits show an alternation of burrowed and unburrowed beds, most likely reflecting a combination of alternating freshwater and brackish-water conditions, and high energy due to dune migration. Studies in the Viking have been instrumental in the elaboration of the brackish-water model.

Reference: MacEachern and Pemberton (1994).

marine sand-plug formed at the seaward, high wave-energy end of the valley (estuary mouth) (Fig. 8.1) (Box 8.1).

Bay-head deltas are extremely stressful environments, being characterized by low salinity values and high sedimentation rates. These deposits are typically unbioturbated to sparsely bioturbated, with burrows displaying a tendency to concentrate on top of sandstone beds; ichnodiversity is very low (e.g. MacEachern and Pemberton, 1994; Buatois *et al*., 1999, 2002b; MacEachern and Gingras, 2007). Trace-fossil assemblages tend to be dominated by dwelling structures of suspension feeders, such as *Palaeophycus* (Fig. 8.2a), *Ophiomorpha* (Fig. 8.2b), *Skolithos* (Fig. 8.2d), *Monocraterion*-like burrows (Fig. 8.2e),

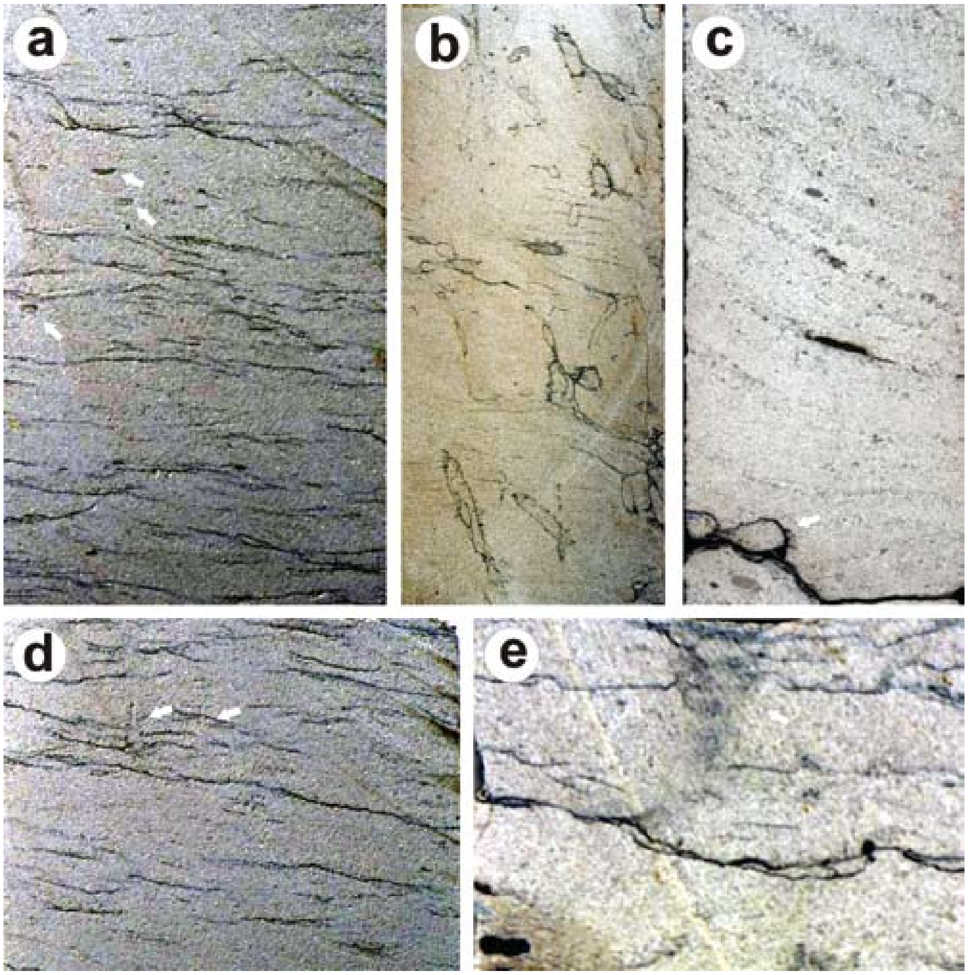


Figure 8.2 Ichnofaunas from bay-head delta deposits as expressed in core. Note tendency to form monospecific suites and small size. (a) Low density of small *Palaeophycus* (arrows) in sandstone with abundant mud drapes. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b). (b) *Ophiomorpha* forming a relatively high-density occurrence in a cross-bedded sandstone with mud drapes. Upper Oligocene–Lower Miocene, Naricual Formation, Pirital Field, Eastern Venezuela Basin. Core width 10 cm. (c) *Rhizocorallium* (arrow) along reactivation surface in a cross-bedded sandstone. Upper Cretaceous, Escandalosa Formation, Caipe Field, Barinas-Apure Basin, southwestern Venezuela. Core width is 10 cm. (d) Scattered tiny specimens of *Skolithos* (arrows) in sandstone with abundant mud drapes. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b). (e) Isolated occurrence of *Monocraterion*-like burrow (arrow) in a sandstone with stylolityzed mud drapes. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al.* (2002b).

and, more rarely, detritus feeders, such as *Cylindrichnus* of *Rhizocorallium* (Fig. 8.2c). These tend to occur in sandstone units commonly recording opportunistic colonization of subaqueous dunes and channels. Feeding trace fossils of deposit feeders are minor components, commonly present in mudstone interbeds associated with pauses in sedimentation (e.g. *Planolites*, *Teichichnus*). Individual beds rarely contain more than a few ichnogenera (MacEachern and Pemberton, 1994). In terms of archetypal ichnofacies, bay-head deltas predominantly contain the *Skolithos* ichnofacies with minor proportions of the impoverished *Cruziana* ichnofacies.

Central-basin settings are characterized by a combination of stress factors, such as brackish-water conditions, water turbidity and oxygen depletion. The degree of bioturbation is typically low, although some intervals may attain moderate to relatively intense bioturbation, reflecting slower depositional rates (e.g. MacEachern and Pemberton, 1994; MacEachern and Gingras, 2007). Ichnodiversity is low; moderate diversity levels most likely reveal less salinity stress. Trace fossils typically occur in heterolithic successions displaying wavy to lenticular bedding. The dominant components are non-specialized feeding traces of deposit feeders (e.g. *Planolites*, *Teichichnus*), although dwelling traces of deposit feeders (e.g. *Thalassinoides*) and detritus feeders (e.g. *Rosselia*), and, more rarely, suspension feeders (e.g. *Palaeophycus*, *Diplocraterion*) may occur. Burrow size reduction and synaeresis cracks are typical features in central-basin deposits (MacEachern and Gingras, 2007). Monospecific or low-diversity suites of *Planolites* (Fig. 8.3) and *Teichichnus* are common (e.g. Buatois *et al.*, 2002b). Storm sands in central-basin deposits commonly contain *Ophiomorpha*, which is thought to reveal transport of burrowing crustaceans rather than opportunistic colonization (Savrda and Nanson, 2003). These authors also noted that in proximal parts of the central bay, rapid event-related accumulation of suspended clays immediately followed sand emplacement, precluding the establishment of a fair-weather suite. Discrete layers with more specialized trace fossils (e.g. *Phycosiphon*, *Chondrites*) either reflect short-lived barrier breaching by storm washovers, incomplete barring of estuary mouths, or permanent barrier breaching during transgressions (MacEachern and Gingras, 2007). Central-basin deposits are characterized by the depauperate *Cruziana* ichnofacies with minor contributions from the *Skolithos* ichnofacies.

Estuary-mouth environments are highly variable in terms of ichnological content and sedimentary facies. The degree of

Figure 8.3 Typical core expression of ichnofaunas from central-basin deposits. Note small *Planolites*, synaeresis cracks, siderite layer (top), and sandstone lenses with very thin mud drapes. Lower Miocene, Oficina Formation, Oritupano Field, eastern Venezuela Basin. Core width is 10 cm.

bioturbation and ichnodiversity is moderate to relatively intense, reflecting near normal marine salinities (Fig. 8.4). Stress factors in this setting mostly consist of high depositional rates and high energy levels rather than reduced salinity (e.g. Savrda *et al*., 1998). As a result, coarser grained deposits (e.g. conglomerate and very coarse-grained sandstone) are sparsely bioturbated in contrast to finer grained deposits that accumulate in more protected sites. Deposits of rapidly migrating large bedforms, such as those of dunes migrating along tidal inlets, are typically unburrowed or sparsely bioturbated (e.g. Savrda *et al*., 1998). Behavioral categories and trophic types are much more varied than in inner- and central-estuarine areas, covering dwelling, feeding, and resting traces of suspension, deposit, and detritus feeders (e.g. MacEachern and Pemberton, 1994; Buatois *et al*., 2002b; MacEachern and Gingras, 2007). *Ophiomorpha*, *Thalassinoides*, *Skolithos*, *Palaeophycus*, *Planolites*, *Cylindrichnus*, *Rosselia*, *Asterosoma*, *Teichichnus*, and *Diplocraterion* are common components, while *Bergaueria*, *Lockeia*, and *Siphonichnus* may be accessory elements.

Figure 8.4 Core expression of intensely bioturbated estuary-mouth coarse-grained deposits. Upper Carboniferous, Lower Morrow Sandstone, Arroyo Field, southwestern Kansas, United States. Core width is 8 cm. See Buatois *et al*. (2002b).

Macaronichnus is commonly present in high-energy tidal-inlet and subtidal-bar sandstone (Savrda and Uddin, 2005), while large *Conichnus* occurs in the same deposits, reflecting equilibrium strategies (Savrda, 2002). *Ophiomorpha* is commonly present in dune deposits associated with slack-water mud drapes, reflecting relatively brief colonization windows (Savrda *et al*., 1998). Deposits that occur on the estuarine side of the barrier are less bioturbated, and display less ichnodiversity than those that accumulate on the seaward side (MacEachern and Pemberton, 1994). On the seaward side, ichnotaxa that are less tolerant to salinity fluctuations may be rather common (e.g. *Chondrites*, *Helminthopsis*, and *Phycosiphon*). Estuarine-mouth deposits are characterized by the mixed depauperate *Cruziana* and *Skolithos* ichnofacies.

The overall distribution of biogenic structures along wave-dominated estuaries is likely controlled by the salinity gradient, displaying a transition from brackish water in the bay-head delta and central basin to near-normal salinity conditions at the seaward end of the valley. Other parameters, such as oxygenation, substrate consistency, and energy regime, play a significant role at a more local scale. For example, dwelling traces of suspension feeders are dominant in high-energy, oxygenated sandy channels and dunes of the bay-head delta, and feeding traces of deposit feeders are more typical of low-energy, poorly oxygenated, fine-grained sediments of the central basin. The importance of salinity becomes evident when facies formed under similar conditions of energy, substrate, and oxygenation are compared (Buatois *et al*., 2002b). Organisms that inhabit bay-head deltas and upper-shoreface environments are adapted to a well-oxygenated sandy substrate under relatively high-energy conditions. However, while animals living in the bay-head delta experience stressful physiological conditions due to brackish water, those from the upper shoreface developed in normal salinity waters. The overall features of both ichnofaunas (e.g. lower ichnodiversity in the bay-head delta than in the shoreface) clearly support the importance of salinity as a limiting factor in trace-fossil distribution.

8.1.2 TIDE-DOMINATED ESTUARIES

The distribution of total energy that produces the tripartite style of sand-to-mud-to-sand fill is less pronounced in tide-dominated systems than in wave-dominated estuaries due to migrating tidal channels in the central zone of the estuary (Dalrymple *et al*., 1992; Boyd *et al*., 2006). Nevertheless, tide-dominated estuarine systems are characterized by: (1) an inner sandy zone representing a straight tidal-fluvial channel (upper estuary); (2) a middle muddy-sandy zone of a meandering to straight tidal channel and tidal flats, tidal creeks, and salt marshes along the sides of the estuary (middle estuary); and (3) an outer zone characterized by elongate tidal sand bars and tidal flats that flanked the estuary valley seaward (lower estuary) (Fig. 8.5).

In the fluvio-estuarine transition zone, tidal influence commonly extends further landward than the saltwater intrusion. This zone is therefore situated between the maximum landward limit of tidal currents and the salinity limit further towards the sea (Buatois *et al*., 1997b). As noted by Allen (1991), upper-estuary channels are rarely affected by brackish water and no marine or brackish-water fauna is able to inhabit this portion of the estuary. The freshwater benthos inhabiting this inner zone does not have the special adaptations necessary to survive in the brackish environment, which results in the middle estuary being a border zone to their distribution area (Wolff, 1983). Tidal rhythmites formed in this innermost zone contain arthropod trackways (e.g. *Dendroidichnites*, *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Stiallia*, *Stiaria*) (Fig. 8.6a), insect resting traces (e.g. *Tonganoxichnus*) (Fig. 8.6a), grazing traces (e.g. *Gordia*, *Helminthoidichnites*, *Helminthopsis*) (Fig. 8.6b–d), subsurface feeding traces (e.g. *Treptichnus*) (Fig. 8.6e), fish locomotion traces (*Undichna*) (Fig. 8.6f), and reptile (e.g. *Notalacerta*, *Pseudobradypus*, *Attenosaurus*, *Alabamasauripus*, *Dimetropus*) and amphibian trackways (e.g. *Cincosaurus*) (Rindsberg, 1990b; Buatois *et al*., 1997b, 1998a; Mángano and Buatois, 2004a; Hunt *et al*., 2004a; Lucas *et al*., 2004a; Lucas and Lerner 2005; Haubold *et al*., 2005; Martin and Pyenson, 2005; Pashin, 2005; Minter and Braddy, 2009).

This ichnofauna reflects the activity of a mixed terrestrial and freshwater biota in low-energy tidal flats (Buatois *et al*., 1997b, 1998a). Root trace fossils (Fig. 8.6g) and autochthonous upright plants are common, representing the only penetrative organic structures in an otherwise unbioturbated substrate characterized by thinly interbedded sandstone–mudstone couplets or siltstone–claystone couplets. Trails and trackways are preserved on mud drapes, and are commonly associated with a wide variety

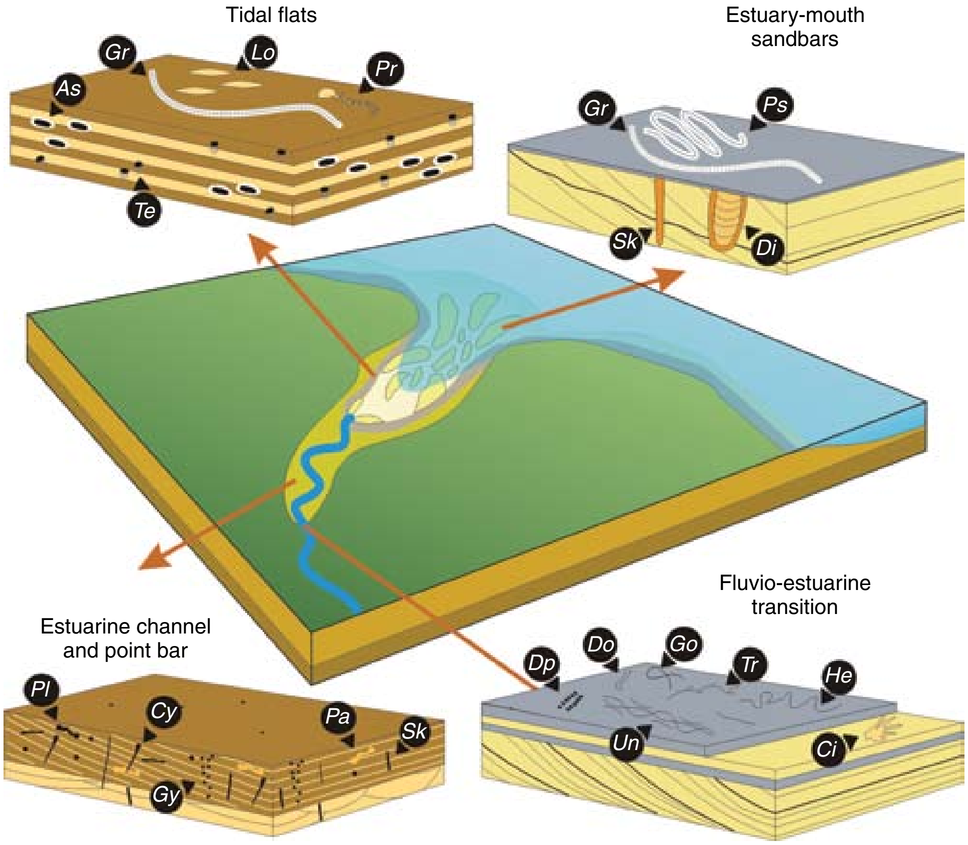


Figure 8.5 Schematic reconstruction of trace-fossil distribution in tide-dominated estuaries. The fluvio-estuarine transition displays relatively high-diversity suites, including *Diplichnites* (*Dp*), *Diplopodichnus* (*Do*), *Gordia* (*Go*), *Treptichnus* (*Tr*), *Helminthopsis* (*He*), *Undichna* (*Un*), and *Cincosaurus* (*Ci*). Estuarine-channel and point-bar deposits are sparsely bioturbated and contain a few ichnotaxa, such as *Gyrolithes* (*Gy*), *Cylindrichnus* (*Cy*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), and *Skolithos* (*Sk*). Associated tidal-flat deposits are slightly more bioturbated, but ichnodiversity remains low, with *Lockeia* (*Lo*), *Protovirgularia* (*Pr*), *Asterosoma* (*As*), *Gyrochorte* (*Gr*), and *Teichichnus* (*Te*) as common forms. Estuary-mouth sandbar deposits may contain *Diplocraterion* (*Di*), *Skolithos* (*Sk*), *Gyrochorte* (*Gr*), and *Psammichnites* (*Ps*).

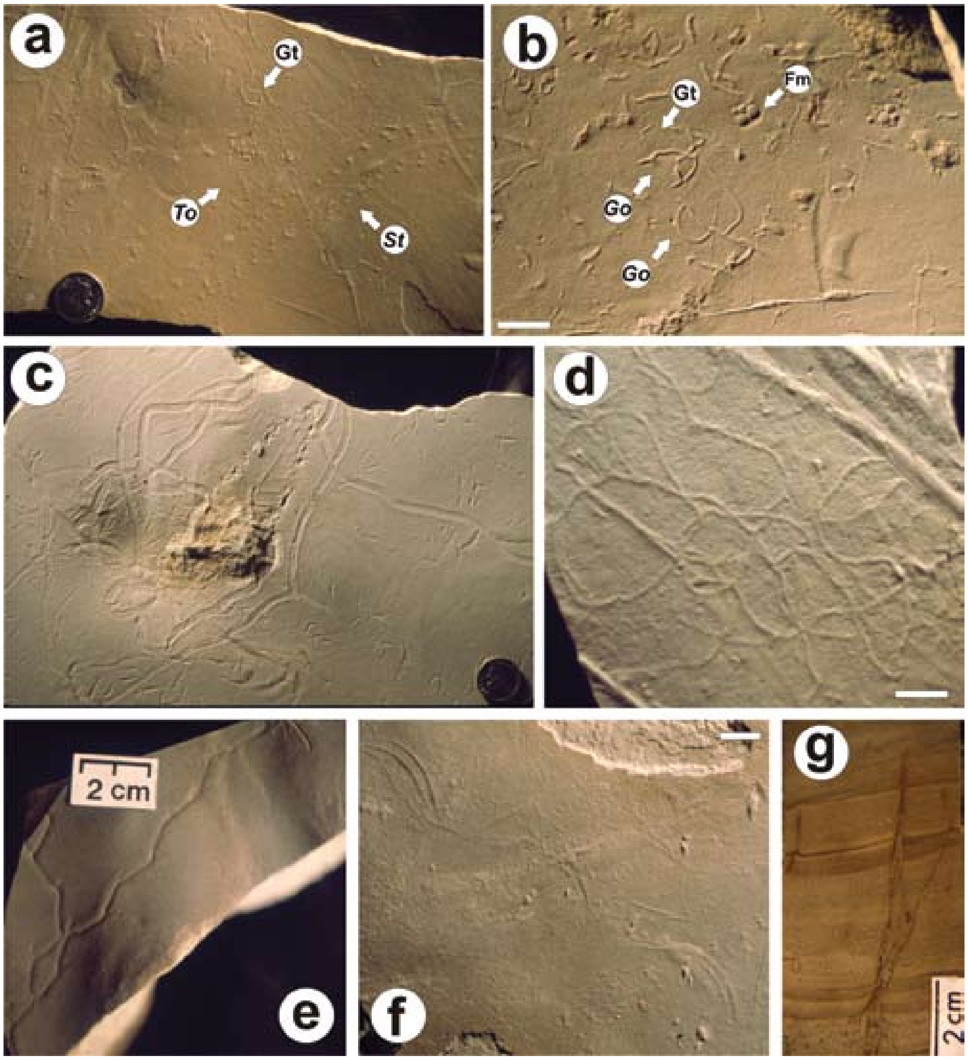


Figure 8.6 Ichnofaunas from fluvio-estuarine transition deposits. Upper Carboniferous, Tonganoxie Sandstone, Stranger Fomation, Buildex Quarry, Kansas, United States. (a) *Stiaria intermedia* (*St*), *Tonganoxichnus ottawensis* (*To*), and indeterminate grazing trails (Gt). Coin is 1.4 cm. (b) *Gordia indianaensis* (*Gi*) indeterminate grazing trails (Gt), and foam marks (Fm). Scale bar is 1 cm. (c) Grazing trails concentrated around a fossil leaf. Coin is 1.4 cm. (d) *Gordia indianaensis*. Scale bar is 1 cm. (e) *Treptichnus bifurcus*. (f) *Undichna britannica*. Scale bar is 1 cm. (g) Core view of a root trace fossil. See Buatois *et al*. (1997b, 1998a).

of bedding-surface structures, including tool marks, drainage or seepage rill marks, runnel marks, runoff washouts, foam marks, raindrop impressions, gas escape structures, falling-water marks, and wrinkle marks, the latter suggestive of microbial matgrounds (Buatois *et al*., 1997b, 1998a; Mángano and Buatois, 2004a; Rindsberg, 2005; Pashin, 2005). In terms of ichnofacies, the fluvial–estuarine transition is characterized by the mixed *Mermia–Scoyenia* ichnofacies, and by the *Serpentichnus* ichnocoenosis of the *Characichichnos* ichnofacies.

Further towards the sea, tidal channels display brackish-water conditions, allowing the establishment of the mixed depauperate *Cruziana* and *Skolithos* ichnofacies. Ichnodiversity reaches a minimum in these highly stressed settings, and bioturbation tends to be sparsely distributed (Ranger and Pemberton, 1992; Gingras *et al*., 1999b). Upper-estuarine channels encompass two main areas, the active portion of the channel and the point bar (MacEachern and Gingras, 2007). Active-channel deposits are typically unburrowed or contain a few trace fossils in mud interbeds or in the toesets of dune bedforms. As noted by MacEachern and Gingras (2007), the scarcity of bioturbation in active channels is for the most part due to the presence of rapidly migrating bedforms rather than brackish-water conditions per se. *Planolites*, *Cylindrichnus*, *Skolithos*, and *Palaeophycus* are among the ichnotaxa most commonly recorded. Logs with *Teredolites* may occur at the base of channels (Fig. 8.7).

The associated point bars, characterized by lateral accretion that produces inclined heterolithic stratification, generally display higher ichnodiversity and degree of bioturbation than the active channels (Box 8.2). Biogenic structures in inclined heterolithic stratification deposits display proximal–distal trends in response to a salinity gradient (Lettley *et al*., 2007b; MacEachern and Gingras, 2007). Landward expressions tend to be sandier, and are either unbioturbated or contain scarce *Planolites* (Fig. 8.8a). The degree of bioturbation and ichnodiversity tend to increase seaward with the progressive addition of *Skolithos*, *Gyrolithes* (Fig. 8.8c–d), and *Cylindrichnus* (Fig. 8.8b). However, mudstone-rich intervals sharply overlying point-bar deposits are commonly unbioturbated, and are thought to record deposition close to or at the turbidity-maximum zone, which promotes clay flocculation and rapid mud accumulation (Bechtel

Figure 8.7 Log with *Teredolites* at the base of an estuarine tidal channel sandstone. Upper Cretaceous, Desert Sandstone Member, Blackhawk Formation, Old Thompson Canyon, Book Cliffs, eastern Utah, United States. Scale bar is 5 cm.

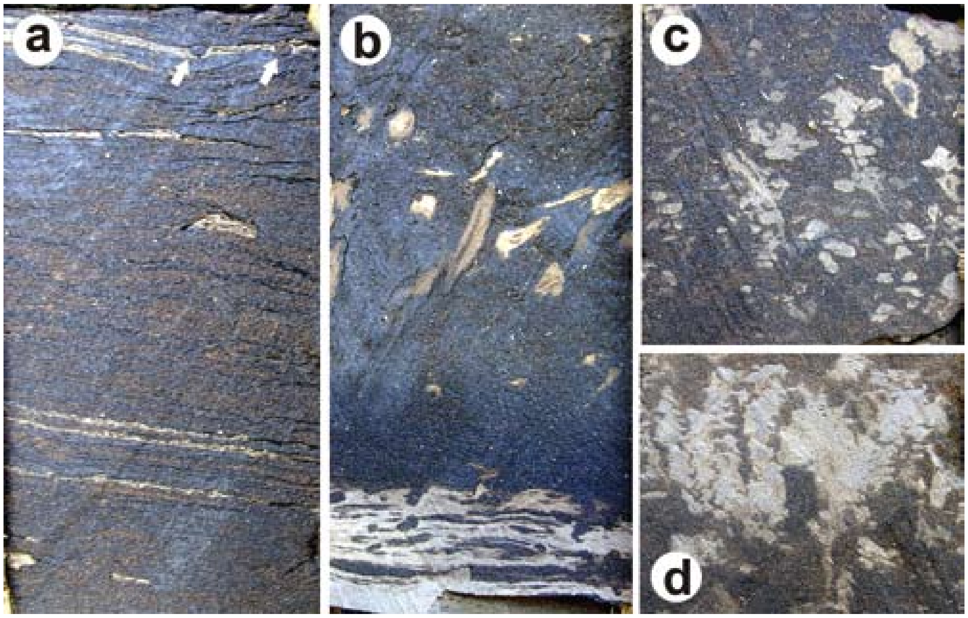


Figure 8.8 Core expression of ichnofaunas from estuarine-channel deposits with inclined heterolithic stratification. Sandstone is impregnated with hydrocarbon and is dark colored, while mudstone is light colored. Lower Cretaceous, McMurray Formation, northern Alberta, Canada. See Lettley *et al.* (2007b). (a) *Planolites* isp. (arrows) in mud drapes. (b) Concentrically laminated *Cylindrichnus* isp. (c) and (d) Vertical spiral burrow *Gyrolithes* isp. Core widths are 8 cm.

et al., 1994; MacEachern and Gingras, 2007; Lettley *et al.*, 2007b). Alternation of intensely bioturbated intervals and mostly unburrowed intervals are, therefore, interpreted as fluctuations in the position of the salt wedge within the turbidity-maximum zone. Notably, many ichnofabrics in estuarine point-bar deposits are composite, reflecting continental trace fossils overprinting brackish-water suites. Typical examples are represented by elements of the *Beaconites–Taenidium* ichnoguild cross-cutting trace-fossil suites with ichnogenera that indicate marine influence (e.g. *Teichichnus*) (Fig. 8.9a–e).

In modern macrotidal estuaries, zonations have been established to differentiate between upper subtidal–lower-intertidal, middle-intertidal, and upper-intertidal zones of muddy point bars and associated tidal flats (Pearson and Gingras, 2006). Upper-subtidal to lower-intertidal zones of the point bars contain incipient *Polykladichnus* and *Skolithos* produced by the capitellid polychaete *Heteromastus*. Middle-intertidal zones contain incipient *Arenicolites* and *Diplocraterion* produced by the amphipod *Corophium volutator*. In the upper-intertidal zone of the point bar and in the tidal flat, the nereid worms *Nereis virens* and *N. diversicolor* (producers of incipient *Polykladichnus*, *Palaeophycus*, and *Planolites*), and the bivalve *Macoma balthica* (producer of incipient *Siphonichnus*) are present. Similar zonations have been documented in sandy point bars of modern mesotidal estuaries (Gingras *et al.*, 1999b). However, *Callianassa* burrows (producers of incipient

Box 8.2 Ichnology of a Lower Cretaceous tide-dominated estuary, the McMurray Formation of Alberta

Understanding of the sedimentary architecture and depositional dynamics of the Lower Cretaceous McMurray Formation is essential because this unit is one of the most important producers of heavy oil in the world. Although the density of well cores is remarkably high, the complex distribution and architecture of these sandstone bodies complicate correlation of tide-dominated estuarine-channel units. Integration of ichnological and sedimentological datasets in the analysis of estuarine-channel deposits displaying inclined heterolithic stratification (IHS) has helped to address longitudinal variations in the character of estuarine point bars. Towards the fluvial end of the estuary, bioturbation is exceedingly rare in IHS deposits and restricted to sporadic occurrences of *Planolites* in interbedded sandstone and siltstone, while associated cross-bedded sandstone is unburrowed. The central zone of the estuary is characterized by fine- and very fine-grained sandstone associated with silt- and clay-rich deposits formed in the zone of turbidity maximum. Bioturbation is highly variable. Fine-grained deposits show little to moderate bioturbation and dominance of monospecific suites of *Planolites*. Sand-dominated deposits show more diversity particularly towards the seaward end of the turbidity maximum zone, where *Planolites* (Fig. 8.8a) and *Teichichnus* dominate, and *Cylindrichnus* (Fig. 8.8b), *Palaeophycus* and *Gyrolithes* (Fig. 8.8c–d) may occur also. The seaward end is characterized by well-sorted very fine- and fine-grained sandstone and minor amounts of mudstone and siltstone. Bioturbation is comparatively abundant and diverse, with *Cylindrichnus*, *Skolithos*, *Teichichnus*, *Palaeophycus*, *Planolites*, *Thalassinoides*, and escape trace fossils as relatively common elements. Seasonal variations in fluvial discharge, together with changes in water circulation and the position of the turbidity maximum played major roles in controlling trace-fossil distribution. This is one of the most detailed ichnological studies of tide-dominated (riverine) estuaries.

Reference: Lettley *et al*. (2007b).

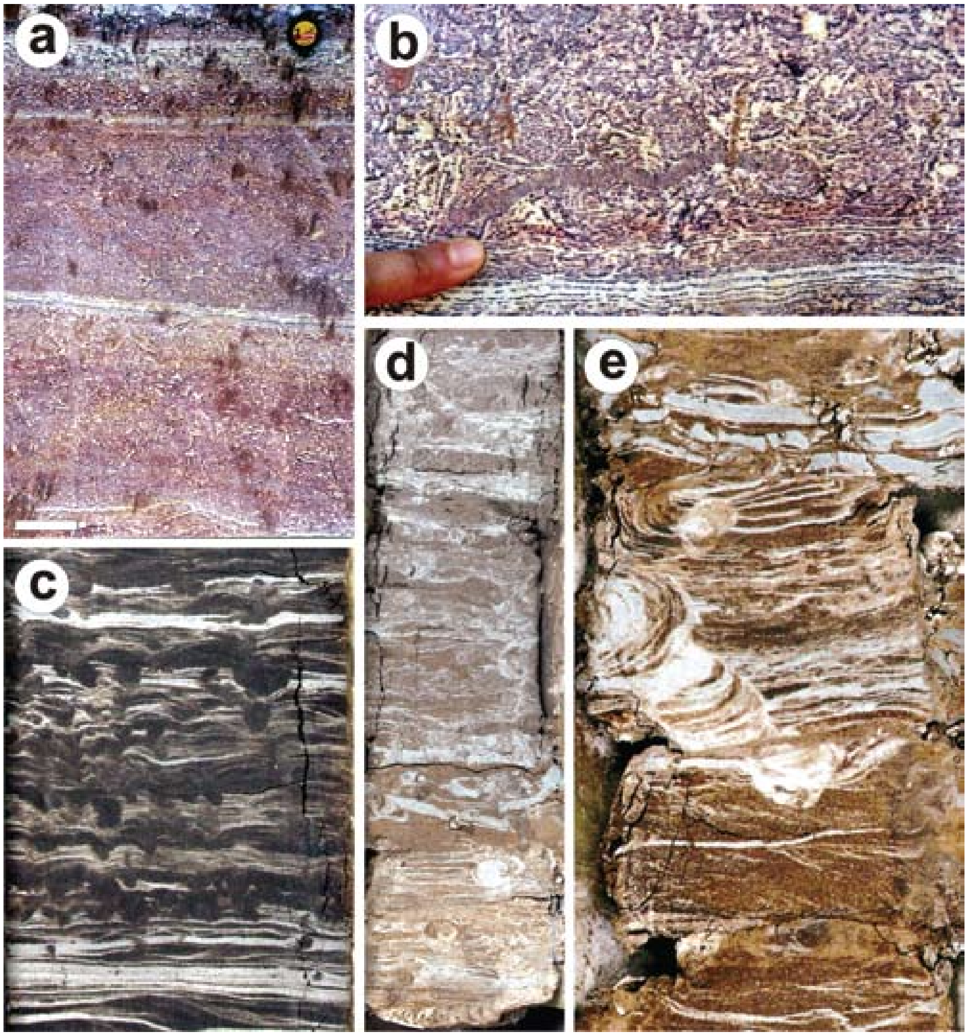


Figure 8.9 Composite ichnofabrics in estuarine-channel deposits with inclined heterolithic stratification. (a) Deposits with alternating intervals having well-preserved inclined heterolithic stratification and intensely bioturbated intervals as a result of the activity of a brackish-water infauna. Measuring tape is 5 cm wide. Lower Miocene Barreiras Formation, Peru Beach, Maranhão State, northern Brazil. See Netto and Rosetti (2003). (b) Close-up showing discrete continental *Taenidium* superimposed to a background brackish-water ichnofabric. Lower Miocene Barreiras Formation, Peru Beach, Maranhão State, northern Brazil. See Netto and Rosetti (2003). (c) *Teichichnus* ichnofabric in the lower interval of an estuarine point bar. Lower Miocene Oficina Formation of the Orinoco Belt, Venezuela. Core is 8 cm wide. (d) Intensely bioturbated upper interval of point-bar deposit shown in (c) The ichnofabric is dominated by continental *Taenidium* and *Beaconites* colonizing the abandoned point bar. Core width is 9.5 cm. (e) Close-up of *Beaconites* colonizing an abandoned point bar. Lower Miocene Oficina Formation of the Orinoco Belt, Venezuela. Core is 8 cm wide.

Thalassinoides and *Ophiomorpha*) tend to occur in these sandier substrates. Point-bar deposits are typically less bioturbated than the associated tidal flats (Gingras *et al.*, 1999b). Some lateral-accretion surfaces identified in the fossil record contain sharp-walled, unlined and passively filled burrows (e.g. *Thalassinoides*, *Skolithos*) of the *Glossifungites* ichnofacies. This suite suggests rapid dewatering and formation of autogenic stiffgrounds (Gingras *et al.*, 2000, 2001; Lettley *et al.*, 2007a). Also, the *Glossifungites* ichnofacies may occur at the base of channels that erode into the underlying bedrock (e.g. Gingras *et al.*, 1999b).

Salt marshes may form along the sides of the estuary. These marshes are dissected by a network of tidal creeks, and are commonly heavily vegetated by salinity tolerant plants (e.g. *Spartina*), resulting in intense bioturbation by root traces (e.g. Edwards and Frey, 1977; Basan and Frey, 1977). In modern salt marshes of macrotidal estuaries, *Corophium volutator* (producer of incipient *Arenicolites* and *Diplocraterion*) and *Mya arenaria* (producer of incipient *Siphonichnus* and *Lockeia*) are common (Dashtgard and Gingras, 2005). Tidal-creek migration may generate *Glossifungites*-demarcated surfaces. In tropical to subtropical estuaries, salt marshes are replaced by mangroves that form along sheltered shores, and consist mostly of trees and woody shrubs that have root adaptations to live in regularly submerged sediment (Cadée, 1998; Schaeffer-Novelli *et al.*, 2002). Robust root traces (e.g. *Avicennia*, *Rhizophora*, and *Sonneratia*) are commonly pervasive. In addition, a number of invertebrates are active bioturbators in mangrove areas (Cadée, 1998). These include mostly crustaceans that construct U-shaped burrows connected to a horizontal segment (*Thalassina anomala*), vertical burrows (*Sesarma* sp. and *Uca* sp.), and U-shaped burrows (*Upogebia* sp.). Horizontal grazing traces by mollusks, although common, have low preservation potential.

Tidal flats also occur along the sides of tide-dominated estuaries. In contrast to tidal flats formed on open coasts, ichnofaunas from middle-estuarine tidal flats are not diverse, but contain ichnotaxa that clearly illustrate marine influence, thereby allowing distinction from intertidal areas at the fluvial–estuarine transition (Mángano and Buatois, 2004a). In strongly tidally dominated settings, tidal flats form under an upper-flow regime (Dalrymple and Choi, 2007), and may be sparsely bioturbated due to high-energy conditions. Common components in low-energy counterparts include resting traces (e.g. *Asteriacites* and *Lockeia*), locomotion traces (e.g. *Gyrochorte* and *Protovirgularia*), grazing traces (e.g. *Nereites* and *Psammichnites*), feeding traces (e.g. *Teichichnus*, *Asterosoma*, *Planolites*, and *Cylindrichnus*), and dwelling traces (e.g. *Diplocraterion*, *Lingulichnus*, and *Palaeophycus*). Although the degree of bioturbation is typically low, *Lingulichnus* and *Lockeia* may occur in profuse densities. Suites are commonly monospecific, but the association of bivalve (*Lockeia*–*Protovirgularia*) and ophiuroid (*Asteriacites*) trace fossils is quite common (Mángano and Buatois, 2004a).

Central-basin deposits, although widespread in wave-dominated estuaries, are rare in tide-dominated estuaries due to a large degree of tidal exchange and the absence of a mouth–barrier system (Dalrymple *et al.*, 1992; Boyd *et al.*, 2006; MacEachern and Gingras, 2007). These deposits typically consist of heterolithic facies that are more bioturbated and exhibit higher diversity levels than the associated point-bar deposits (MacEachern and Gingras, 2007). Some of the ichnotaxa recorded in central-basin deposits are *Teichichnus*, *Planolites*, *Cylindrichnus*, *Palaeophycus*, and *Skolithos*.

The outer region of tide-dominated estuaries is characterized by the establishment of elongate tidal bars that may be associated with upper-flow regime sand flats (Dalrymple *et al.*, 1992; Boyd *et al.*, 2006; Dalrymple and Choi, 2007). Although this region displays normal-marine salinities, high tidal velocities and high rates of sedimentation commonly preclude bioturbation (e.g. Buatois *et al.*, 2006b). Locally, assemblages dominated by vertical burrows of suspension feeders, such as *Skolithos* (Fig. 8.10a–b), *Diplocraterion* (Fig. 8.10c) and *Ophiomorpha* (Fig. 8.10d), may occur in high densities reflecting colonization during short breaks in sedimentation or tidal-bar abandonment during transgression. Horizontal grazing and feeding traces, such as *Gyrochorte* (Fig. 8.10e) and *Psammichnites* (Fig. 8.10f), typically occur in mud drapes that result from longer breaks or in more protected sites showing interfingering with middle-estuarine deposits (Mángano and Buatois, 2004a). Vertical burrows of detritus or deposit feeders, such as *Asterosoma* (Fig. 8.10f), *Patagonichnus* (Fig. 8.10g), *Rosselia* (Fig. 8.11a), and *Teichichnus* (Fig. 8.11b) may occur also in this setting.

As in the case of wave-dominated estuaries, the salinity gradient plays a major role in distribution of biogenic sedimentary structures in tide-dominated estuaries. Ichnofaunas tend to display proximal–distal trends revealing the activity of freshwater and terrestrial biotas near or at the fluvial–estuarine transition, brackish-water faunas in the central zone of the estuary and fully marine biotas at the estuary mouth (Mángano and Buatois, 2004b). However, other factors may be equally important, albeit at a more local scale, including clay flocculation near the turbidity-maximum zone and high tidal energy at the elongate tidal-bar complex.

8.2 BAYS

In recent years, ichnologists have begun to recognize that some marginal-marine successions containing brackish-water assemblages do not strictly represent the infill of estuarine systems, but record deposition in embayments instead (e.g. MacEachern *et al.*, 1998). The ichnology of these bay settings is less understood than that of other marginal marine environments. Comparatively little has been written on these environments and only a few case studies have been documented (e.g. MacEachern *et al.*, 1998, 1999c; Pemberton *et al.*, 2001; Spila *et al.*, 2005; Buatois *et al.*, 2007b; Desjardins *et al.*, 2010b). MacEachern and Gingras (2007) suggested subdividing bay environments into restricted or barrier-barred bays and open or non-barred bays, a classification framework that is adopted here.

8.2.1 RESTRICTED BAYS

Restricted bays correspond to embayments that have limited or intermittent connection to the open sea (MacEachern and

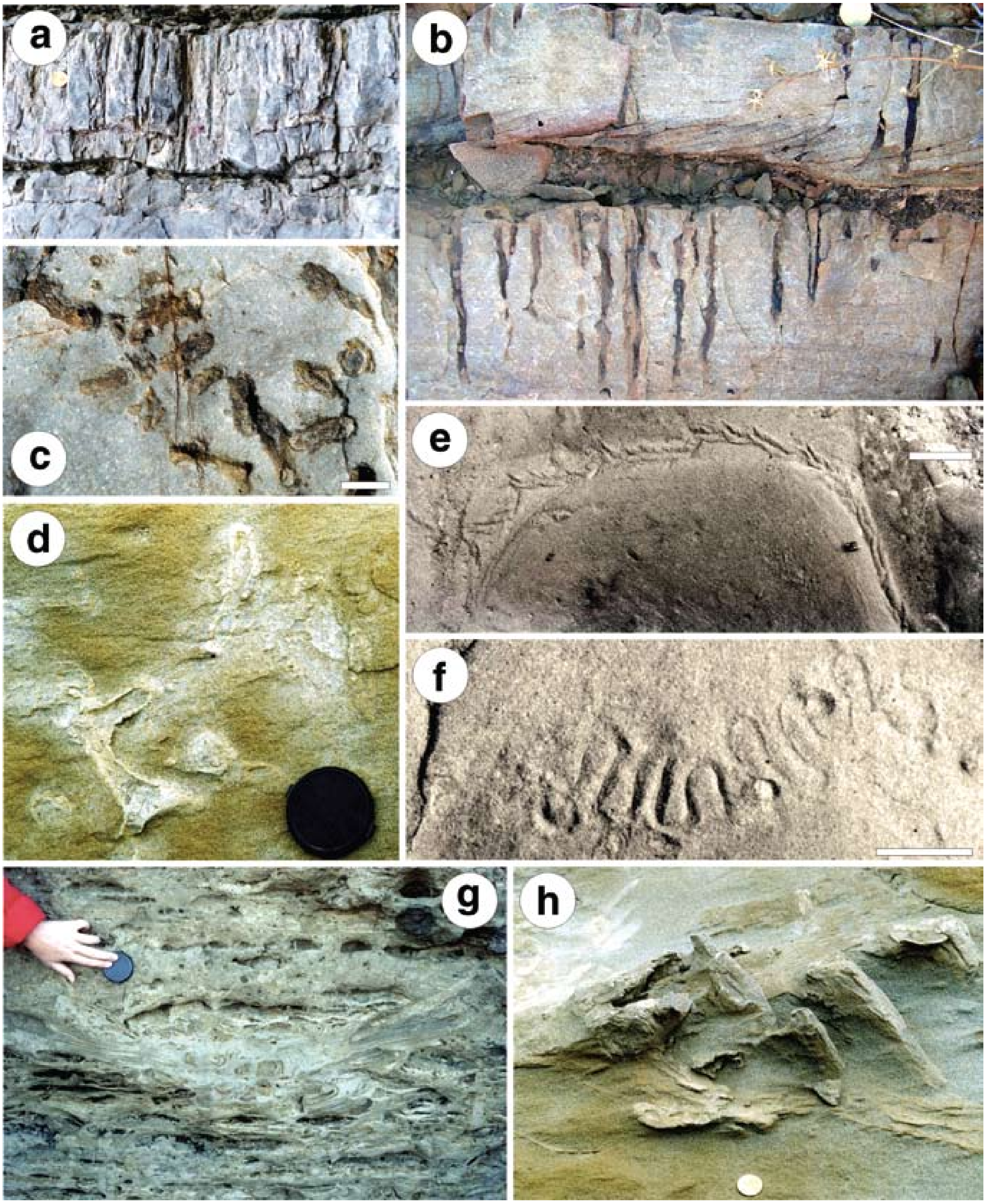


Figure 8.10 Ichnofaunas from deposits formed in the outer region of tide-dominated estuaries as expressed in outcrop. (a) *Skolithos linearis* forming a pipe rock. Upper Cambrian, Pico de Halcón Member, Quebrada del Salto Alto, Cordillera Oriental, northwest Argentina. Coin (upper left) is 1.8 cm. See Mángano and Buatois (2003a). (b) *Skolithos gyratus* in planar cross-bedded sandstone with abundant intraclasts and mud drapes. Upper Cambrian, Pico de Halcón Member, Quebrada del Abra Blanca, Cordillera Oriental, northwest Argentina. Coin (upper right) is 1.8 cm. (c) High density of *Diplocraterion parallelum* in bedding-plane view. Upper Cambrian, Pico de Halcón Member, Arroyo de Sapagua, Cordillera Oriental, northwest Argentina. Scale bar is 1 cm. (d) *Ophiomorpha nodosa*. Lower Miocene, Chenque Formation, roadcut near Comodoro Rivadavia, Patagonia, southern Argentina. Lens cap is 5.5 cm. (e) *Gyrochorte* isp. Upper Carboniferous, Bandera Shale, Bandera Sandstone Quarry, Bourbon County, eastern Kansas. Scale bar is 1 cm. See Mángano and Buatois (2004a). (f) *Psammichnites implexus*. Upper Carboniferous, Bandera Shale, Bandera Sandstone Quarry, Bourbon County, eastern Kansas. Scale bar is 1 cm. See Mángano and Buatois (2004a). (g) *Asterosoma radiciforme* displaying typical concentrically laminated ichnofabric. Lower Miocene, Patagonia Formation, cliff between Las Grutas and La Rinconada, Patagonia, southern Argentina. Lens cap is 5.5 cm. See Olivero and López-Cabrera (2005). (h) *Patagonichnus stratiformis*. Note associated mud drapes. Lower Miocene, Chenque Formation, roadcut near Comodoro Rivadavia, Patagonia, southern Argentina. Coin is 1.8 cm.

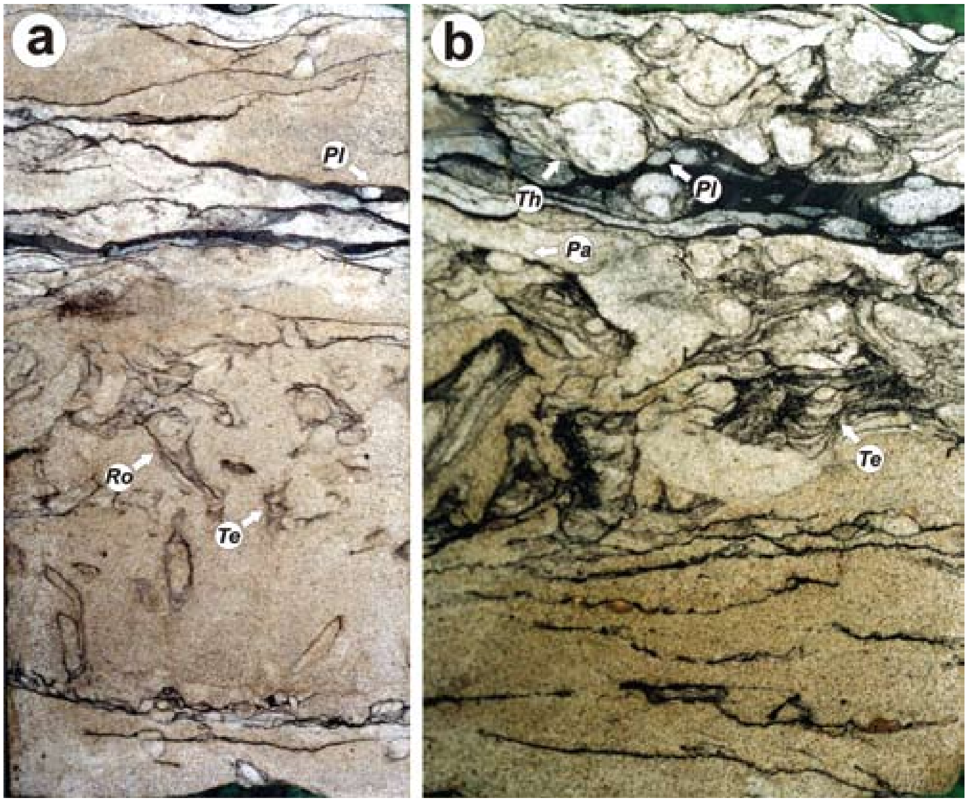


Figure 8.11 Core expression of ichnofaunas from the outer region of tide-dominated estuaries. (a) *Rosselia* isp. (*Ro*) and *Teichichnus rectus* (*Te*) in a sandstone bed. Note *Planolites* isp. (*Pl*) in mud drapes. Upper Cretaceous, Napo Formation, Auca Field, Oriente Basin, Ecuador. Core width is 10 cm. (a) *Thalassinoides* isp. (*Th*), *Teichichnus rectus* (*Te*), *Planolites* isp. (*Pl*) and *Palaeophycus* (*Pa*). Note abundant mud drapes and flaser bedding. Upper Cretaceous, Napo Formation, Shushufindi Field, Oriente Basin, Ecuador. Core width is 10 cm.

Gingras, 2007). Accordingly, they are typically characterized by brackish-water assemblages representing the mixed depauperate *Cruziana* and *Skolithos* ichnofacies (Fig. 8.12). Salinity fluctuations take place on a variety of temporal scales (e.g. daily, monthly and seasonally), imparting a stress signature to the associated biota (MacEachern and Gingras, 2007). This stress results in poorly diverse ichnofaunas and sparse bioturbation, *Teichichnus* (Fig. 8.13a–b) and *Planolites* (Fig. 8.13a–c), being some of the most common ichnogenera in severely restricted settings. Other common ichnogenera are *Rosselia* (Fig. 8.13a) and *Siphonichnus* (Fig. 8.13d). An increase in ichnodiversity, more intense bioturbation, and the presence of certain ichnogenera, such as *Asterosoma* and *Phycosiphon*, commonly suggest less restricted conditions or sporadic breaching of barriers as a result of storms (MacEachern and Gingras, 2007).

Bay-margin deposits consist of heterolithic facies with abundant synaeresis cracks and siderite nodules (MacEachern and Gingras, 2007). Trace fossils are sparsely distributed, with some intervals reaching relatively intense bioturbation. Ichnodiversity is low to rarely moderate. Monospecific suites are common. Typical ichnogenera are *Teichichnus*, *Planolites*, *Rosselia*, *Gyrolithes*, *Cylindrichnus*, *Palaeophycus*, and *Siphonichnus*. The *Glossifungites* ichnofacies is commonly associated with autogenic firmgrounds due to local erosion (MacEachern and Gingras, 2007).

The distal-bay deposits accumulate in the deepest parts of the bays or the most sheltered areas, and tend to be mud-dominated (MacEachern and Gingras, 2007). Thin tempestites layers may occur in strongly storm-affected bays, while dark parallel-laminated mudstones are typical of low-energy anoxic to dysaerobic embayments. Sandy tempestites may bear low-diversity assemblages consisting of *Palaeophycus*, *Planolites*, *Halopoa* (Fig. 8.13e), and *Rhizocorallium* (Fig. 8.13f) (Desjardins *et al.*, 2010b). Oxygen-depleted deposits are either unbioturbated, or contain sporadically distributed small *Planolites* (MacEachern and Gingras, 2007).

Bay-mouth deposits are sedimentologically and ichnologically more variable, and resemble wave-dominated estuary mouths (see Section 8.1.1). The salinity stress is not typically high because the outer region of the bay environment experiences slightly brackish to fully marine conditions. However, high-energy conditions predominate and, therefore, deposits are typically sparsely bioturbated (MacEachern and Gingras, 2007). Vertical burrows of suspension feeders are common in sandstone layers, including *Ophiomorpha*, *Skolithos*, and *Arenicolites*; horizontal traces of both deposit feeders (*Planolites*) and suspension feeders (*Palaeophycus*) occur in associated finer-grained intervals.

8.2.2 OPEN BAYS

Open bays have virtually unrestricted connection to the open sea (MacEachern and Gingras, 2007). As a result, the salinity stress is significantly lower than in restricted bays. However, these authors noted that salinity in the bay is in any case dependent of that of the adjacent seaway, which may be brackish. In addition, substrates are typically sandier than in restricted bays because of the deeper-water position of the wave base.

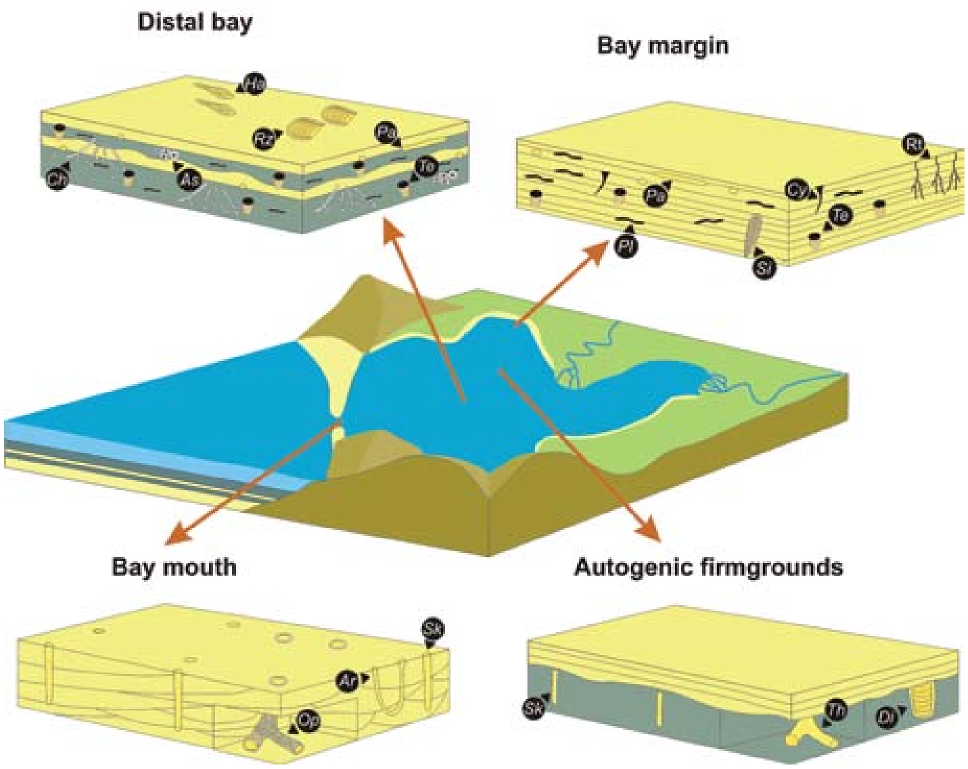


Figure 8.12 Schematic reconstruction of trace-fossil distribution in restricted bays. Bay-margin deposits commonly display low-diversity trace-fossil suites, including *Palaeophycus* (*Pa*), *Planolites* (*Pl*), *Siphonichnus* (*Si*), *Teichichnus* (*Te*), *Cylindrichnus* (*Cy*), and root trace fossils (Rt). Distal-bay deposits may contain more complex forms indicative of slightly less-stressful conditions. Typical ichnotaxa are *Rhizocorallium* (*Rz*), *Halopoa* (*Ha*), *Chondrites* (*Ch*), *Asterosoma* (*As*), *Palaeophycus* (*Pa*), and *Teichichnus* (*Te*). Bay-mouth deposits tend to contain ichnotaxa indicative of relatively high-energy conditions, such as *Ophiomorpha* (*Op*), *Arenicolites* (*Ar*), and *Skolithos* (*Sk*). Autogenic firmgrounds may contain *Skolithos* (*Sk*), *Diplocraterion* (*Di*), and *Thalassinoides* (*Th*).

As a result, open-bay deposits resemble shoreface successions (e.g. Pemberton *et al.*, 2001; MacEachern and Gingras, 2007). Depauperate expressions of the mixed *Cruziana* and *Skolithos* ichnofacies tend to alternate with more archetypal expressions of these ichnofacies (Fig. 8.14). A replacement of the *Skolithos* ichnofacies in bay-margin deposits by elements of the *Cruziana* ichnofacies in distal-bay deposits have been observed in some open bays (MacEachern *et al.*, 1998, 1999c).

Bay-margin deposits are very similar to shoreface successions both in physical and biogenic attributes (see Sections 7.1.3, 7.1.4, and 7.1.5), particularly in bays that are deep or not sheltered from wave approach (MacEachern and Gingras, 2007). Under strong tidal influence, heterolithic tidal-flat deposits become common. The degree of bioturbation is highly variable, with some deposits displaying intense bioturbation. Ichnodiversity is low to relatively high. Typical ichnotaxa include *Teichichnus*, *Thalassinoides*, *Planolites*, *Palaeophycus*, *Arenicolites*, *Cylindrichnus*, *Ophiomorpha*, and *Conichnus*, among many other forms. The presence, albeit restricted, of *Chondrites*, *Zoophycos*, and *Phycosiphon* suggests periods of fully marine conditions. *Teichichnus*, *Palaeophycus*, *Lingulichnus* (Fig. 8.15a), *Asteriacites* (Fig. 8.15b), *Protovirgularia* (Fig. 8.15b), and *Lockeia* (Fig. 8.15b) are common in tidal-flat areas; the latter three may display remarkable size reduction (Mángano *et al.*, 1999; Mángano and Buatois, 2004a).

Distal-bay deposits are mudstone-dominated, but contain a significant proportion of interbedded storm sandstones (MacEachern and Gingras, 2007). Sedimentologically and ichnologically these deposits closely resemble offshore and offshore-transition deposits. The degree of bioturbation is highly variable. Low to moderate bioturbation indexes tend to be common because of high rates of sedimentation in comparison with offshore deposits. However, intense bioturbation has been detected in some basins (Pemberton *et al.*, 2001; Spila *et al.*, 2005). Ichnodiversity varies from low to relatively high. Ichnotaxonomic composition is similar to that of proximal-bay deposits, but with a tendency to show lower proportions of elements of the *Skolithos* ichnofacies. As in the case of proximal-bay deposits, intervals containing less tolerant forms, such as *Chondrites*, *Zoophycos*, and *Phycosiphon*, are probably formed under fully marine conditions. Ichnodiversity levels commonly increase immediately above surfaces containing the *Glossifungites* ichnofacies, indicating transgressive events (MacEachern *et al.*, 1998, 1999c).

8.3 DELTAS

Deltas consist of discrete shoreline protuberances occurring where a river enters a standing body of water, supplying sediments more rapidly than they can be redistributed by basin processes, such as tides and waves (Bhattacharya, 2006). In this section, we will restrict our discussion to marine deltas. In recent years, deltaic systems have become the focus of increased scrutiny and a growing volume of new information is emerging (e.g. Sidi *et al.*, 2003; Giosan and Bhattacharya, 2005; Bhattacharya, 2006). As discussed above (see Section 8.1), ichnological information has been traditionally used to detect stresses associated with dilution of marine salinity in marginal-marine, brackish-water environments, most typically

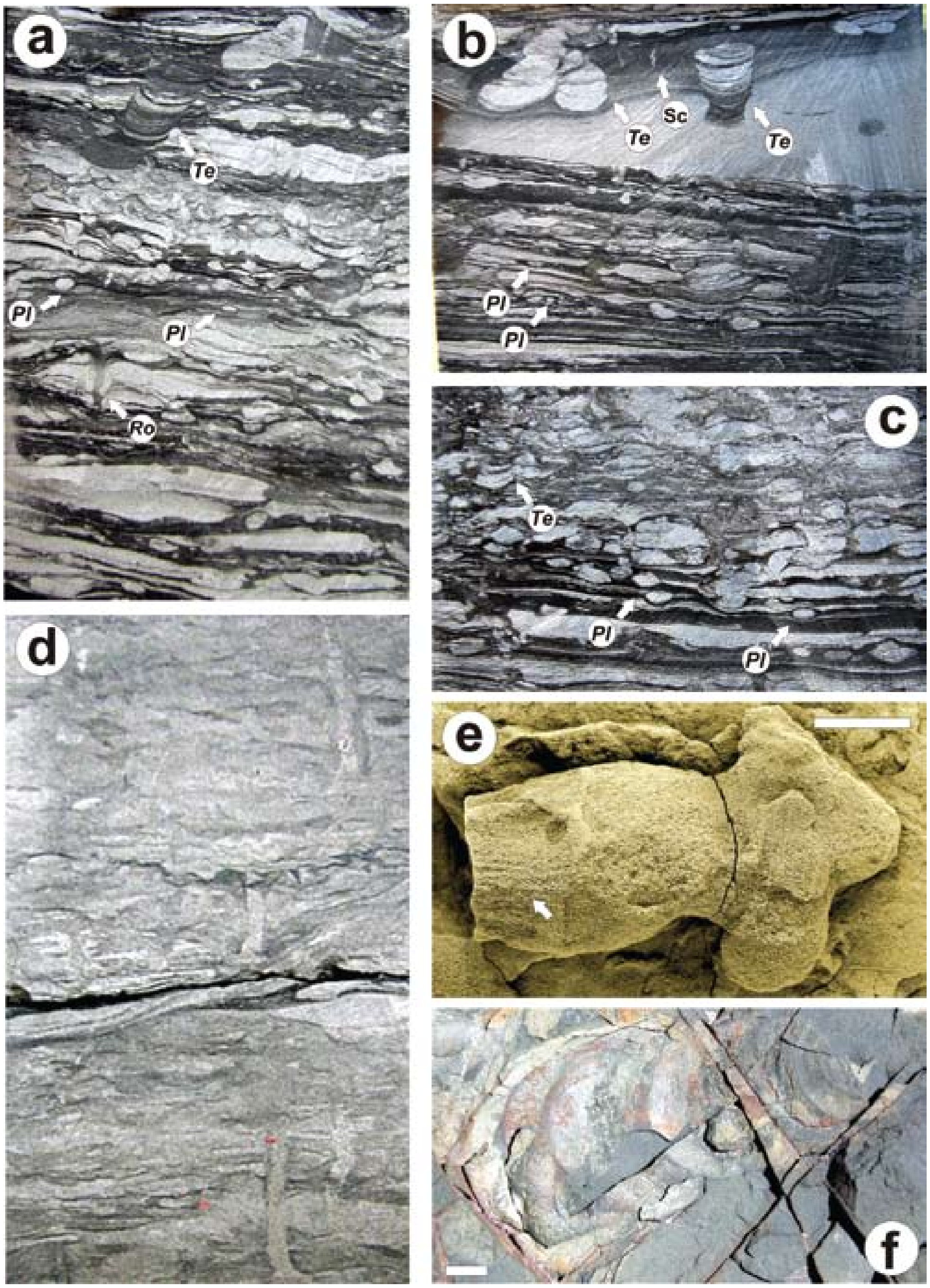


Figure 8.13 Outcrop and core expression of ichnofaunas from restricted bays. (a) Irregularly bioturbated heterolithic deposits containing *Teichichnus rectus* (*Te*), *Planolites montanus* (*Pl*), and small *Rosselia* isp. (*Ro*). Note abundant mud drapes. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (b) *Teichichnus rectus* (*Te*) at the top of a sharp-based tempestite. Note associated tiny *Planolites montanus* (*Pl*), synaeresis cracks (Sc), and mud drapes. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (c) Irregularly bioturbated heterolithic deposits containing *Teichichnus rectus* (*Te*) and *Planolites montanus* (*Pl*). Note well-developed wavy bedding and mud drapes. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (d) Deep-tier vertical *Siphonichnus eccacensis* overprinted to a background ichnofabric. Upper Devonian–Lower Carboniferous, Bakken Formation, southeastern Saskatchewan, central Canada. Core width is 7 cm. See Angulo and Buatois (2010). (e) *Halopoa* isp. with longitudinal striations (arrow). Upper Carboniferous, Tupe Formation, Cuesta de Huaco, Precordillera, Argentina. Scale bar is 1 cm. See Desjardins *et al.* (2010b). (f) *Rhizocorallium commune* with rod-like pellets organized in a spreiten structure. Upper Carboniferous, Tupe Formation, Cuesta de Huaco, Precordillera, Argentina. Scale bar is 1 cm. See Desjardins *et al.* (2010b).

estuarine deposits accumulated in incised valleys, resulting in the brackish-water model (Howard and Frey, 1975; Pemberton and Whightman, 1992; MacEachern and Pemberton, 1994; Buatois *et al.*, 2005) (see Section 6.1.4). However, there are relatively few studies that integrate ichnological information in the context of deltaic dynamics. Our understanding of the ichnology of deltas still suffers from several problems. One of these is the virtual absence of ichnological studies in modern deltas. In addition, some of these problems result from the incomplete picture available from sedimentological studies. In particular, while relatively detailed facies models are available for river- and wave-dominated deltas, the same is not true with respect to tide-dominated deltas (Willis, 2005). Unsurprisingly, tide-dominated deltas are also the least understood from an ichnological standpoint. Furthermore, while the brackish-water model is clearly of use in understanding ichnofaunas from embayment areas associated with the delta plain, its applicability in delta-front and prodelta settings is not straightforward (MacEachern *et al.*, 2005).

MacEachern *et al.* (2005) discussed the most important environmental controls and processes that represent stress factors in deltas. These factors result from the complex interplay of

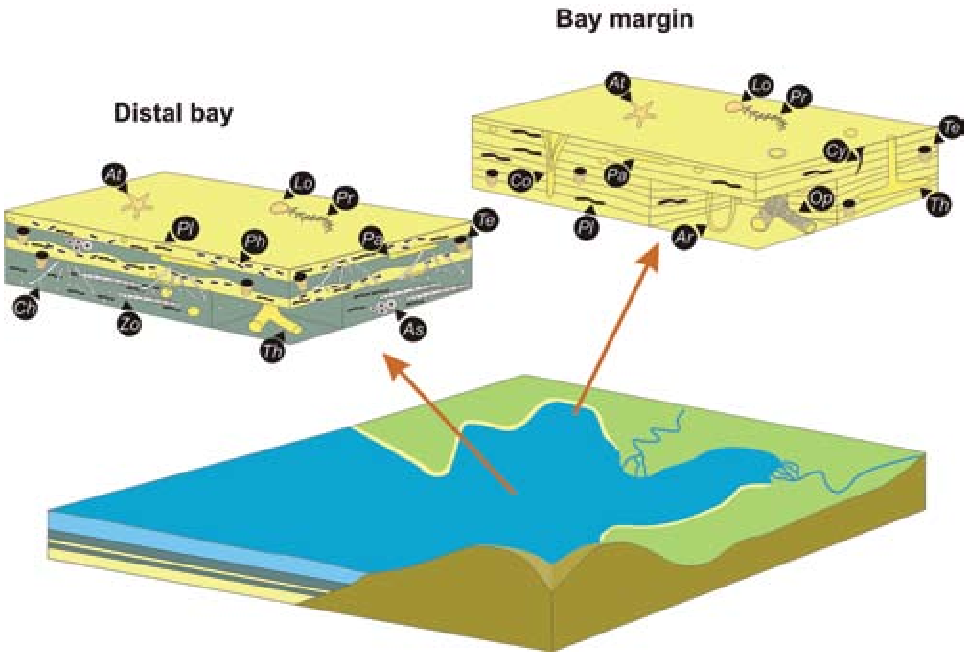


Figure 8.14 Schematic reconstruction of trace-fossil distribution in open bays. Ichnofaunas from open bays are more diverse than those in restricted bays. Bay-margin deposits may contain *Teichichnus* (*Te*), *Thalassinoides* (*Th*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Arenicolites* (*Ar*), *Cylindrichnus* (*Cy*), *Ophiomorpha* (*Op*), *Conichnus* (*Co*), *Asteriacites* (*At*), *Protovirgularia* (*Pr*), *Phycosiphon* (*Ph*), and *Lockeia* (*Lo*). Distal-bay deposits are ichnologically similar to proximal-bay deposits, but may also include ichnotaxa that are even less tolerant of brackish-water conditions, such as *Chondrites* (*Ch*), *Zoophycos* (*Zo*), and *Asterosoma* (*As*).

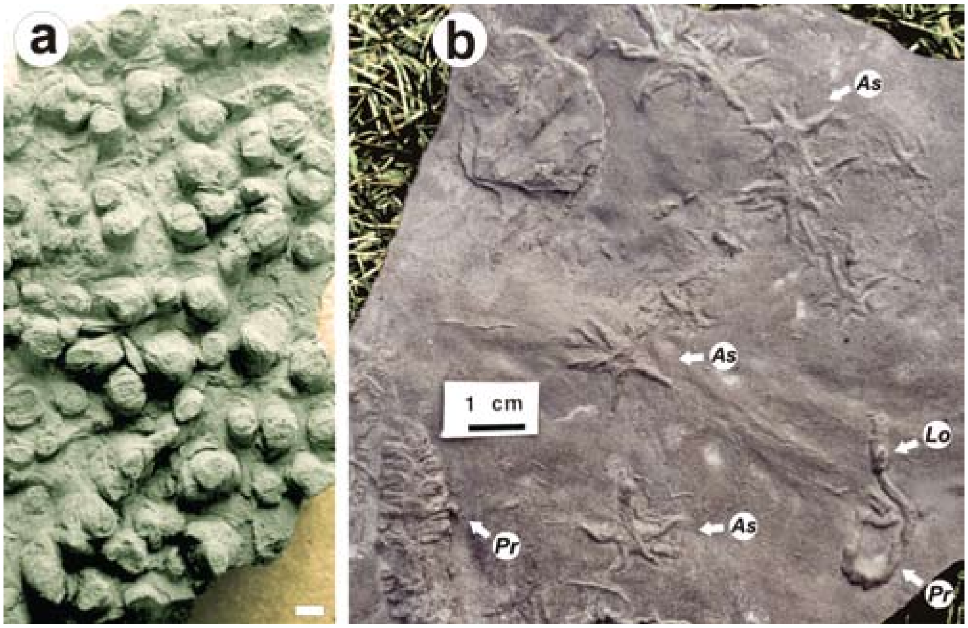


Figure 8.15 Ichnofaunas from open-bay deposits in outcrop. See Mángano and Buatois (2004b). (a) The lingulid dwelling trace *Lingulichnus* isp. on the base of a sandstone bed. Upper Carboniferous, Rock Lake Shale, Stanton Limestone, Lansing Group, quarry near Coleman Creek, southeast of Eudora, northeastern Kansas, United States. Scale bar is 1 cm. (b) The ophiuroid resting trace *Asteriacites lumbricalis* (*As*), and the bivalve traces *Lockeia siliquaria* (*Lo*) and *Protovigularia rugosa* (*Pr*) on the base of a sandstone bed. Note the small size of the compound bivalve trace fossil. Upper Carboniferous, Stull Shale, Kanwaka Shale Formation, Shawnee Group, roadcut along Country Road 6, south of Stull, northeastern Kansas, United States.

fluvial, wave, and tidal processes. River-induced stresses include heightened sedimentation rates, water turbidity, salinity changes (freshets), episodic sediment gravity deposition, hyperpycnal flows, and phytodetrital pulses. Wave-induced stresses include wave energy levels, repeated erosion, and longshore drift. Tidal-induced stresses comprise clay flocculation and fluid-mud deposition. Identification of these stress factors is essential to distinguish deltas from prograding strandplains. In this section, we address the ichnology of river-, wave- and tide-dominated deltas, following the genetic classification of Galloway (1975). However, this framework works at its best when combined with other classification schemes, which take into consideration other factors, such as sediment caliper (Orton and Reading, 1993) and site of emplacement (Porębski and Steel, 2006). In addition, most deltas are mixed, reflecting variable contributions of fluvial, wave, and tidal processes (e.g. Giosan *et al*., 2005).

8.3.1 RIVER-DOMINATED DELTAS

River-dominated deltas arguably rank among the most stressful of all deltas. This is mostly due to the overwhelming predominance of river-induced stresses. As a consequence, river-dominated

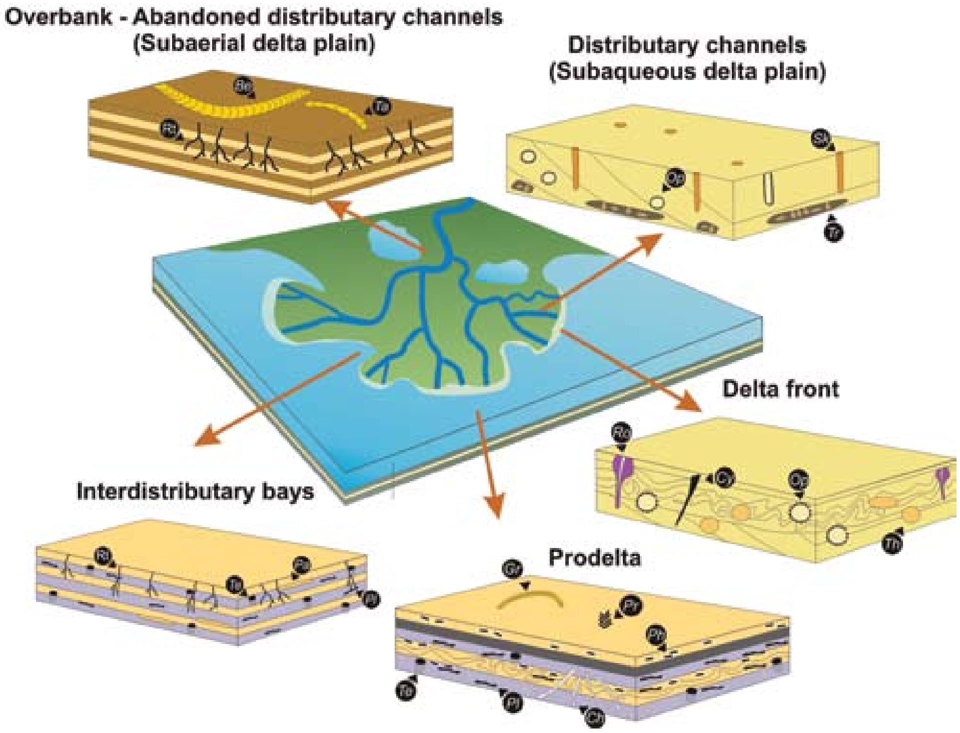


Figure 8.16 Schematic reconstruction of trace-fossil distribution in river-dominated deltas. Abandoned-channel and overbank deposits of the subaerial delta plain typically contain *Beaconites* (*Be*), *Taenidium* (*Ta*), and root traces (Rt). Distributary-channel deposits of the subaqueous delta plain may contain *Ophiomorpha* (*Op*) and *Skolithos* (*Sk*); *Teredolites* (*Tr*) may occur in wood logs at the base of the channel. Interdistributary-bay deposits typically host *Planolites* (*Pl*), *Teichichnus* (*Te*), *Palaeophycus* (*Pa*), and root traces (Rt). Delta-front deposits may contain *Rosselia* (*Ro*), *Ophiomorpha* (*Op*), *Cylindrichnus* (*Cy*), and *Thalassinoides* (*Th*). Prodelta deposits typically exhibit *Teichichnus* (*Te*), *Planolites* (*Pl*), *Phycosiphon* (*Ph*), *Chondrites* (*Ch*), *Protovirgularia* (*Pr*), and *Gyrochorte* (*Gr*).

Box 8.3 Ichnology of a late Quaternary fan-delta complex, South Island, New Zealand

Nearly continuous outcrops along the depositional strike of a late Quaternary fan delta in the South Island of New Zealand allows careful examination of its sedimentological and ichnological attributes. The complex consisted of a number of alluvial fans that prograded into the sea directly feeding small gravel and loess fan deltas separated by embayment areas. The embayment deposits consist of reworked loess, and sand and pebble forming bars. Trace fossils are remarkably well preserved, commonly showing full three-dimensional relief. No trace fossils occur in the subaerial fan delta-plain deposits, but marine biogenic structures are abundant in embayment, bar, and prodelta facies. Proximal deposits of the embayment contain abundant root trace fossils but not animal trace fossils, while distal loess deposits are characterized by the local presence of monospecific assemblages of *Phycosiphon incertum*, forming intensely bioturbated layers. Distal-embayment deposits also contain a trace-fossil association dominated by *Diplocraterion parallelum* with subordinate occurrences of other ichnotaxa, such as *Asterosoma* isp. and *Piscichnus* isp. The bar facies is also dominated by *Diplocraterion parallelum*; other trace fossils such as *Arenicolites* isp., *Cylindrichnus concentricus*, *Skolithos linearis*, and escape traces are locally abundant. Prodelta deposits are intensely bioturbated by poorly preserved specimens of *Planolites montanus*, with other ichnotaxa (e.g. *Diplocraterion parallelum*) locally present. A number of stress factors, such as salinity, interstitial oxygen, sediment composition and texture, hydrodynamic energy, and sedimentation rate, controlled the distribution of trace fossils in the fan-delta complex. Brackish water and reduced interstitial oxygen may have been limiting factors, particularly in the distal embayment, judging from the common occurrence of monospecific suites. This is consistent with limited circulation due to the presence of bars that partially isolated the embayment from the open sea. The presence of *Phycosiphon incertum* is restricted to fine-grained loess, indicating a strong substrate control. Loess cohesiveness may have allowed the *Phycosiphon* producer to keep its tunnel system open, allowing for respiration in poorly oxygenated substrate. High hydrodynamic energy in bar environments is suggested by the predominance of vertical burrows. In addition, high sedimentation rates in these settings are indicated by the presence of escape trace fossils.

Reference: Ekdale and Lewis (1991b), and Lewis and Ekdale (1991).

deltas tend to contain more depauperate ichnofaunas than wave- and tide-dominated deltas (Gingras *et al.*, 1998; MacEachern *et al.*, 2005) (Fig. 8.16) (Box 8.3). Ichnofaunas from the subaerial delta plain consist of a combination of terrestrial and freshwater trace fossils because they record conditions in the portion of the delta that is located above the high tide. Therefore, distributary channel and overbank ichnofaunas closely resemble those of fluvial channels and overbanks of alluvial plains (see Section

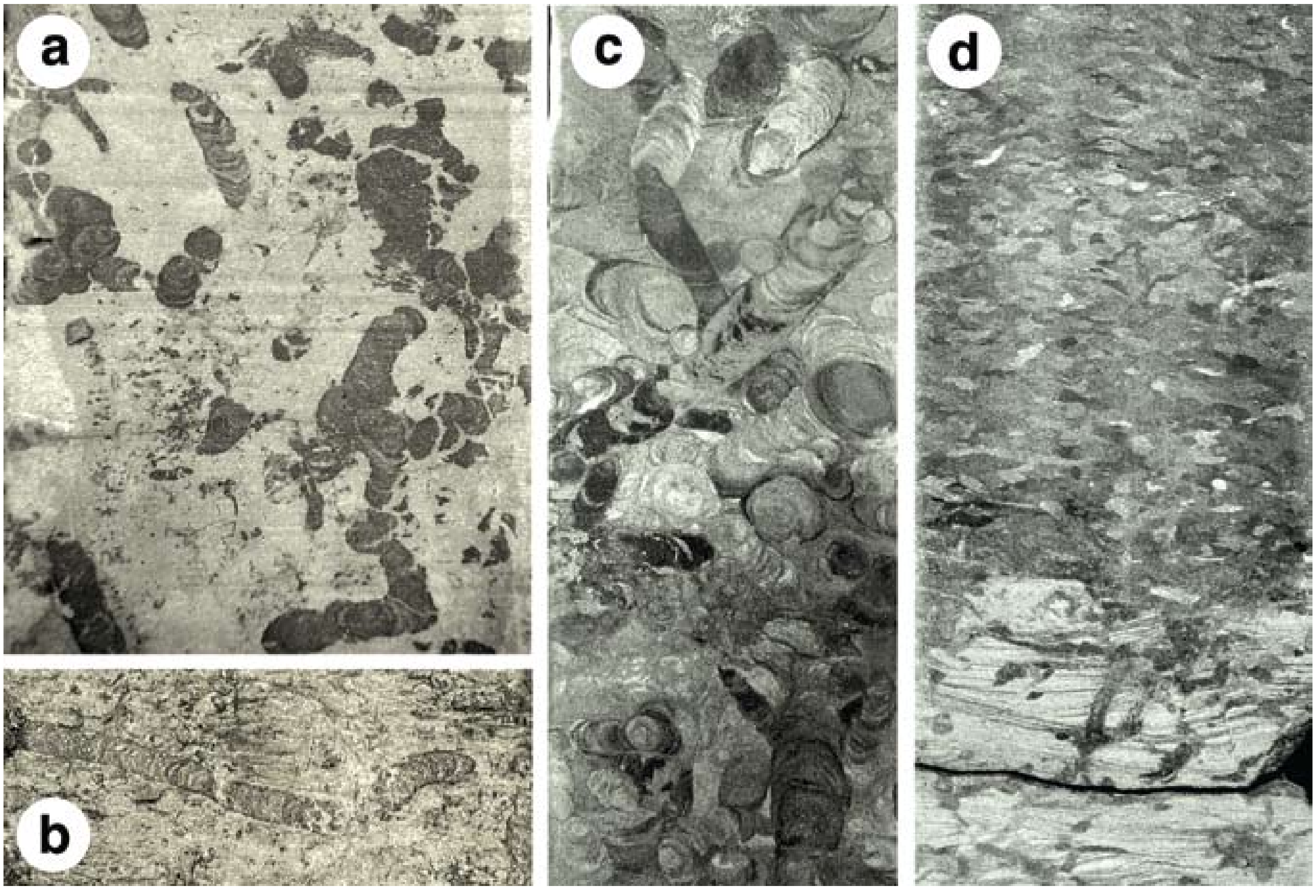


Figure 8.17 Core expression of ichnofaunas from subaerial delta-plain deposits. Oligocene–Middle Miocene, Guafita Formation, Guafita Field, Apure, Venezuela. (a) The meniscate trace fossil *Taenidium* in red siltstone. Core width is 10 cm. (b) Close-up of *Taenidium*. Core width is 10 cm. (c) High-density of meniscate trace fossils in red siltstone. Core width is 10 cm. (d) Crevasse-splay sandstone (lower interval) and floodplain siltstone (upper interval). Note colonization by *Taenidium* and high intensity of bioturbation in the siltstone. Core width is 9 cm.

10.2). *Taenidium* and *Beaconites* are typical components of the *Scoyenia* ichnofacies in these settings (Fig. 8.17a–d). Because of the high frequency of crevassing and overbank events, the *Scoyenia* ichnofacies tends to be common in the subaerial delta plain of river-dominated systems (e.g. Pollard, 1988). Bivalve (*Lockeia*) and xiphosurid (*Kouphichnium* and *Selenichnites*) trace fossils may occur also (Eagar *et al.*, 1985). However, during times of reduced or no discharge, the salt wedge may extend upstream, generating brackish-water conditions across the delta plain and colonization by elements of the mixed depauperate *Cruziana* and *Skolithos* ichnofacies (e.g. Corbeanu *et al.*, 2004; Garrison and van der Berg, 2004).

Brackish-water conditions are persistent in the proximal regions of deltas, particularly the subaqueous delta plain, interdistributary bays, and the distributary mouth bars at the proximal delta front (MacEachern *et al.*, 2005). Ichnofaunas in these subenvironments basically display the diagnostic features outlined by the brackish-water model (see Section 6.1.4). Bioturbation is remarkably sparse and ichnodiversity levels are very low. *Ophiomorpha* and *Diplocraterion* occur locally in abandoned delta-plain distributary-channel, abandoned terminal distributary-channel and mouth-bar sandstone (e.g. Hobday and Tavener-Smith, 1975). Retrusive forms of *Diplocraterion* may be common, indicating high sedimentation rates (e.g. Turner *et al.*, 1981). Logs with *Teredolites* are common on channel floors (e.g. MacEachern *et al.*, 2005). Escape trace fossils may occur locally reflecting rapid sedimentation within the channels. Interdistributary-bay mudstone commonly contains *Planolites* and *Teichichnus* as dominant components, typically associated with synaeresis cracks. Root traces record the presence of waterlogged paleosols in swamp areas.

Periodic salinity fluctuations due to freshwater input from rivers (freshets of MacEachern *et al.*, 2005) may take place in more distal areas, and, in fact, play a major role in delta-front and prodelta environments. As a result, even in these distal settings, ichnofaunas from river-dominated deltas are impoverished. Freshets are typically revealed by the association of synaeresis cracks, siderite bands and nodules, and depauperate occurrences of the *Cruziana* ichnofacies (MacEachern *et al.*, 2005). Low ichnodiversity of individual suites (Fig. 8.18a–b) reveals a stress factor due to reduced salinity, and allows distinction from non-deltaic strandplain–shoreface successions. However, the local occurrence

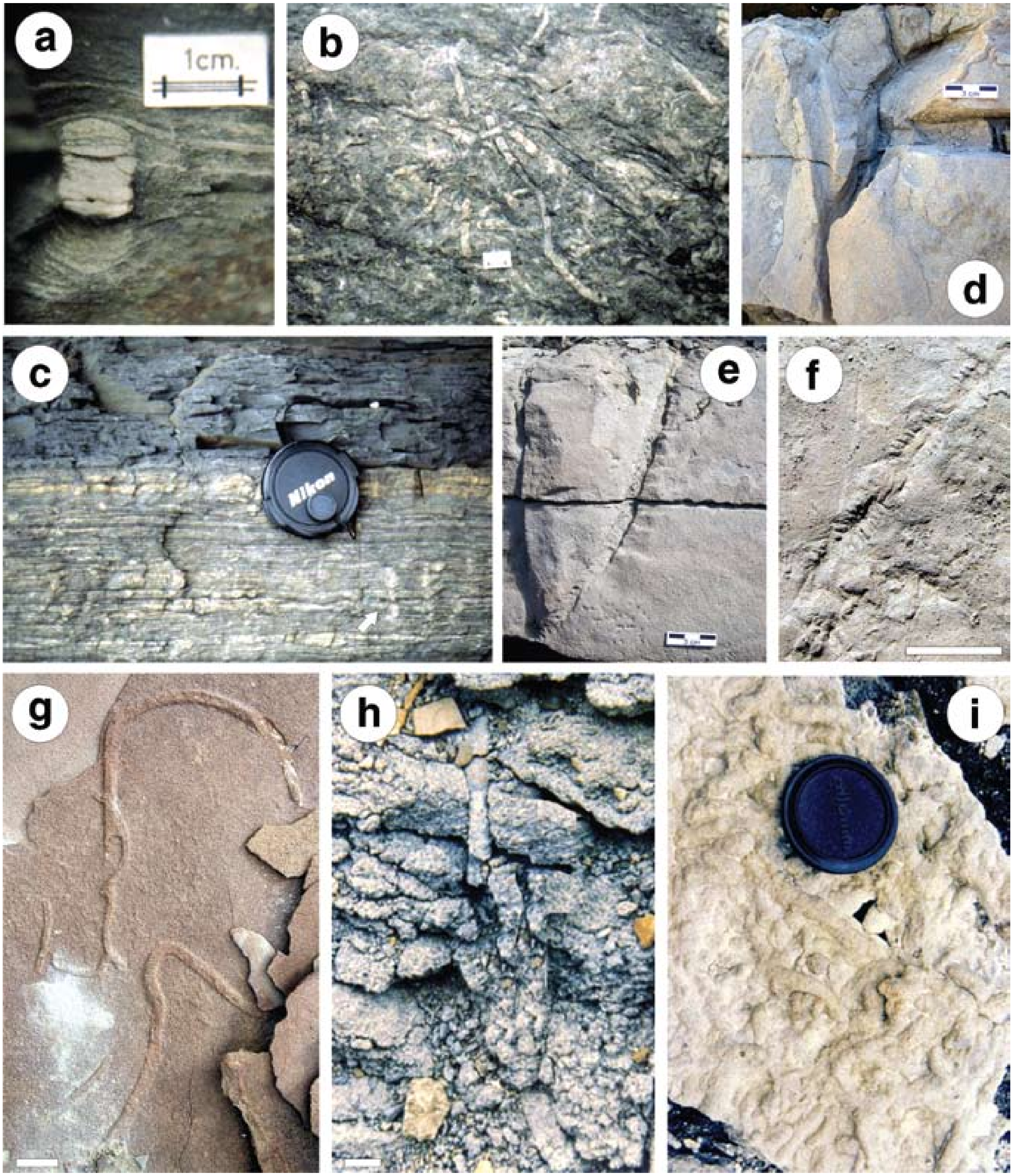


Figure 8.18 Outcrop expression of ichnofaunas from river-dominated delta-front and prodelta deposits. (a) *Teichichnus rectus* with well-defined causative burrow in prodelta siltstone-rich deposits. Upper Carboniferous, Westward Ho! Formation, Bideford Group, north Devon coast, southwestern England. (b) Bedding-plane view of a monospecific suite of *Teichichnus rectus* in prodelta siltstone-rich deposits. Upper Carboniferous, Westward Ho! Formation, Bideford Group, north Devon coast, southwestern England. Scale bar is 1 cm. (c) Escape trace fossils (arrow) in prodelta siltstone-rich deposits. Note overlying unburrowed fluid mudstone. Upper Carboniferous, Westward Ho! Formation, Bideford Group, north Devon coast, southwestern England. Lens cover is 5 cm. (d) *Rosselia chonoides* in delta-front turbidites. Upper Cretaceous, Panther Tongue, Star Point Formation, Gentile Wash, near Price, Book Cliffs, eastern Utah, United States. See Bhattacharya *et al*. (2007). (e) Vertical *Ophiomorpha nodosa* in delta-front turbidites. Upper Cretaceous, Panther Tongue, Star Point Formation, Gentile Wash, near Price, Book Cliffs, eastern Utah, United States. See Bhattacharya *et al*. (2007). (f) *Protovirgularia* isp. in prodelta-lobe deposits. Upper Cretaceous, Kennilworth Member, Blackhawk Formation, Hatch Mesa, Book Cliffs, eastern Utah, United States. Scale bar is 1 cm. (g) *Gyrochorte* isp. in prodelta-lobe deposits. Upper Cretaceous, Kennilworth Member, Blackhawk Formation, south entrance to Tusher Canyon, Book Cliffs, eastern Utah, United States. Scale bar is 1 cm. (h) *Skolithos* isp. in coarse-grained fan-delta front deposits. Upper Cretaceous, Hidden Lake Formation, Bajo de la Angustia, James Ross Island, Antarctica. Scale bar is 1 cm. See Buatois and López Angriman (1992a). (i) *Palaeophycus tubularis* in coarse-grained fan-delta front deposits. Upper Cretaceous, Hidden Lake Formation, Bajo de la Angustia, James Ross Island, Antarctica. Lens cover is 5 cm. See Buatois and López Angriman (1992a).

of ichnotaxa more typical of open-marine environments (e.g. *Phycosiphon*, *Chondrites*) suggests periods of normal-marine salinity that alternated with dilution due to fluvial discharge.

In addition to freshwater discharge, water turbidity represents another stress factor in river-dominated deltas (see Section 6.1.8). Deltas that developed under hypopycnal conditions are commonly characterized by buoyant plumes leading to rapid flocculation of clays (Bates, 1953; Wright, 1977; Kineke *et al*., 1996). High suspended loads of fine-grained material related to river influx clog the filter-feeding apparatus of suspension feeders, therefore resulting in an impoverishment or direct suppression of the *Skolithos* ichnofacies (Gingras *et al*. 1998; MacEachern *et al*. 2005). In addition, accumulation of fluid muds in distal delta fronts and prodeltas imparts a substrate stress by reducing boundary shear stress, preventing benthic organisms from constructing permanent structures or actively backfill tunnels (see Section 6.1.2). Sediment swimming is the only possible strategy in these soupy substrates (Schieber, 2003). Even in the case that benthic organisms are able to burrow into these substrates, preservation of these structures is unlikely (Ekdale, 1985). As a result, fluid mud is typically unbioturbated or, more rarely, contains "mantle and swirl" biogenic structures (Schieber, 2003; Bhattacharya and MacEachern, 2009).

The delta front and prodelta of river-dominated deltas is also influenced by rapid rates of sedimentation. Under hyperpycnal conditions, underflow currents move off river mouths along the sea floor. Underflow triggering is particularly common at the mouth of small- to medium-sized rivers (Mulder and Syvitski, 1995). Hyperpycnal flows are commonly conducive to rapid deposition. Also, rapid rates of sedimentation are associated with sediment gravity flows produced by delta-front bar failure. In both situations, colonization of the substrate by benthic organisms is inhibited or reduced due to a combination of rapid deposition and high frequency of sedimentation events (MacEachern *et al*., 2005). As a consequence, these rapidly emplaced layers tend to be sparsely bioturbated, may contain escape trace fossils (Figs. 8.18c and 8.19e), and commonly display a colonization surface at the top of the event bed (Fig. 8.18d–e). The low degree of bioturbation of these event beds may contrast with the more intense bioturbation of associated finer-grained deposits if background sedimentation rate is not high (Fig. 8.19a). Under more continuous deposition from river-fed density underflows, ichnological evidence indicates animal activity contemporaneous with sedimentation instead of colonization after a major break in deposition. Highly compressed specimens of *Thalassinoides* filled with parallel-laminated sand may occur in sandy hyperpycnites, suggesting high rates of sedimentation and emplacement of water-saturated sand (Buatois *et al*., 2011) (Fig. 8.19b). Associated trace fossils are *Teichichnus* (Fig. 8.19c) and *Diplocraterion* (Fig. 8.19d). In some case, lobes may consist of a complex facies mosaic of classic turbidites, sandy hyperpycnites, wave-modified turbidites, and storm-generated beds (Pattison, 2005; Pattison *et al*., 2007). Common ichnogenera in these deposits are *Protovirgularia* (Fig. 8.18f), *Palaeophycus*, *Skolithos*, *Gyrochorte* (Fig. 8.18g), *Phycosiphon*, and *Rosselia* (Buatois *et al*., 2010b). MacEachern *et al*. (2005) noted that hyperpycnal events are commonly linked to freshets and increased phytodetrital influx (Fig. 8.19e) creating a whole set of stress factors to benthic life. In turn, phytodetrital pulses are linked to oxidation of organic carbon and oxygen depletion. It is therefore unsurprising that *Chondrites* is one of the dominant forms in many river-dominated prodelta mudstones (MacEachern *et al*., 2005). Freshwater discharge may be extreme in glaciated basins significantly affecting coastal ecosystems (see Section 8.4).

The importance of sediment caliper in deltaic depositional systems has long been recognized (Orton and Reading, 1993). In the case of coarse-grained systems, such as fan deltas, high-energy conditions, high rates of sedimentation and dominance of coarse grain size are major factors leading to reduced diversity and bioturbation restricted to localized levels (e.g. Ekdale and Lewis, 1991b; Buatois and López Angriman, 1992a) (Fig. 8.18h–i). However, Ekdale and Lewis (1991b) noted relatively high diversity levels in bar deposits of a gravel and loess fan-delta complex (Box 8.3). Robust dwelling structures (e.g. *Thalassinoides*, *Ophiomorpha*) seem to be the dominant components of fan-delta ichnofaunas (e.g. Buatois and López Angriman, 1992a; Siggerud and Steel, 1999). Fan-delta plain deposits are typically unbioturbated (Ekdale and Lewis, 1991b).

8.3.2 WAVE-DOMINATED DELTAS

In terms of the importance of stress factors, wave-dominated deltas rank among the least stressful of all deltaic systems (Fig. 8.20) (Box 8.4). In fact, distinction of wave-dominated delta front and prodelta from wave-dominated strandplain deposits is exceedingly difficult and the precise depositional setting of many successions remains controversial (e.g. Howell and Flint, 2003; Bhattacharya and Giosan, 2003; Bhattacharya, 2006). Ichnofaunas from the subaerial delta plain are identical to those from river-dominated deltas (see Section 8.3.1), although frequency of crevassing and overbank events is lower and, therefore, the *Scoyenia* ichnofacies is not as widespread.

The subaqueous delta plain is by far the most stressful setting in wave-dominated deltas. Distributary-channel and interdistributary-bay deposits are sparsely bioturbated and contain typical brackish-water assemblages. In fact, distributary-channel deposits are commonly unbioturbated; *Ophiomorpha* (Fig. 8.21a) and *Skolithos* may locally occur at colonization surfaces typically reflecting pauses in sedimentation or channel abandonment. Escape trace fossils may occur also. Interdistributary-bay deposits contain suites that reflect lower-energy conditions. *Planolites* (Fig. 8.21b), *Palaeophycus*, *Teichichnus* (Fig. 8.21b), and root trace fossils (Fig. 8.21c) are the dominant components in protected bay areas. *Rosselia* (Fig. 8.21d) and *Cylindrichnus* may be present locally. Subaqueous delta-plain assemblages display all the characteristics of brackish-water ichnofaunas, namely low ichnodiversity, forms typically found in marine environments, dominance of infaunal traces rather than epifaunal trails, simple structures produced by trophic generalists, mixture of vertical and horizontal traces from the *Skolithos*

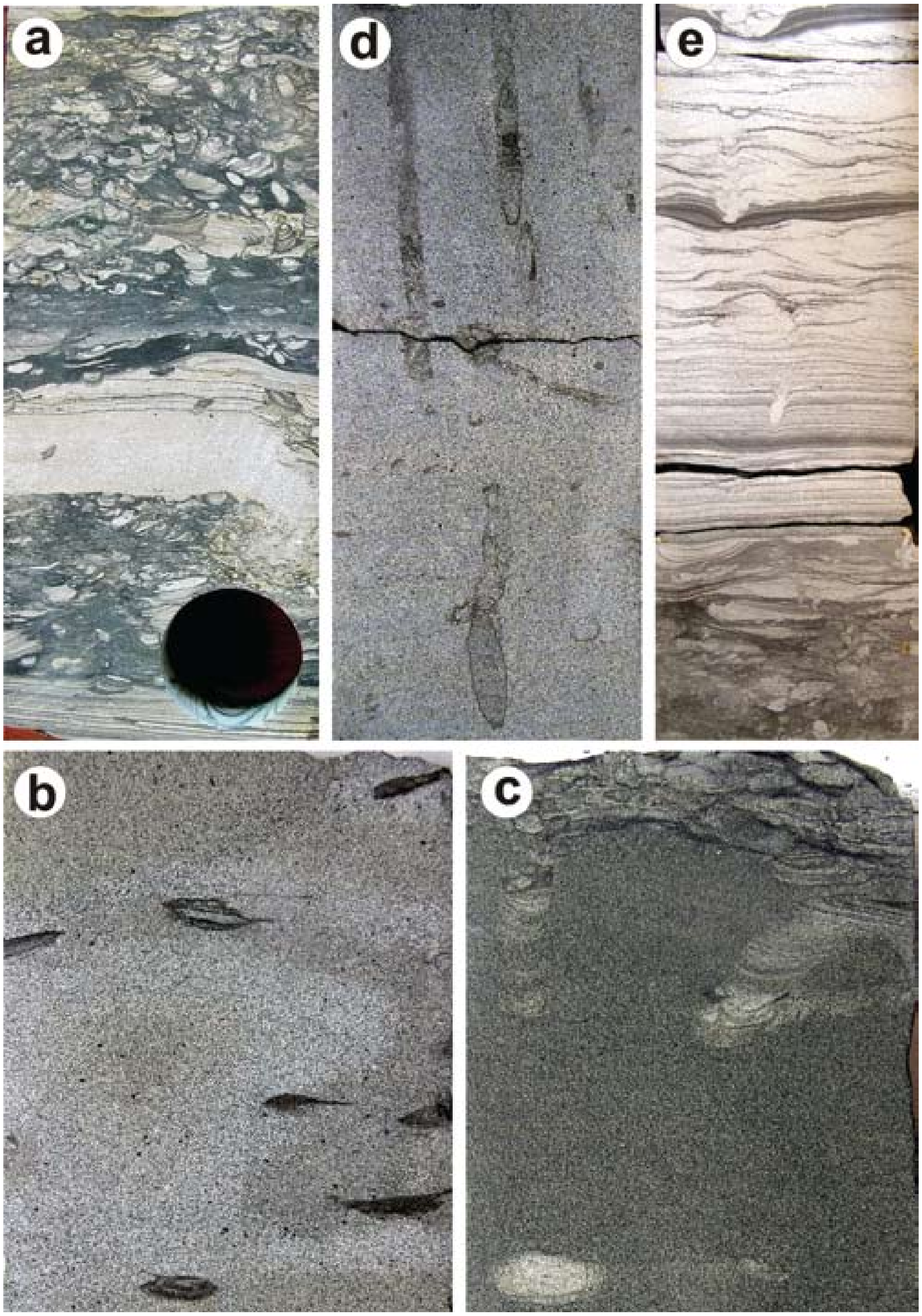


Figure 8.19 Core expression of ichnofaunas from river-dominated delta-front and prodelta deposits. (a) Proximal-prodelta sharp-based sparsely bioturbated event sandstone layer interbedded with intensely bioturbated finer-grained deposits containing a trace-fossil suite dominated by *Teichichnus rectus*. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (b) Highly compressed, mud-lined *Thalassinoides* isp. showing infill with passive parallel lamination in sandy hyperpycnal-lobe deposits. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (c) Retrusive *Teichichnus* isp. in sandy hyperpycnal-lobe deposits. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (d) Long U-shaped *Diplocraterion* isp. burrows in sandy hyperpycnal-lobe deposits. Upper Cretaceous, Magallanes Formation, Estancia Agua Fresca area, Austral Basin, southern Patagonia, Argentina. Core width is 10 cm. See Buatois *et al.* (2011). (e) Escape trace fossils in distal delta-front deposits. Note more intense bioturbation in underlying mudstone. Thin dark lamina of carbonaceous detritus record phytodetrital pulses. Upper Cretaceous, Ferron Sandstone, Ivie Creek #3, Ivie Creek area, eastern Utah, United States. Core width is 9 cm. See MacEachern *et al.* (2007b).

and *Cruziana* ichnofacies, abundance of some ichnotaxa, and presence of monospecific suites (see Section 6.1.4).

Proximal to distal delta-front deposits of wave-dominated deltas are commonly characterized by a combination of the *Skolithos* and *Cruziana* ichnofacies (MacEachern *et al.*, 2005). As in the case of river-dominated deltas, *Ophiomorpha* is common in terminal distributary-channel deposits (Fig. 8.21e). Some detritus-feeding traces (e.g. *Cylindrichnus*) are components of the *Skolithos* ichnofacies in proximal delta-front deposits. Impoverishment of the *Skolithos* ichnofacies rather than suppression seems to be the norm in wave-dominated deltas in contrast to more stressful river-dominated ones. In storm-dominated settings, periodic fluvial discharges alternate with storm events and suspension fallout, leaving diagnostic ichnological signatures in the deposits. Repeated storm events rank among the most important controlling factors in these deltas. Storm-influenced clastic deposits comprise two contrasting trace-fossil assemblages that reflect the behavioral response of the benthic fauna that developed under two successive and contrasting environmental conditions (see Section 7.1). The

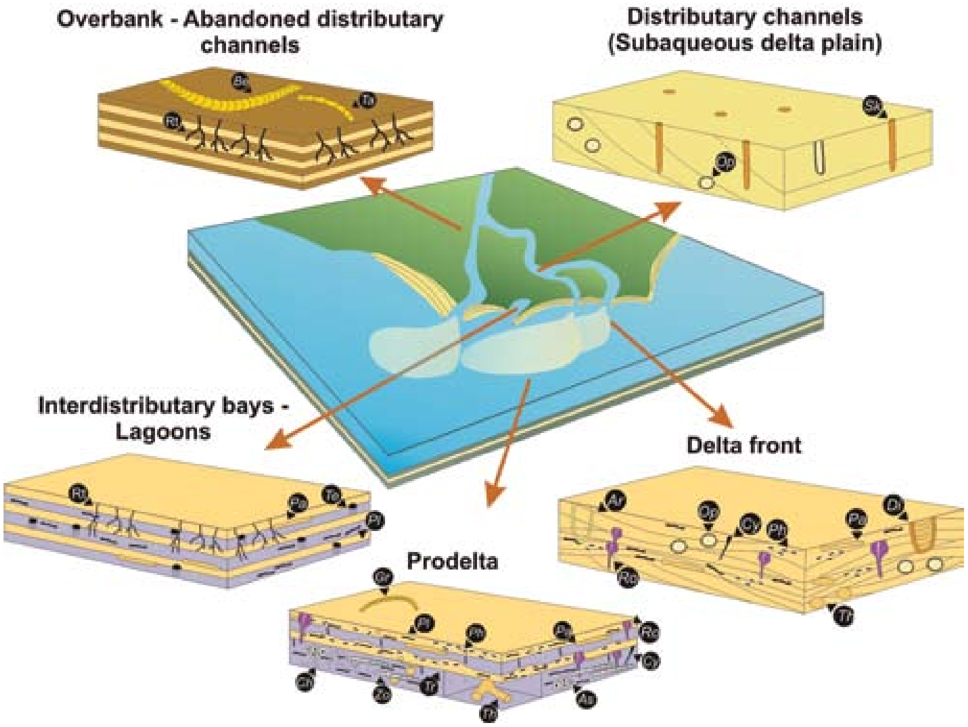


Figure 8.20 Schematic reconstruction of trace-fossil distribution in wave-dominated deltas. As in the case of river-dominated deltas, abandoned-channel and overbank deposits of the subaerial delta plain typically contain *Beaconites* (*Be*), *Taenidium* (*Ta*), and root traces (Rt). Distributary-channel deposits of the subaqueous delta plain may contain *Ophiomorpha* (*Op*) and *Skolithos* (*Sk*). Interdistributary-bay and lagoonal deposits typically display *Planolites* (*Pl*), *Teichichnus* (*Te*), *Palaeophycus* (*Pa*), and root traces (Rt). Delta-front deposits may contain *Rosselia* (*Ro*), *Ophiomorpha* (*Op*), *Cylindrichnus* (*Cy*), *Thalassinoides* (*Th*), *Palaeophycus* (*Pa*), *Diplocraterion* (*Di*), *Phycosiphon* (*Ph*), and *Arenicolites* (*Ar*). Prodelta deposits exhibit various ichnotaxa, such as *Teichichnus* (*Te*), *Planolites* (*Pl*), *Phycosiphon* (*Ph*), *Chondrites* (*Ch*), *Protovirgularia* (*Pr*), *Zoophycos* (*Zo*), *Trichichnus* (*Tr*), *Asterosoma* (*As*), *Thalassinoides* (*Th*), *Palaeophycus* (*Pa*), and *Gyrochorte* (*Gr*).

Box 8.4 Ichnology of a Lower Miocene wave-dominated delta in the subsurface of the Eastern Venezuela Basin

The Eastern Venezuela Basin hosts a number of deltaic sandstones that have been intensely explored petroleum targets. Detailed ichnological and sedimentological observations in cores allow the interpretation of Lower Miocene deposits in the Tácata field as the result of progradation of a wave-dominated delta complex. Repeated storms were one the most important controlling factors on the front of the Tácata deltas and on the lower/middle shoreface of associated strandplains. Amalgamated, thick-bedded storm deposits are typically unburrowed or contain deep vertical *Ophiomorpha* (Fig. 8.22a). Delta-front and prodelta deposits, although being characterized by sparse bioturbation and depauperate trace-fossil suites (Fig. 8.22b–c), contain some ichnotaxa that typically do not occur in brackish-water settings, such as *Chondrites* and *Phycosiphon* (Fig. 8.22d). Preservation of very thin storm layers was regarded as more common of wave-dominated deltas than of strandplain systems because deltaic stresses preclude the establishment of an abundant infauna that otherwise would have completely reworked such thin sandstone layers. Tidal influence was subordinate and restricted to distributary-channel and, particularly, interdistributary-bay deposits. Interdistributary-bay deposits are sparsely bioturbated and their ichnofaunas, typically dominated by *Teichichnus* (Fig. 8.21b) and *Planolites*, tend to display all the characteristics expected from brackish-water settings. Distributary-channel deposits are sparsely bioturbated, but the presence of certain ichnotaxa (e.g. *Ophiomorpha*; Fig. 8.21e) allows distinction from freshwater fluvial channels. Ichnological evidence has been essential to differentiate between deltaic and associated along-strike strandplain–shoreface successions, and to detect possible delta asymmetry. In particular, *Scolicia* ichnofabrics (Fig. 8.22e–f) are restricted to fully marine offshore deposits that accumulated on the updrift side of the river mouths. Associated fully marine deposits are also characterized by an overall increase in ichnodiversity and degree of bioturbation (Fig. 8.22g). This study illustrates how ichnological data used in conjunction with sedimentological evidence helps to identify deltaic signatures that otherwise may remain undetected.

Reference: Buatois *et al*. (2008).

resident, fair-weather trace-fossil assemblage records the establishment of a benthic community developed under stable and rather predictable conditions, and commonly belongs to the *Cruziana* ichnofacies. The storm-related trace-fossil assemblage reflects colonization after storm deposition and records the establishment of an opportunistic community, commonly represented by the *Skolithos* ichnofacies (Fig. 8.23a–b). Deep, vertical *Ophiomorpha*, *Cylindrichnus*, *Rosselia*, *Palaeophycus*, *Arenicolites*, *Diplocraterion*, *Skolithos*, robust *Thalassinoides*, and escape trace fossils are common components in delta fronts of wave-dominated deltas characterized by frequent and intense storm events. In these settings the fair-weather suite is poorly

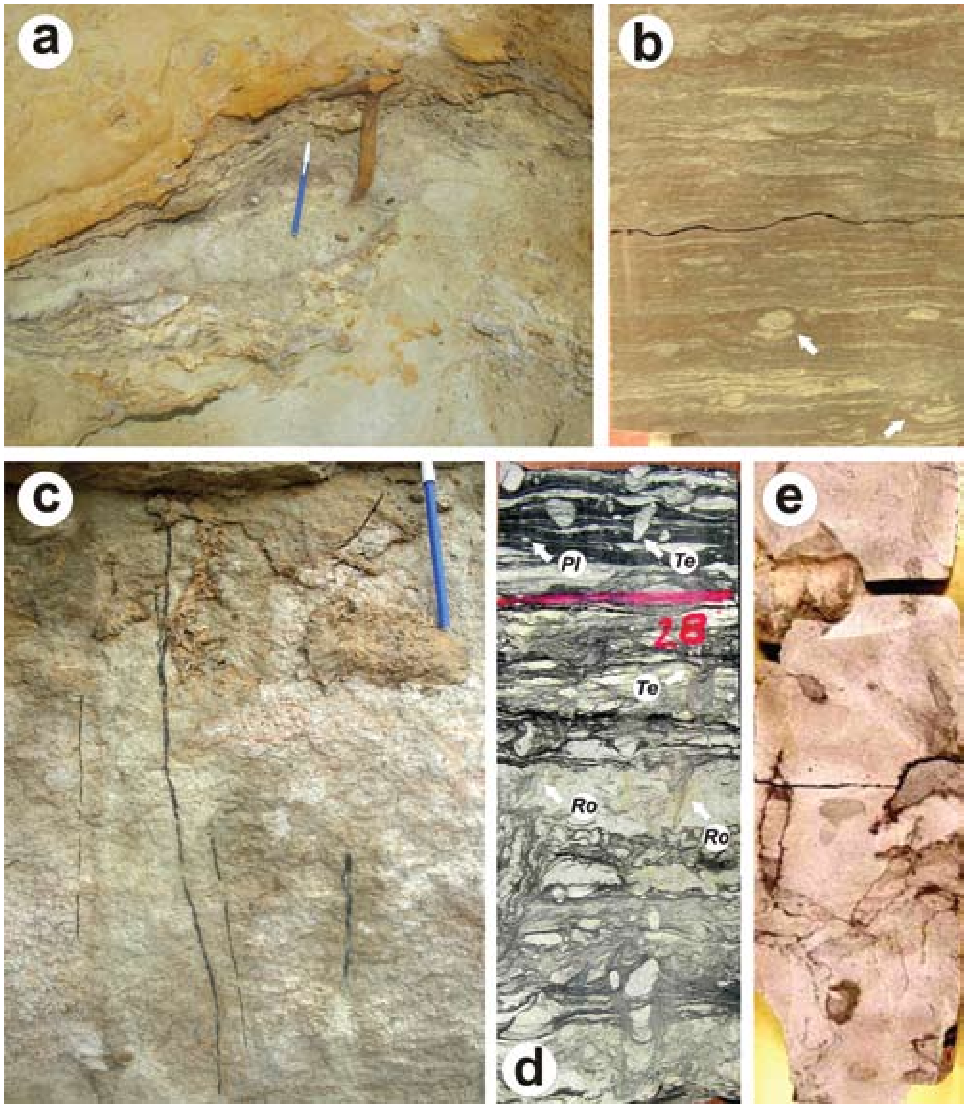


Figure 8.21 Outcrop and core expression of ichnofaunas from subaqueous delta-plain and terminal distributary-channel deposits in wave-dominated deltas. (a) *Ophiomorpha* isp. at the top of a distributary-channel deposit. Upper Miocene, Urumaco Formation, Urumaco River, northwest Venezuela. Pen is 15 cm. (b) Sparsely bioturbated interdistributary bay/lagoonal deposits containing a low-diversity trace-fossil suite dominated by *Teichichnus rectus* (arrows). Lower Miocene, Tácata Field, Eastern Venezuela Basin. Core width is 7 cm. See Buatois *et al.*, (2008). (c) Root trace fossils in crevasse-splay deposits in an interdistributary bay. Upper Miocene, Urumaco Formation, Urumaco River, northwest Venezuela. Pen is 15 cm. (d) Interdistributary-bay deposits containing a low-diversity suite dominated by *Rosselia* isp. (*Ro*). *Teichichnus rectus* (*Te*) and *Planolites montanus* (*Pl*) are also abundant. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (e) *Ophiomorpha nodosa* in terminal distributary-channel deposits. Lower Miocene, Tácata Field, Eastern Venezuela Basin. Core width is 7 cm. See Buatois *et al.*, (2008).

developed or directly absent and the storm-related suite dominates. Storm-dominated delta-front deposits formed under less frequent and intense events display a laminated to burrowed pattern (lam-scram), and are characterized by the alternation of the storm-related and fair-weather assemblages (Fig. 8.23c–f). The storm-related suite is similar to that of strongly storm-dominated types. *Rosselia*, *Planolites*, *Palaeophycus*, *Teichichnus*, *Phycosiphon*, *Chondrites*, “Terebellina”, *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Rhizocorallium*, *Gyrochorte*, and *Thalassinoides* are common components of the fair-weather suite. Some ichnogenera, such as *Chondrites*, *Phycosiphon* (Fig. 8.24a) and *Thalassinoides* (Fig. 8.24b) can penetrate relatively deep into storm sandstone beds. This suite becomes more diverse in the distal delta front (Fig. 8.24c–d). Overall, ichnofaunas from wave-dominated delta fronts are relatively diverse and very similar to those from shoreface settings (see Section 7.1).

The prodelta of wave-dominated deltas is commonly characterized by the alternation of suspension fall-out silt and clay during fair-weather times and sand emplacement during storms. In general, prodelta deposits contain diverse trace-fossil assemblages of the *Cruziana* ichnofacies, including *Rosselia* (Fig. 8.24e), *Asterosoma*, *Cylindrichnus, Planolites*, *Palaeophycus*, *Teichichnus*, *Helminthopsis*, *Chondrites*, *Phycosiphon* (Fig. 8.24f), “Terebellina”, *Cruziana*, *Rusophycus*, *Dimorphichnus*, *Rhizocorallium*, *Phycodes*, *Gyrochorte*, *Zoophycos*, *Taenidium*, and *Thalassinoides* (Fig. 8.23g) as common elements. Escape trace fossils may occur in distal storm beds (Fig. 8.24g).

In any case, the sporadic occurrence of other stress factors related with fluvial discharge (e.g. freshets, high sedimentation rates), although not as significant as in river-dominated deltas, still imparts a signature in the ichnological record. As noted by MacEachern *et al.* (2005), the juxtaposition of “open marine ichnogenera” (e.g. *Zoophycos*, *Phycosiphon*, “Terebellina”, *Chondrites*) and stressed suites (e.g. dominated by *Teichichnus* or *Planolites*) seems to be particularly typical of distal delta-front and proximal prodelta settings. In addition to ichnodiversity, the

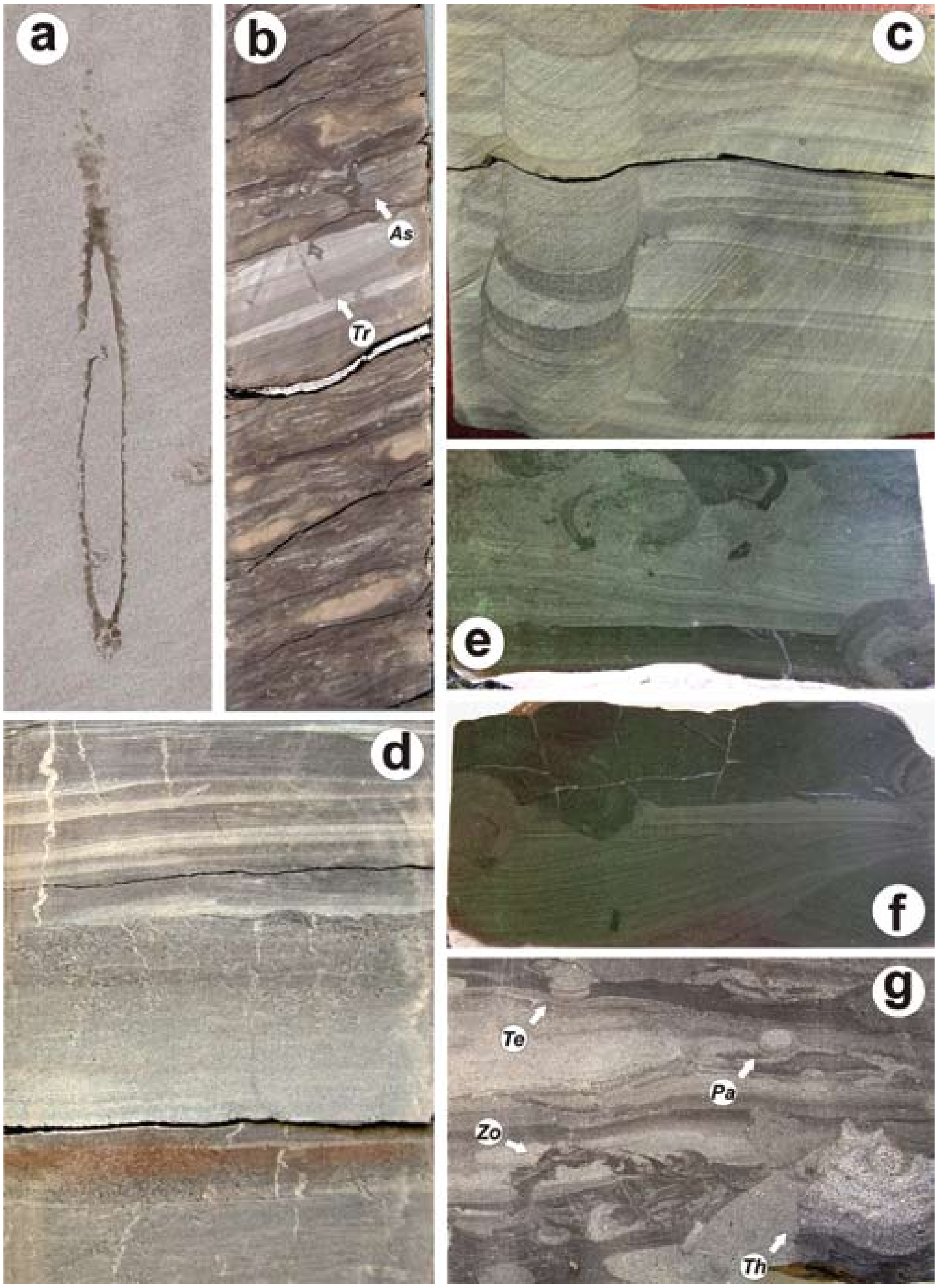


Figure 8.22 Contrasting trace-fossil assemblages in deltaic and strandplain shorelines. (a) *Ophiomorpha* representing the storm-related suite of proximal delta-front deposits. Lower Miocene, Tácata Field, Eastern Venezuela Basin. See Buatois *et al.* (2008). (b) *Trichichnus* isp. (*Tr*) colonizing a distal-prodelta tempestite. *Asterosoma* isp. (*As*) represents the re-establishment of the background suite. (c) *Diplocraterion* isp. colonizing hummocky bed in distal delta-front deposits. (d) Proximal-prodelta deposits displaying unburrowed to sparsely bioturbated hummocky cross-stratified very fine-grained sandstone with synaeresis cracks and high-density suite of *Phycosiphon incertum* in fair-weather mudstone. (e) *Scolicia* isp. displaying characteristic backfill in fully marine offshore deposits. Note trace-fossil emplacement within the storm sandstone and at the sandstone–mudstone interface. (f) *Scolicia* isp. concentrated at the top of the offshore storm sandstone layer. (g) Intensely bioturbated lower-offshore deposits displaying *Thalassinoides* isp. (*Th*), *Zoophycos* isp. (*Zo*), *Teichichnus* isp. (*Te*), and *Palaeophycus* isp. (*Pa*). Core widths are 7 cm.

degree of bioturbation shows some departures from that typical of non-deltaic fully marine settings. Intensity of bioturbation in prodelta and delta-front deposits may range from low to moderate. This results in the common preservation of very thin tempestites that otherwise would have been totally destroyed by the infauna under fully marine conditions. The links between bioturbation and event-bed preservation have been analyzed by Wheatcroft (1990), who noted that if the transient time (i.e. time required to advect the signal through the biologically active zone) is less than the dissipation time (i.e. time required to destroy the event bed), then some evidence of the event layer should be preserved in the stratigraphic record (see Section 7.1). Locally, higher degrees of bioturbation are attained in discrete layers dominated by fully marine ichnotaxa, indicating times of little deltaic influence. Wave-dominated settings do not seem to be conducive to emplacement of fluid muds. However, distal delta-front and proximal prodelta deposits may locally display unbioturbated, dark gray mudstone layers that may reflect fluid-mud sedimentation, and the influence of deltaic-related buoyant plumes.

Integration of ichnological and sedimentological data may help to detect asymmetry in wave-dominated deltas. Bhattacharya and Giosan (2003) noted that in wave-dominated settings with strong longshore drift currents, an asymmetric delta may result due to preferential sediment movement

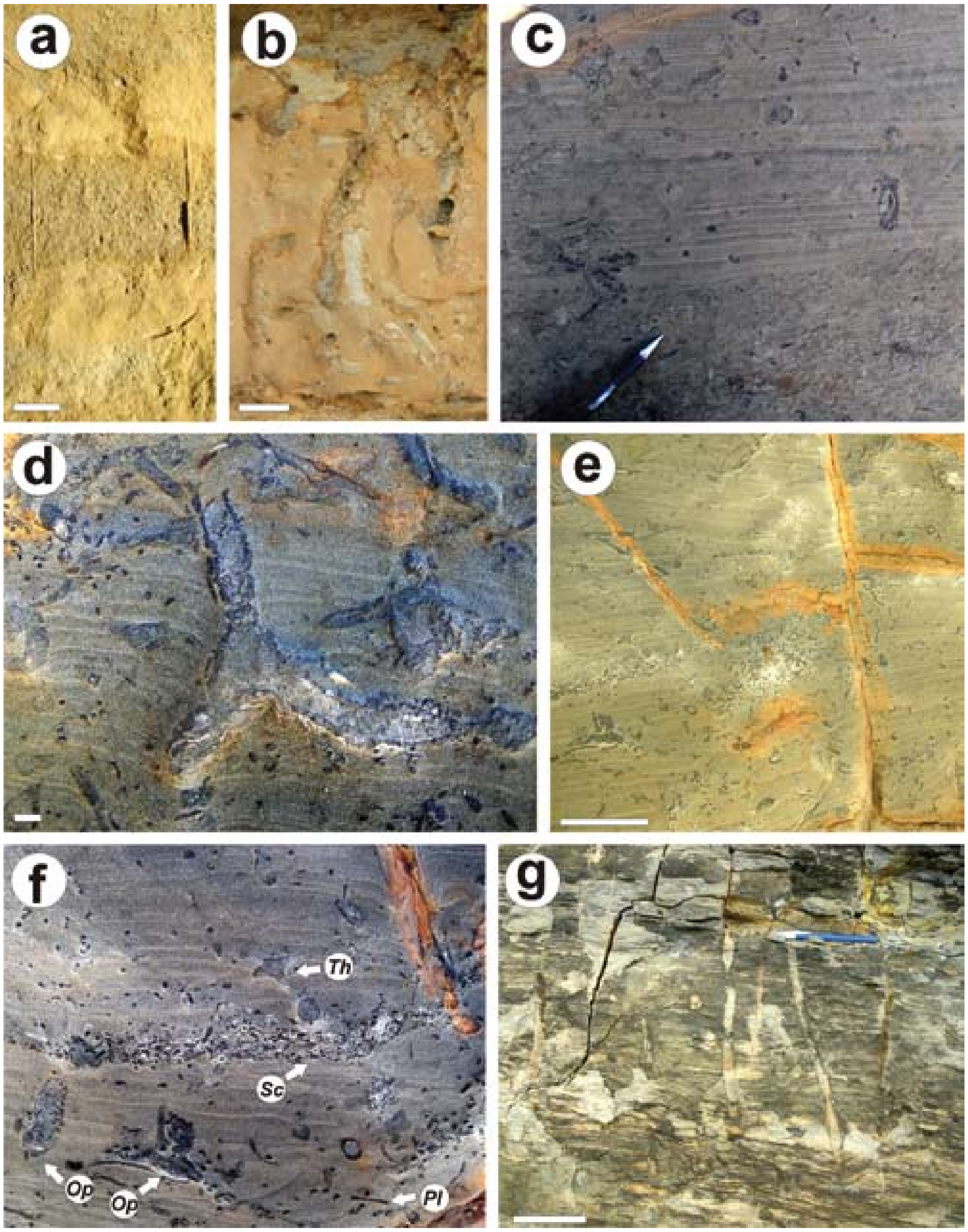


Figure 8.23 Ichnofaunas in outcrops of wave-dominated delta-front and prodelta deposits. (a) Deep *Skolithos* in distal delta-front tempestite. Upper Cretaceous, Ferron Sandstone, Ivie Creek, eastern Utah, United States. Scale bar is 10 cm. See Bhattacharya *et al.* (2007). (b) Vertical *Ophiomorpha* in distal delta-front tempestite. Upper Miocene, Urumaco Formation, Quebrada Bejucal, northwest Venezuela. Scale bar is 5 cm. (c) Intensely burrowed fair-weather deposit overlain by a sharp-based sparsely bioturbated hummocky cross-stratified sandstone emplaced in a proximal delta front. Pliocene, Caleta Godoy Formation, Mar Brava, near Carelmapu, southern Chile. Pencil is 15 cm. (d) Close-up of a specimen of *Ophiomorpha nodosa* penetrating deep into a proximal delta-front hummocky layer. Pliocene, Caleta Godoy Formation, Mar Brava, near Carelmapu, southern Chile. Scale bar is 1 cm. (e) General view of sparsely bioturbated thick hummocky cross-stratified sandstone formed in a proximal delta front. Pliocene, Caleta Godoy Formation, Mar Brava, near Carelmapu, southern Chile. Scale bar is 10 cm. (f) Close-up of (e) showing *Ophomorpha nodosa* (*Op*), patches of *Schaubcylindrichnus coronus* (*Sc*), *Thalassinoides suevicus* (*Th*), and *Planolites beverleyensis* (*Pl*) commonly reworking crustacean burrows. (g) Deep vertical *Thalassinoides* penetrating into proximal-prodelta deposits. Upper Miocene, Urumaco Formation, Urumaco River, northwest Venezuela. Scale bar is 10 cm.

downdrift of the distributary mouth. Delta asymmetry is commonly reflected by trace-fossil distribution with suites displaying a strong deltaic signature downdrift, but with establishment of strandplain shoreface complexes having more marine, less stressed suites in an updrift direction (MacEachern *et al.*, 2005; Hansen and MacEachern, 2007; Buatois *et al.*, 2008).

8.3.3 TIDE-DOMINATED DELTAS

In comparison with river- and wave-dominated deltas, tide-dominated deltas are less understood from both sedimentological and ichnological viewpoints (Fig. 8.25). The subaerial delta plain is similar in terms of ichnological content to that of river- and wave-dominated settings and is dominated by structures produced by freshwater and terrestrial elements. The subaqueous delta plain combines a set of stress factors, mostly consisting of clay flocculation and fluid-mud deposition (MacEachern *et al.*, 2005). Distributary-channel deposits are sparsely bioturbated, and trace fossils commonly occur along surfaces that reflect colonization windows during slack-water periods. *Diplocraterion*, *Ophiomorpha*, and *Planolites* are common components, the latter typically present along mud drapes (e.g. Martinius *et al.*, 2001). Retrusive forms of *Diplocraterion* tend to be dominant, reflecting equilibrium behaviors under relatively high rates of sedimentation (e.g. Martinius *et al.*, 2001; MacEachern *et al.*, 2005). Some tide-dominated distributary channels, however, are the site of fluid-mud emplacement and are, therefore, unbioturbated (e.g. Dalrymple *et al.*, 2003). Interdistributary-bay deposits are dominated by *Teichichnus* and *Planolites*, commonly associated with synaeresis cracks.

Box 8.5 Ichnology of Lower Miocene delta-front and prodelta deposits of a tide-dominated delta of Patagonia, Argentina

Excellent deltaic outcrops of the Lower Miocene Chenque Formation are exposed along cliff areas near Caleta Olivia, Patagonia, Argentina. Their ichnological and sedimentological study allows recognition of clear tidal signatures in prodelta and delta-front deposits, which are stacked forming a progradational coarsening-upward succession. Heterolithic prodelta deposits with lenticular and wavy bedding are sparsely bioturbated and display sporadic distribution of trace fossils. Deposit-feeder structures, such as *Planolites montanus* (Fig. 8.26a), *Protovirgularia* isp. (Fig. 8.26b), and *Teichichnus rectus*, are dominant, representing an impoverished expression of the *Cruziana* ichnofacies. Flaser-bedded sandstone characterizes the prodelta-delta front transition. These deposits are almost completely obliterated by equilibrium/adjustment trace fossils of large bivalves (*Atrina*) (Fig. 8.26c and d). Associated trace fossils are *Nereites missouriensis*, *Teichichnus rectus* (Fig. 8.26e), *Phycosiphon incertum* (Fig. 8.26f), *Thalassinoides* isp. (Fig. 8.26f), and *Schaubcylindrichnus freyi*. Trough and planar cross-stratified distal delta-front sandstone is dominated by large *Rosselia socialis* and *Macaronichnus segregatis* (Fig. 8.26g). The associated mud drapes blanketing the sandstone foresets commonly contain *Nereites missouriensis* and *Protovirgularia* isp. Proximal delta-front deposits are characterized by sigmoidal cross-stratification and very sparse bioturbation, represented by *Macaronichnus segregatis* and isolated specimens of *Rosselia socialis*. Changes in salinity, water turbidity, fluid mud substrates, and fluctuations in energy and in sedimentation rates are among the most important stress factors that affected these deltaic infaunal communities. Overall, this ichnofauna is characterized by shallow-tiered communities, impoverished trace-fossil assemblages, dominance of deposit-feeder structures, and inhibition of suspension-feeder elements. This study helps to explain how tide-influenced deltaic ichnofaunas are shaped by the relative influence of the different stress factors.

References: Carmona *et al*. (2009).

Root traces occur in interdistributary-bay deposits and at the top of channel-abandonment successions. In general, ichnofaunas from the subaqueous delta plain of tide-dominated deltas follow the tenets of the brackish-water model (see Section 6.1.4).

Delta-front and prodelta environments contain representatives of the *Cruziana* ichnofacies, including *Gyrochorte*, *Thalassinoides*, *Phycosiphon*, *Chondrites*, *Siphonichnus*, *Diplocraterion*, *Teichichnus*, *Palaeophycus*, *Planolites*, and *Rhizocorallium*, among other ichnotaxa (McIlroy, 2004b, 2007b; MacEachern *et al*., 2005; Carmona *et al*., 2008, 2009) (Box 8.5). Equilibrium structures (*Rosselia*, bivalve adjustment structures) are rather common (Carmona *et al*., 2008, 2009). High-energy subtidal sandbars and dunes are either unbioturbated or contain elements of the *Skolithos* ichnofacies, such as *Skolithos* and *Diplocraterion*, reflecting short-term colonization windows during breaks in sedimentation. Mud drapes along foresets are sparsely bioturbated, and typically contain *Planolites*. Synaeresis cracks occur locally probably in relation with salinity fluctuations (MacEachern *et al*., 2005). Ichnodiversity levels in tide-dominated delta-front and prodelta environments are poorly understood. MacEachern *et al*. (2005) summarized known occurrences and noted size reduction, sparse bioturbation, and low diversity levels, with trace fossils concentrated along pause planes. In contrast, McIlroy (2004b) documented relatively diverse ichnofaunas in a case study of deltaic ichnology. Nevertheless, there is general agreement that tide-dominated delta fronts and prodeltas are less diverse than their wave-dominated counterparts (McIlroy, 2004b; MacEachern *et al*., 2005). However, ichnodiversity levels seem to be higher than in river-dominated deltas (McIlroy, 2007b).

8.4 FJORDS

Fjords are deep, high-latitude estuaries that have been excavated or modified by land-based ice (Syvitski *et al*., 1987). The ichnology of fjords remains poorly explored, with only a few papers dealing with modern (e.g. Aitken *et al*., 1988), Cenozoic (e.g. Eyles *et al*., 1992; Corner and Fjalstad, 1993), and late Paleozoic (e.g. Nogueira and Netto, 2001; Buatois and Mángano, 2003b; Balistieri *et al*., 2002, 2003; Gandini *et al*., 2007; Buatois *et al*., 2006a, 2010a; Schatz *et al*., 2011) examples (Fig. 8.27). However, ichnological evidence is essential to resolve paleoenvironmental interpretations in fjord successions, commonly representing the only available biological data because of the low preservation potential of shelly faunas in marine environments adjacent to glaciated margins (Aitken, 1990).

Fjords include a wide variety of environmental stresses that affect benthic colonization, including extreme salinity dilution, high rates of sedimentation, variable degree of substrate consolidation, oxygen-depleted conditions, high water turbidity, and intense storm activity. In polar areas, seasonal light restriction and floating ice masses contributing to ice-rafted debris rainfall may be important stress factors.

Salinity dilution is undoubtedly one of the most significant stress factors because fjords are characterized by strong meltwater discharge issuing from seasonal glacial melting. Increased precipitation and runoff during summer lead to reduced salinity (e.g. Feder and Keiser, 1980). As a result, most Cenozoic and Holocene fjords are dominated by brackish-water ichnofaunas (Eyles *et al*., 1992; Corner and Fjalstad, 1993). High freshwater discharges due to glacier melting and associated catastrophic outburst floods are known for a number of glaciated margins, such as the Baltic

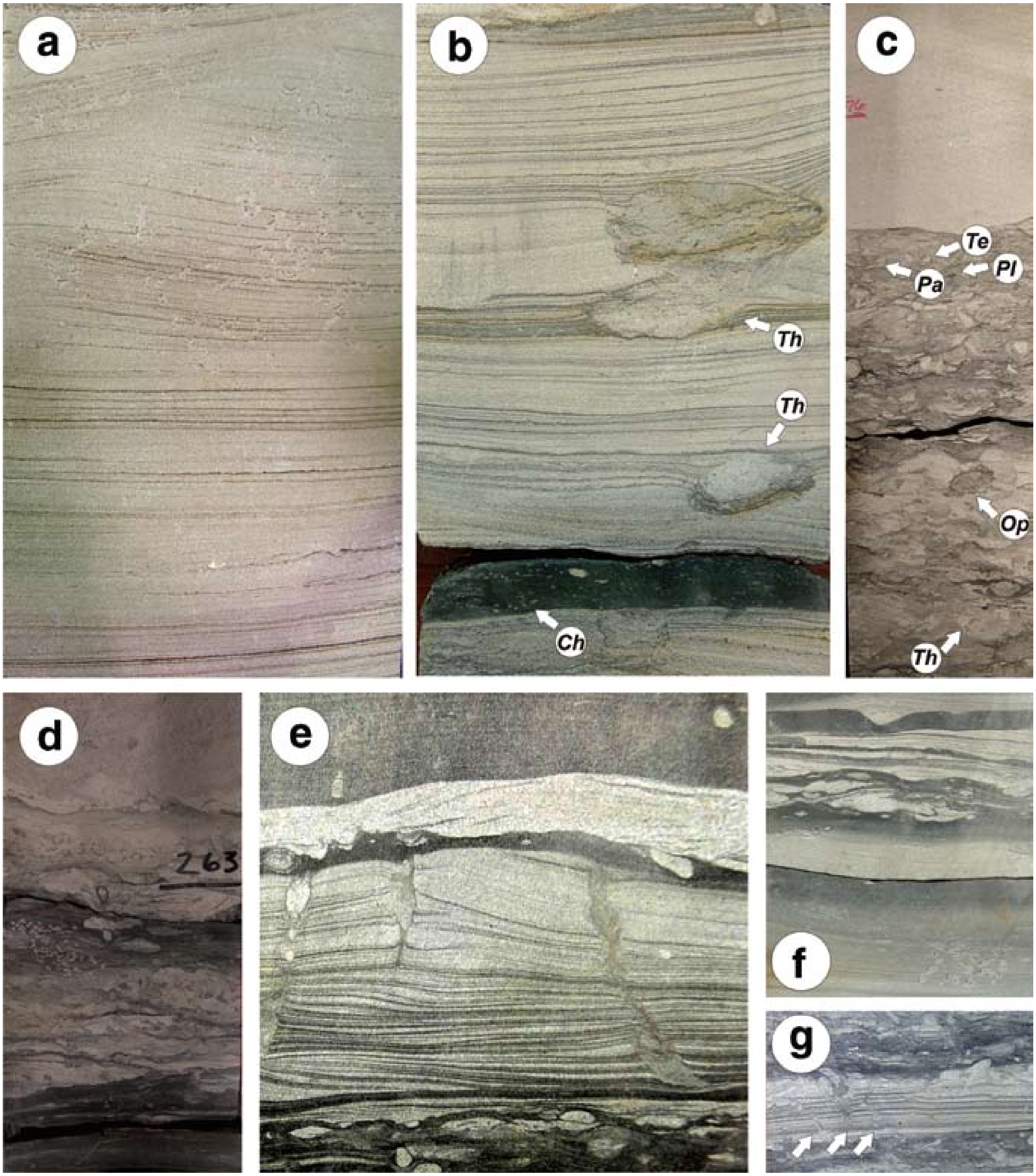


Figure 8.24 Core expression of ichnofaunas from wave-dominated delta-front and prodelta deposits. (a) *Phycosiphon* penetrating into a hummocky cross-stratified sandstone emplaced in the proximal delta front. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (b) Distal delta-front sandstone tempestite containing deeply emplaced *Thalassinoides* isp. (*Th*). *Chondrites* isp. (*Ch*) occurs in associated fair-weather deposits. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (c) Distal delta-front heterolithic deposits containing a diverse fair-weather trace-fossil suite consisting of *Teichichnus rectus* (*Te*), *Ophiomorpha nodosa* (*Op*), *Palaeophycus* isp. (*Pa*), *Thalassinoides* isp. (*Th*), and *Planolites* isp. (*Pl*). Note the presence of an overlying sharp-based storm sandstone bed. Upper Cretaceous, Ferron Sandstone, Ivie Creek #11, Ivie Creek area, eastern Utah, United States. Core width is 9 cm. See MacEachern *et al.* (2007b). (d) Sparsely bioturbated to locally moderately bioturbated distal delta-front deposits containing well-defined *Chondrites*. Upper Cretaceous, Ferron Sandstone, Muddy Creek #11, Muddy Creek area, eastern Utah, United States. Core width is 9 cm. See Pemberton *et al.* (2007). (e) *Rosselia* isp. in thin storm sandstone layers emplaced in a proximal prodelta. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm. (f) *Phycosiphon* penetrating into a distal sandstone tempestite emplaced in a proximal prodelta. Note associated mud drapes indicative of tidal influence, load cast at the base of an overlying tempestite, and unbioturbated mudstone units interpreted as fluid muds. Middle Jurassic, Plover Formation, Sunrise and Troubadour fields, Timor Sea, northern Australia. Core width is 10 cm. (g) Escape trace fossils (arrows) in proximal-prodelta sandstone tempestites. Upper Permian, San Miguel Formation, Mallorquín # 1 core, Paraguay. Core width is 8 cm.

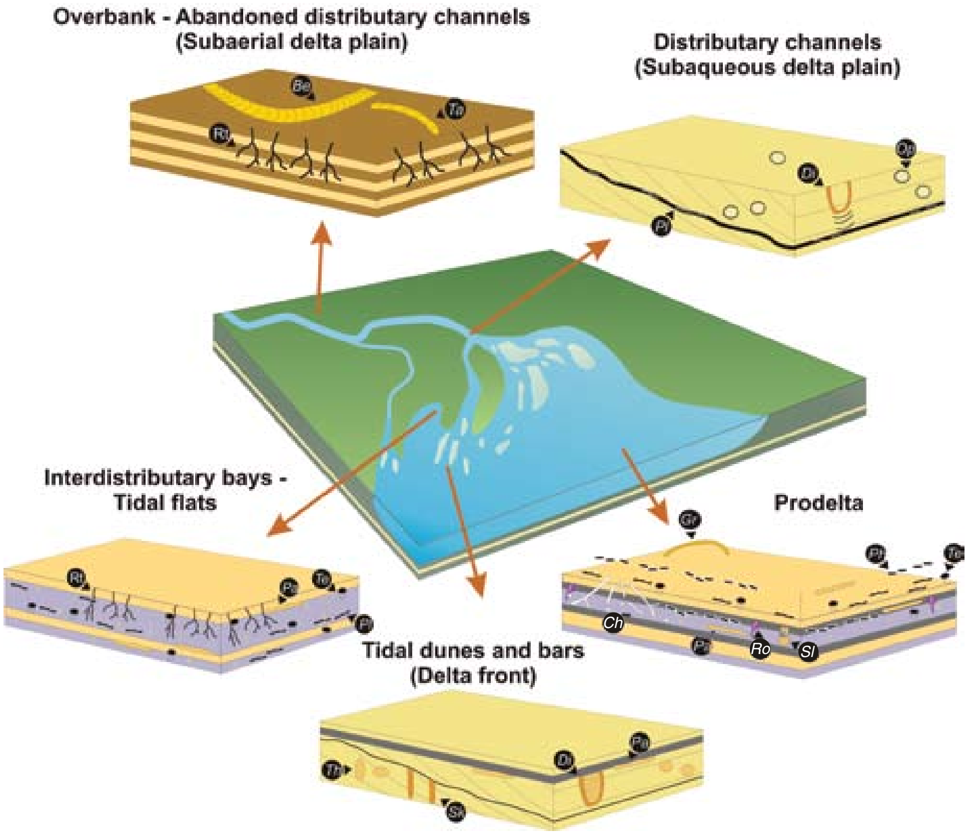


Figure 8.25 Schematic reconstruction of trace-fossil distribution in tide-dominated deltas. Abandoned-channel and overbank deposits of the subaerial delta plain may contain *Beaconites* (*Be*), *Taenidium* (*Ta*), and root traces (Rt). Distributary-channel deposits of the subaqueous delta plain may contain *Ophiomorpha* (*Op*) and *Diplocraterion* (*Di*); *Planolites* (*Pl*) may occur on mud drapes along foresets. Interdistributary-bay and tidal-flat deposits typically exhibit *Planolites* (*Pl*), *Teichichnus* (*Te*), *Palaeophycus* (*Pa*), and root traces (Rt). Tidal-dune and bar deposits of the delta-front may host *Thalassinoides* (*Th*), *Palaeophycus* (*Pa*), *Diplocraterion* (*Di*), and *Skolithos* (*Sk*). Prodelta deposits exhibit various ichnotaxa, such as *Teichichnus* (*Te*), *Phycosiphon* (*Ph*), *Chondrites* (*Ch*), *Rosselia* (*Ro*), *Palaeophycus* (*Pa*), *Scalichnus* (*Sl*), and *Gyrochorte* (*Gr*).

and Labrador Seas (Lord, 1990; Shaw and Lesemann, 2003). Some of the most extreme cases of freshwater discharges occur during deglaciation times. In fact, glacial melting may lead to the formation of extensive freshwater bodies that are physically connected with the open sea. For example, the Holocene Yoldia Sea was freshwater in the northern Baltic Sea Basin due to high input meltwater during deglaciation during most of its history (Virtasalo *et al.*, 2006). Times of elevated concentration of suspended sediment promote formation of hyperpycnal flows in fjord environments (Syvitski *et al.*, 1987). Only exceptional discharges overcome the buoyancy effect of seawater in modern examples, but high-discharge hyperpycnal flows may have been the norm during deglaciation. In addition, because large discharges reduce the salinity of the fjord, the likelihood of hyperpicnal flows is increased providing a positive feedback. In these situations marine benthic fauna are inhibited due to reduced salinity, allowing colonization by a freshwater biota. This situation seems to have been quite common in late Paleozoic glaciated margins of Gondwana, which display ichnological signatures of extreme freshwater release during deglaciation (Buatois *et al.*, 2006a, 2010a). In fact, some Gondwana fjord ichnofaunas are virtually identical to those from Pleistocene glacial lakes (e.g. Gibbard and Stuart, 1974; Gibbard, 1977; Gibbard and Dreimanis, 1978; Walter and Suhr, 1998; Gaigalas and Uchman, 2004; Uchman *et al.*, 2009; Benner *et al.*, 2009; Knecht *et al.*, 2009) (see Section 10.3.2) (Fig. 8.28a–c). Although some of these settings have been referred to as "brackish seas", in fact they may be more appropriately called "freshwater seas" because of the dominance of freshwater conditions due to extensive melting during postglacial times (Buatois *et al.*, 2006a, 2010a; Buatois and Mángano, 2007). In many cases, however, brackish-water ichnofaunas also occur in these late Paleozoic successions, reflecting increased marine influence.

High rates of sedimentation are persistent in the fjord environment as a result of high fluvial input. In addition, mass-sediment transport, eolian transport, and input from wave and tidal erosion also play a role (Syvitski *et al.*, 1987). In particular, high sedimentation rate affects the epifauna by subjection to floc and agglomerate rain, microturbidity flows due to biological resuspension of unstable slope sediment, and disturbances due to major slides (Farrow *et al.*, 1983). Bioturbation is commonly inhibited close to the bay-head delta due to rapid sediment accumulation. Abundance of escape trace fossils and dwelling structures, such as *Conichnus* and *Diplocraterion*, has been linked to rapid sedimentation (e.g. Eyles *et al.*, 1992). Rapid sedimentation is also a limiting factor for larval settlement (Farrow *et al.*, 1983). As a result of high sedimentation rates and steep margins, fjords are strongly affected by sediment gravity flows, most commonly turbidity currents and debris flows. High frequency of sediment gravity flows carrying significant amounts of food seems to have prevented establishment of the *Nereites* ichnofacies, allowing extension of the *Cruziana* ichnofacies into deeper water (Eyles

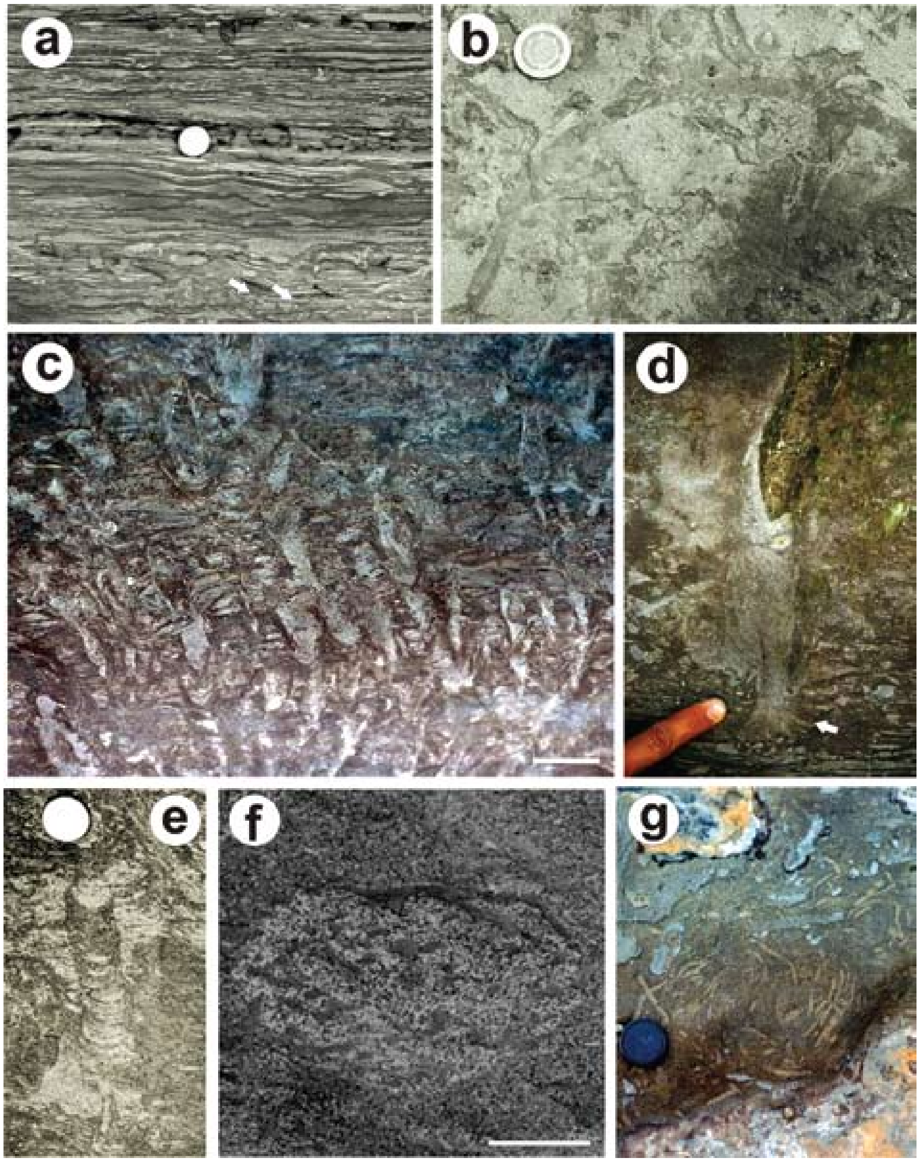


Figure 8.26 Ichnofaunas from delta-front and prodelta deposits of a Lower Miocene tide-dominated delta, Chenque Formation, Caleta Olivia, Patagonia, Argentina. See Carmona *et al.* (2008, 2009). (a) Heterolithic proximal-prodelta deposits containing a monospecific suite of small *Planolites montanus* (arrows). Note abundance of synaeresis cracks. Coin is 2.4 cm. (b) *Protovirgularia* isp. in proximal-prodelta deposits. Coin is 2.4 cm. (c) High density of equilibrium/adjustment trace fossils produced by the bivalve *Atrina* in deposits emplaced at the transition between the delta front and the prodelta. Scale bar is 10 cm. (d) Close-up of equilibrium/adjustment trace fossil showing structures left by the byssal threads (arrow) and the body fossils of their tracemakers at the end of the trace fossil. (e) Transitional prodelta-delta front deposits containing *Teichichnus rectus*. Coin is 1.8 cm. (f) *Thalassinoides* isp. reworked by *Phycosiphon incertum* in transitional deposits. Scale bar is 1 cm. (g) *Macaronichnus segregatis* in distal delta-front deposits. Lens cover is 5.5 cm.

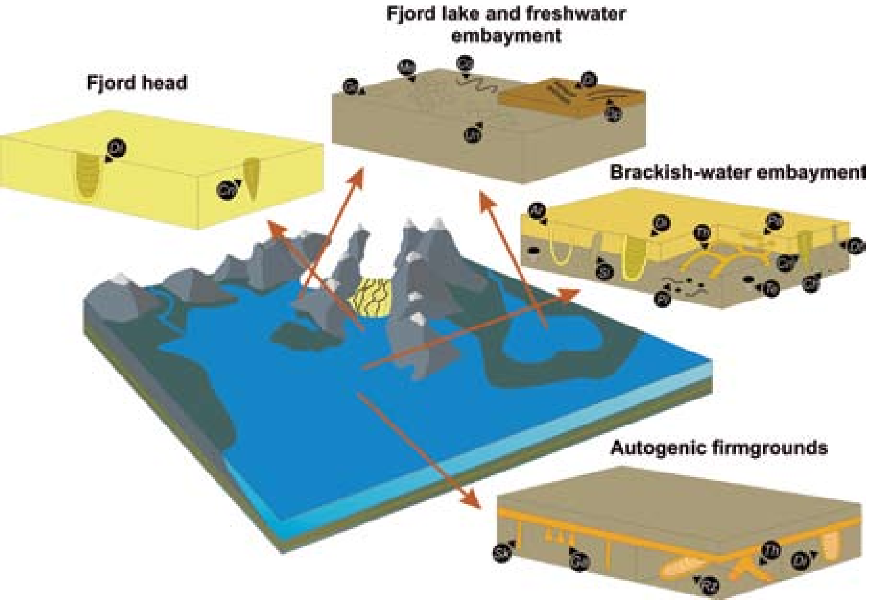


Figure 8.27 Schematic reconstruction of trace-fossil distribution in fjords. Fjord-head-deposits are sparsely bioturbated, and contain a few forms, such as robust *Diplocraterion* (*Di*) and *Conichnus* (*Cn*). An increase in degree of bioturbation and trace-fossil diversity characterizes brackish-embayment deposits, which may contain *Arenicolites* (*Ar*), *Diplocraterion* (*Di*), *Siphonichnus* (*Si*), *Teichichnus* (*Te*), *Thalassinoides* (*Th*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Conichnus* (*Cn*), *Chondrites* (*Ch*), and *Diopatrichnus* (*Dt*). Fjord-lake and freshwater-embayment deposits are characterized by *Undichna* (*Un*), *Mermia* (*Me*), *Cochlichnus* (*Co*), *Gordia* (*Go*), *Diplopodichnus* (*Dp*), and *Diplichnites* (*Di*). Associated firmground surfaces contain *Skolithos* (*Sk*), *Gastrochaenolites* (*Ga*), *Rhizocorallium* (*Rz*), *Diplocraterion* (*Di*), and *Thalassinoides* (*Th*).

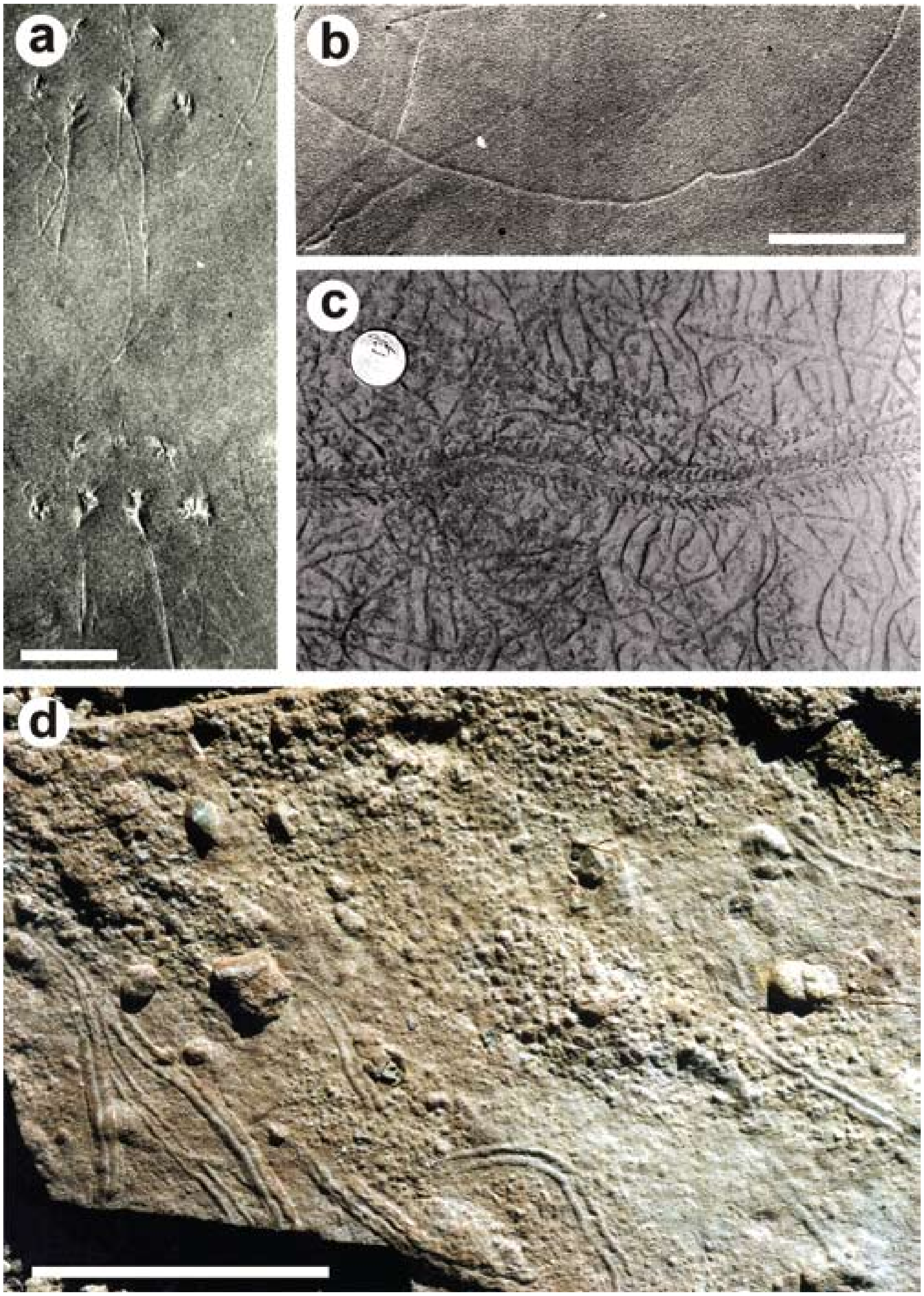


Figure 8.28 Ichnofaunas from late Paleozoic fjord deposits of Gondwana. (a) *Orchesteropus atavus*. Upper Carboniferous, Guandacol Formation, Huerta de Huachi, Paganzo Basin, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003b). (b) *Helminthoidichnites tenuis*. Upper Carboniferous, Guandacol Formation, Huerta de Huachi, Paganzo Basin, western Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003b). (c) *Diplichnites* isp. cross-cutting a high-density suite consisting of *Helminthoidichnites tenuis*. Upper Carboniferous–Lower Permian, Rio do Sul Formation, Trombudo Central, Santa Catarina State, Paraná Basin, southern Brazil. Coin is 2 cm. See Nogueira and Netto (2001). (d) *Diplopodichnus biformis* and *Cruziana* isp. with associated dropstones. Upper Carboniferous, Guandacol Formation, Cuesta de Huaco, Paganzo Basin, western Argentina. Scale bar is 10 cm. See Schatz *et al*. (2011).

et al., 1992). Ice-rafted debris rainfall also represents a stress factor on the benthic biota, and the presence of trace fossils in direct association with dropstones is not uncommon in late Paleozoic fjord deposits (e.g. Schatz *et al*., 2011) (Fig. 8.28d).

A number of papers have documented the role of water turbidity in modern fjords (e.g. Feder and Matheke, 1980; Farrow *et al*., 1983). Modern fjord waters contain high concentrations of fine-grained particles that commonly preclude the establishment of suspension-feeder organisms (see Section 6.1.8). The dominance of horizontal feeding traces of deposit and detritus feeders, and the absence of vertical burrows of suspension feeders in ancient fjord deposits is also suggestive of high amounts of suspended fine-grained material (Buatois *et al*., 2006a). The abundance of deeply plowing deposit feeders may also have contributed to the exclusion of suspension feeders (Feder and Matheke, 1980; Eyles *et al*., 1992) (see Section 6.7).

The degree of substrate consolidation is extremely variable in fjord environments. Muddy soupgrounds seem to be rather common close to the glacier margin, imparting a strong stress to epifaunal communities (see Section 6.1.2). Eyles *et al*. (1992)

noted that polychaetes and deposit-feeding bivalves are the dominant components in these soupy substrates. Suspension feeders are typically absent. Softground communities containing more varied epifauna and infauna tend to occur towards more distal positions. Fluid muds are typically unbioturbated. In addition, current-winnowed substrates commonly contain firmgrounds with associated suites of the *Glossifungites* ichnofacies characterized by deep gravel-filled *Skolithos* and *Gastrochaenolites* (Dale *et al*., 1989; Eyles *et al*., 1992).

Dissolved oxygen concentration in fjord bottom waters is extremely variable (Syvitski *et al*., 1987). The bottom of some fjords may be characterized by oxygen depletion, particularly in enclosed basins with a high concentration of organic matter. In these settings, the redox discontinuity surface is very close to the sediment–water interface, restricting the activity of infaunal organisms (Syvitski *et al*., 1987). As a result, shallow-tier structures of small deposit feeders tend to be the dominant components (Pearson, 1980). Anoxic to dysaerobic conditions are particularly common at times. However, the activity of bottom currents may supply oxygen to the fjord floor in some basins (e.g. Eyles *et al*., 1992).

Some fjords are subjected to intense wave action due both to wind funneled from the interior to the sea and to large shoreward-traveling swells (Syvitski *et al*., 1987). This results in the deep emplacement of the storm wave base in some Arctic and Antarctic fjords. For example, the storm wave base is deeper than 200 m in the Gulf of Alaska, influencing the entire shelf bottom (O'Clair and Zimmerman, 1987). Therefore, repeated storms impart a strong stress in benthic communities and affect populations established in relatively deep water (see Section 7.1). This stress is expressed by deep erosion and strong resuspension of sediment that remains close to the sediment–water interface.

As a consequence of these series of commonly interconnected stress factors, the taxonomic composition of fjord ichnofaunas is highly variable. Late Paleozoic fjord ichnofaunas typically contain representatives of the *Mermia* and *Scoyenia* ichnofacies as a result of the predominance of freshwater conditions (e.g. Buatois and Mángano, 2003b). Simple grazing trails (e.g. *Cochlichnus*, *Gordia*, *Helminthoidichnites, Helminthopsis, Mermia*), feeding traces (e.g. *Circulichnis*, *Treptichnus*), resting traces (e.g. *Rusophycus*), arthropod trackways (e.g. *Diplichnites, Maculichna*, *Umfolozia*, *Orchesteropus*), and fish trails (e.g. *Undichna*) are common ichnotaxa. Because these structures are preserved along bedding planes, recording emplacement in very shallow tiers, the degree of bioturbation is typically zero. Associated brackish-water intervals are slightly more bioturbated, and contain the depauperate *Cruziana* ichnofacies (Buatois *et al*., 2010a). Most Cenozoic and modern fjords contain ichnofaunas that record the activity of organisms adapted to brackish water (e.g. Aitken *et al*., 1988; Eyles *et al*., 1992). Common components include bivalve vertical burrows (*Siphonichnus*), U-shaped vertical burrows (e.g. *Arenicolites*, *Diplocraterion*), gravel-lined polychaete burrows (*Diopatrichnus*), and crustacean galleries (*Thalassinoides*), among other forms. The degree of bioturbation is typically low to moderate.

9 Ichnology of deep-marine clastic environments

> Y cuando me hundo en el mar
> de la fertilidad,
> un silencio visual:
> es la fauna abisal
> reflejando el color del sol
>
> Gustavo Cerati
> *Lisa* (1993)

Deep-marine trace fossils have long fascinated ichnologists with their amazing variety of shapes and sizes, arranged in regular and recurrent patterns (Fuchs, 1895). Graphoglyptids preserved at the base of sandy turbidites have represented a challenging puzzle. Trace fossils preserved in turbidites exposed mostly in European Mountain Chains (Fuchs, 1895; Azpeitia-Moros, 1933; Seilacher, 1962, 1977a; Książkiewicz, 1970, 1977; Crimes, 1977; Crimes *et al*., 1981), but also in South (Macsotay, 1967) and North (Chamberlain, 1971) America rapidly captured the attention of ichnologists. These structures were originally interpreted as post-turbidite (Seilacher, 1960), but after further research Seilacher (1962) was able to demonstrate that graphoglyptids were in fact pre-turbidite trace fossils formed as shallow-tier open burrow systems in the hemipelagic mud and preserved due to uniform stripping of the uppermost muddy layer by the incoming turbidity current and subsequent casting with sand. In another seminal paper, Seilacher (1977a) introduced a morphological classification of these structures, including continuous meanders (e.g. *Helminthorhaphe* and *Cosmorhaphe*), uniramous meanders (e.g. *Belorhaphe*, *Helicolithus*, and *Urohelminthoida*), biramous meanders (e.g. *Desmograpton* and *Paleomeandron*), radial structures (e.g. *Glockerichnus* and *Lorenzinia*), irregular networks (e.g. *Megagrapton* and *Acanthorhaphe*), and regular networks (e.g. *Paleodictyon*). The fact that these structures were originally described and interpreted from the fossil record, and only later recorded in the modern deep sea has been regarded as an example of reverse uniformitarianism, in which the past is the key to the present (Frey and Seilacher, 1980). Recent years have witnessed extraordinary progress in our understanding of the ichnotaxonomy of deep-marine trace fossils. Following a long tradition started by Polish ichnologist Marian Książkiewicz, a number of monographs have been published during the last 15 years or so (Uchman, 1995, 1998, 1999, 2001), allowing the establishment of a systematic framework to classify deep-marine trace fossils. Parallel to this, significant progress was attained in our knowledge of biogenic structures formed in the modern deep sea (e.g. Werner and Wetzel, 1982; Wetzel, 1981, 1984, 1991, 2002, 2008). Integration of modern observations and detailed systematic work are now resulting in more finely tuned ichnological and sedimentological models of turbidite systems (e.g. Wetzel and Uchman, 2001; Ponce *et al*., 2007; Olivero *et al*., 2010; Wetzel, 2010; Carmona and Ponce, 2011), including studies in based on cores (Knaust, 2009). In all probability, future work will emphasize the search for comparative ichnological signatures of various deep-sea processes, such as episodic turbidity currents, hyperpycnal flows, and bottom currents (e.g. Wetzel *et al*., 2008). In this chapter, we will review the ichnology of deep-marine environments, covering both slopes and base-of-slope turbidity systems. In order to do so, we will subdivide slopes in topographically simple and topographically complex, and turbidite systems into fine-grained and coarse-grained.

9.1 SLOPES

The continental slope extends from the slope break at the shelf edge to the basin plain (Stow, 1985; Pickering *et al*., 1989; Flint and Hodgson, 2005). Slopes are topographically variable ranging from relatively simple to complex, including depressions and highs that result from faulting, folding, salt tectonics, and mud diapirism (Smith, 2004). Because most ichnological studies of deep-marine deposits have focused on the diverse suites present in thin-bedded sandstone turbidites that typically accumulate in base of slope–basin–plain submarine fans, those ichnofaunas present on the slope itself have received comparatively little attention. However, examination of a number of studies (e.g. Werner and Wetzel, 1982; Wetzel, 1981, 1983; Buatois and Mángano, 1992; Fu and Werner, 1994; Savrda *et al*., 2001; Löwemark *et al*., 2004; Shultz and Hubbard, 2005; Encinas *et al*., 2008) allows some generalizations to be established. Slope systems are herein classified in topographically simple and topographically complex, which should be regarded as end members (see also Smith, 2004). Oxygen content is a first-order limiting factor on slope benthic faunas, and is in turn a reflection of topographic confinement which controls water circulation (Pickering *et al*., 1989).

9.1.1 TOPOGRAPHICALLY SIMPLE SLOPES

Topographically simple slopes are characterized by open unconfined areas separated by confined incised canyons

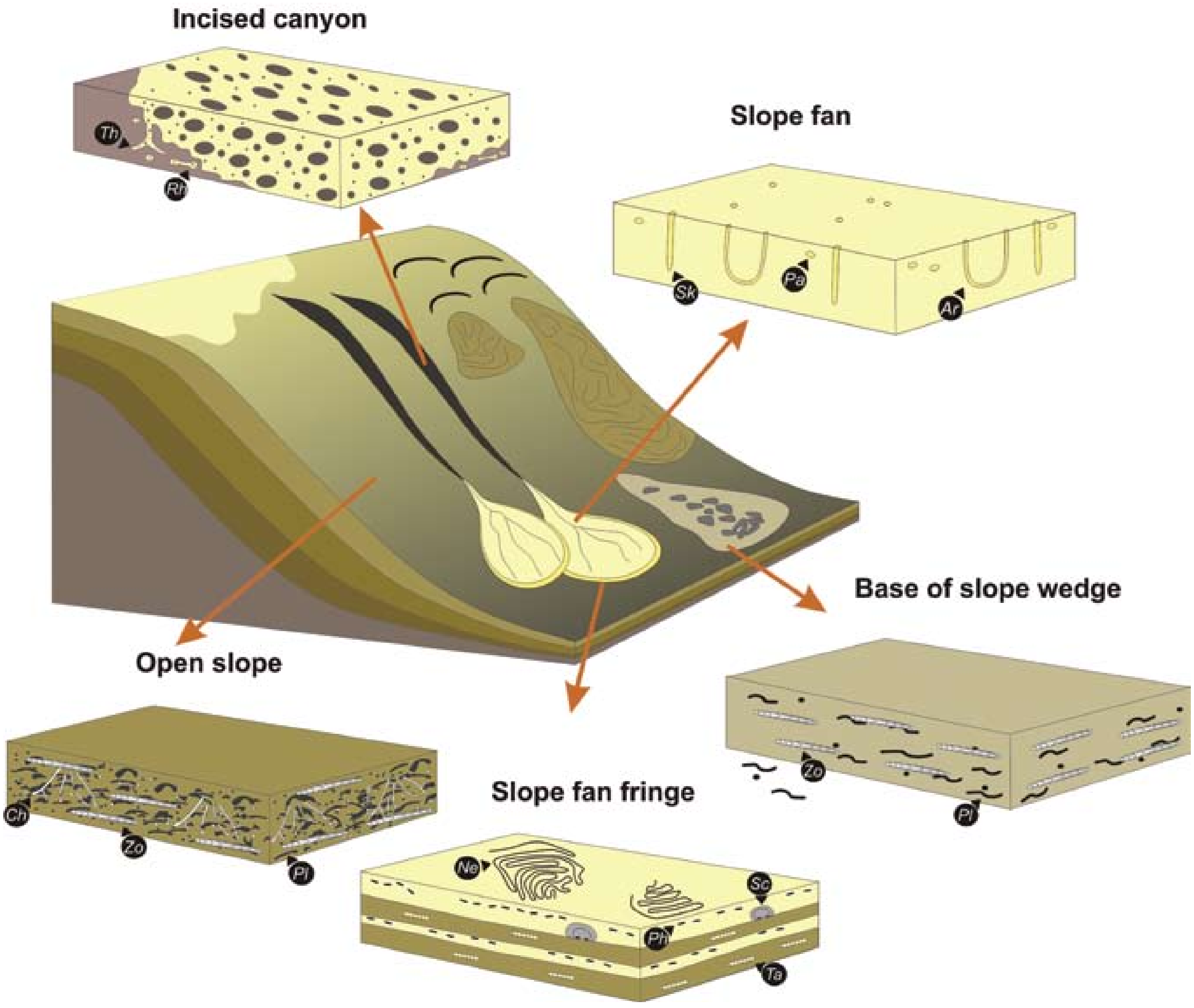


Figure 9.1 Schematic reconstruction of trace-fossil distribution in topographically simple slopes. Trace-fossil associations may be relatively diverse. Firmground *Thalassinoides* (*Th*) and *Rhizocorallium* (*Rh*) are relatively common at the base of incised canyon surfaces. Slope-fan deposits are characterized by dwelling traces of suspension feeders, such as *Skolithos* (*Sk*), *Arenicolites* (*Ar*), and *Palaeophycus* (*Pa*). Slope-fan fringe deposits tend to display feeding and grazing traces of deposit feeders, such as *Nereites* (*Ne*), *Scolicia* (*Sc*), *Phycosiphon* (*Ph*), and *Taenidium* (*Ta*). Base-of-slope-wedge deposits are sparsely bioturbated, and may contain *Zoophycos* (*Zo*) and *Planolites* (*Pl*). Open-slope deposits are intensely bioturbated, and typically display *Zoophycos* (*Zo*), *Chondrites* (*Ch*), and *Planolites* (*Pl*).

(Fig. 9.1). Levee channels may be locally present (Posamentier and Walker, 2006). Slope fans flanked by fringe areas occur on the open unconfined areas. The base of the slope is commonly characterized by a wedge of coarse-grained sediment. Examples include both passive margins, such as the continental slope off northwest Africa (Wetzel, 1981) and active margins, such as the Sulu Sea (Wetzel, 1983). In these settings, ponded intra-slope minibasins are relatively rare. Topographically simple slopes display less stressful conditions and tend to have higher oxygen content than in ponded systems as a result of water circulation. The base of the incised canyons may be delineated by elements of the *Glossifungites* ichnofacies (see Section 12.2.2). Bioturbation is commonly inhibited within the canyon due to high frequency of sediment gravity flows, but open unconfined areas of the slope are typically completely bioturbated (Wetzel, 1981, 1983; Uchman, 1995) (Box 9.1).

Topographically simple slope systems contain a much wider diversity of oxygen-related suites, reflecting more variable conditions of water circulation (Wetzel, 1983; Buatois and Mángano, 1992; Löwemark *et al.*, 2004) (Fig. 9.1). Ichnofaunas are dominated by feeding traces of deposit feeders, particularly in the unconfined open-slope and slope-fan fringe deposits. *Zoophycos*, *Chondrites* (Fig. 9.2a), *Trichichnus*, *Teichichnus* (Fig. 9.2a), and *Planolites* are typically abundant in both modern and ancient examples, and *Scolicia* and *Taenidium* may be

Box 9.1 Ichnology of modern slope to deep-sea sediments in the Sulu Sea Basin of the Philippines

Studies of cores from modern slope to deep-sea deposits of the Sulu Sea Basin provide valuable information to understand environmental distribution of biogenic structures, as well as controls on the benthic fauna and preservation potential of animal traces. Three main ichnocoenoses have been identified. The slope and rise ichnocoenose occurs in sediments down to water depths of 3800 m. Slope and rise muds and oozes are thoroughly bioturbated, and the ichnocoenose is dominated by incipient *Helminthopsis*, *Planolites*, and *Thalassinoides*, with the subordinate presence of *Chondrites*, *Scolicia*, *Trichichnus*, *Skolithos*, and *Zoophycos*. Biodeformational structures are also common. This ichnocoenose essentially represents the *Zoophycos* ichnofacies. The transitional slope to abyssal-plain ichnocoenose occurs between 3800 and 4400 m deep. The degree of bioturbation is lower than in adjacent slope and abyssal-plain environments, and biogenic structures tend to be rather small. *Planolites* is the dominant discrete trace. The abyssal-plain ichnocoenose is present below water depths of 4400 m, in areas with abundant intercalation of turbidites. Although the degree of bioturbation is only 20%, the diversity of biogenic structures is the highest, with 15 ichnotaxa recognized. *Taenidium* and *Phycosiphon* are dominant. Graphoglyptids are absent, most likely reflecting a combination of erosion by turbidity currents, high rates of sedimentation, high nutrient availability, and destruction by deep-tier burrows. Biogenic structures are of small size and maintain a connection with the sea bottom to allow circulation of oxygenated waters essential for animal respiration. Overall, the Sulu Sea ichnofauna is clearly limited by oxygen content; high sedimentation rates and abundant food supply also play a role.

Reference: Wetzel (1983).

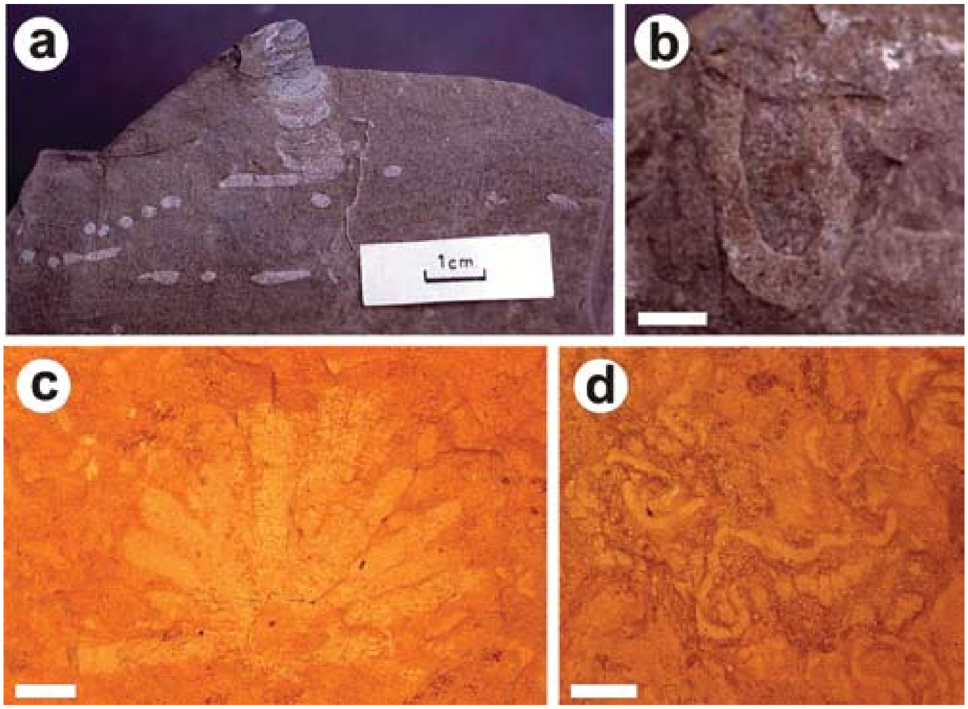


Figure 9.2 Characteristic trace fossils of slope deposits from the Lower Cretaceous Kotick Point Formation, Kotick Point, James Ross Island, Antarctica. (a) *Chondrites* isp. and *Teichichnus rectus*. (b) *Arenicolites* isp. (c) *Cladichnus fischeri* reworked by *Phycosiphon incertum*. (d) *Nereites missouriensis*. All scale bars are 1 cm. See Buatois and Mángano (1992).

also present. Dwelling structures of suspension feeders, such as *Palaeophycus*, *Skolithos*, and *Arenicolites* (Fig. 9.2b) and burrow systems (*Thalassinoides*) occur locally, mostly in slope-fan deposits. The radial trace fossil *Cladichnus* (Fig. 9.2c), the spreite structure *Phycosiphon* (Fig. 9.2c), and grazing trails of deposit feeders, such as *Nereites missouriensis* (Fig. 9.2d) occur in sandy turbidite layers (Buatois and Mángano, 1992). Base-of-slope-wedge deposits are typically sparsely bioturbated, and only locally may contain *Zoophycos* (*Zo*) and *Planolites* (*Pl*). Ichnofabrics tend to show more complex tiering structures than in topographically complex slopes (Buatois and Mángano, 1992). Moderately diverse ichnofaunas are also present in partially ponded slope minibasins, which tend to contain abundant sand-rich turbidites (Shultz and Hubbard, 2005). Although ichnodiversity levels are higher than in the *Zoophycos* ichnofacies of topographically complex slopes, these are remarkably lower than those in the *Nereites* ichnofacies. Substrates are nutrient rich, and therefore highly complex systems, such as those

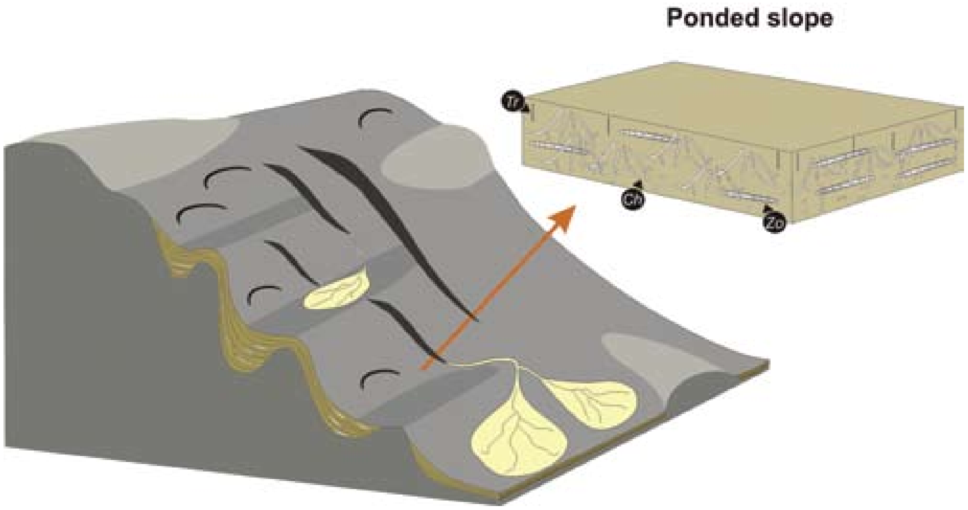


Figure 9.3 Schematic reconstruction of trace-fossil distribution in topographically complex slopes. These deposits are only locally bioturbated, and may contain *Zoophycos* (*Zo*), *Chondrites* (*Ch*), and *Trichichnus* (*Tr*).

illustrated by graphoglyptids, are not present (Wetzel, 1983). Overall, ichnofaunas from topographically simple slopes illustrate the *Zoophycos* ichnofacies with the addition of elements more typical of a distal *Cruziana* ichnofacies.

9.1.2 TOPOGRAPHICALLY COMPLEX SLOPES

Topographically complex slopes exhibit local topographic depressions and highs induced by deformation in the substrate (Smith, 2004) (Fig. 9.3). The classic example of topographically complex slopes is the Gulf of Mexico (Prather *et al.*, 1998; Pirmez *et al.*, 2000), but silled basins also occur in active-plate margins, such as the southern California borderland (Ingle, 1980). Available information indicates that these slopes are characterized by the formation of fault-controlled, silled, intra-slope minibasins, display limited deep-water circulation, and are commonly anoxic or dysaerobic. Turbidite systems tend to show various degrees of confinement, from cascades of silled sub-basins to connected tortuous corridors (Smith, 2004). Low current velocities and enhanced deposition of particulate organic matter in ponded areas lead to low pore-water oxygen levels (Löwemark *et al.*, 2004). Ingle (1980) noted that if the depth of the sill is within the oxygen-minimum layer, all of the water below sill depth will be anoxic regardless of the maximum depth of the basin floor. Therefore, silled intra-slope minibasins are commonly non-bioturbated due to anoxic conditions or, more rarely, may contain very low-diversity ichnofaunas due to dysaerobia (Fig. 9.3). Monospecific assemblages of *Chondrites* are the most abundant suites in ponded slopes (Fu and Werner, 1994; Encinas *et al.*, 2008). *Zoophycos* and *Trichichnus* may also be present. In any case, bioturbation is restricted to discrete intervals, which alternate with non-bioturbated units. Increased intensity of bioturbation and ichnodiversity may in some cases reflect shallowing (Conybeare *et al.*, 2004). If bioturbated at all, topographically complex slope systems are characterized by the *Zoophycos* ichnofacies.

9.2 DEEP-MARINE TURBIDITE SYSTEMS

Deep-marine turbidite systems or submarine fans are formed by deposition of sediment gravity flows. Turbidite systems are remarkably complex and a wide variety of classification schemes and facies models have been proposed over the years (e.g. Mutti and Ricci Lucchi, 1972; Walker, 1978; Mutti, 1979, 1985, 1992; Mutti and Normark, 1991; Reading and Richards, 1994). A useful subdivision that helps to frame observations on deep-marine ichnofaunas is that of fine-grained and coarse-grained turbidite systems (Bouma, 2000a, b, 2004).

9.2.1 FINE-GRAINED TURBIDITE SYSTEMS

Fine-grained turbidite systems are characterized by (1) high sandstone/shale ratio at the base-of-slope and outer fan, but low ratio in the mid fan; (2) fine- and very fine-grained sand with abundant silt and clay particles; and (3) interfingering with basin deposits (Bouma, 2000a, b, 2004). Because of the abundance of very fine-grained sediment, fine-grained turbidite systems are efficient systems (Mutti, 1979). These systems are more typical of passive margins (although examples are known from foreland basins), and tend to occur in basins with wide shelves and coastal plains. A channel complex is formed at the base of the slope, consisting of channels flanked by levees and overbanks, and separated by interchannel areas. The breaching of levees results in the formation of crevasse-splay deposits (Posamentier and Kolla, 2003). Channels bifurcate, forming distributary channels in the mid fan, which feed sheet-sand depositional lobes in the outer fan, also known as frontal-splay complexes (Bouma, 2000a, b, 2004; Posamentier and Kolla, 2003).

Fine-grained turbidite systems commonly contain some of the most spectacular ichnofaunas described from the fossil record with respect to diversity, abundance, and complexity (e.g. Książkiewicz, 1970, 1977; Seilacher, 1977a; Crimes, 1977; Crimes *et al.*, 1981; Leszczyński, 1992a; Uchman, 1995, 1998, 1999,

Box 9.2 Ichnology of Eocene fine-grained turbidite systems of the Hecho Group in the Ainsa–Jaca Basin of the Spanish Pyrenees

The Eocene Hecho Group is well known among turbidite sedimentologists because many deep-marine depositional models have resulted from its study. However, its ichnological content remained poorly documented until very recently when a monographic work and an integrated ichnological–sedimentological study were performed. More confined channelized environments are recorded in the more proximal Ainsa sub-basin, while more distal and unconfined deposits are present in the Jaca sub-basin. Ninety five ichnospecies and 49 ichnogenera have been recorded. In the Ainsa sub-basin there is an increase in ichnodiversity and intensity of bioturbation from channel to inter-channel deposits. Channel deposits are dominated by crustacean burrows, such as *Ophiomorpha rudis*, *O. annulata*, *Ophiomorpha* isp., and *Thalassinoides suevicus*. *Scolicia prisca* and *Arenicolites* isp. occur in some sandstone beds. The assemblage illustrates the *Ophiomorpha rudis* ichnosubfacies. Low ichnodiversity and sparse bioturbation are typical of channelized facies elsewhere. Interchannel deposits, both channel-margin and levee facies, contain a high diversity of trace fossils, including graphoglyptids, such as *Megagrapton irregulare* and *Paleodictyon minimum*, together with dwelling structures (e.g. *Ophiomorpha rudis* and *Thalassinoides suevicus*), feeding structures (e.g. *Phycosiphon incertum*) and grazing trails (e.g. *Gordia arcuata* and *Gordia marina*). This assemblage illustrates a mixed *Ophiomorpha rudis* and *Paleodictyon* ichnosubfacies. In the Jaca sub-basin, there is an increase in ichnodiversity and intensity of bioturbation from the channel-lobe transition to the lobe fringe. The channel-lobe transition is characterized by moderate ichnodiversity and sparse bioturbation. Deposits display a dominance of dwelling burrows (e.g. *Ophiomorpha annulata, Thalassinoides suevicus*, and *Palaeophycus tubularis*), but grazing trace fossils (*Nereites irregularis*), feeding trace fossils (*Halopoa imbricata*), and graphoglyptids (*Paleodictyon maximum*) are present locally. In the depositional lobe (frontal splay), a wide variety of trace fossils is preserved, including feeding structures (e.g. *Halopoa storeana*, *Halopoa imbricata*, and *Chondrites intricatus*), dwelling structures (*Ophiomorpha annulata*, *O. rudis*, and *Thalassinoides* isp.), grazing trace fossils (*Nereites irregularis*, *Scolicia prisca*, and *Scolicia strozzi*), and graphoglyptids (*Helminthorhaphe flexuosa*, *Spiroraphe involuta*, *Cosmorhaphe lobata*, and *Paleodictyon strozzi*). Lobe-fringe deposits display the highest trace-fossil diversity and intensity of bioturbation, representing a typical *Paleodictyon* ichnosubfacies of the *Nereites* ichnofacies. Although feeding, dwelling, and grazing trace fossils are present, suites tend to be dominated by graphoglyptids, including *Paleomeandron robustum*, *Desmograpton dertonensis*, *Helmithorhaphe flexuosa*, *Protopaleodictyon spinata*, and various ichnospecies of *Paleodictyon*. A decrease in trace-fossil diversity and degree of bioturbation is detected from the lobe fringe to the basin plain. Basin-plain deposits are characterized by a sharp increase in the proportion of feeding structures (e.g. *Phycosiphon incertum*, *Zoophycos* isp.), a high proportion of graphoglyptids (e.g. *Megagrapton submontanum* and "*Rotundusichnium*" *zumayense*), and a decrease in dwelling structures (e.g. *Ophiomorpha rudis*). The overall high trace-fossil diversity is typical of deep-marine deposits of similar age, and has been attributed to moderate oligotrophy as a result of large-scale oceanographic and climatic changes. The Hecho Group illustrates the most diagnostic ichnological features of a fine-grained turbidite system.

References: Uchman (2001); Heard and Pickering (2008).

2007; Wetzel and Uchman, 1997; Kozur *et al.*, 1996; Buatois *et al.*, 2001; Wetzel *et al.*, 2007; Rodríguez-Tovar *et al.*, 2010a) (Box 9.2) (Fig. 9.4). In deep-marine environments, low-energy conditions and temporal stability promote the establishment of a wide variety of graphoglyptids and grazing trails, representing the *Nereites* ichnofacies. The overall abundance of graphoglyptids is indicative of reduced food supply and appropriate bottom energy conditions allowing their preservation. This is consistent with the site of emplacement of fine-grained turbidite systems, typically far away from the source area, and separated from the nearshore zone by a wide continental shelf. Interestingly, although delta-fed turbidite systems represent a departure to this standard scenario, graphoglyptids are also present in these organic-rich turbidites and related deposits (Olivero *et al.*, 2010).

Graphoglyptid ichnofaunas, illustrating the *Paleodictyon* ichnosubfacies of the *Nereites* ichnofacies, occur in thin-bedded sandy turbidites, and are mostly present in the outer fan, more precisely in frontal splays (e.g. Crimes, 1977; Crimes *et al.*, 1981; McCann, 1993; Uchman, 1995, 2001; Uchman and Demircan, 1999; Wetzel and Uchman, 2001; Demircan and Toker, 2003; Uchman *et al.*, 2004a; López-Cabrera *et al.*, 2008; Heard and Pickering, 2008; Rodríguez-Tovar *et al.*, 2010a). Together with a large number of graphoglyptids, such as *Paleodictyon* (Fig. 9.5a–b), *Desmograpton* (Fig. 9.5c), *Protopaleodictyon*, *Megagrapton*, *Helicolithus* (Fig. 9.5d), *Spirorhaphe* (Fig. 9.5e), *Helminthorhaphe* (Fig. 9.5f), *Lorenzinia* (Fig. 9.5g–h), *Cosmorhaphe*, and *Urohelminthoida*, there are other basic morphological types. These include the circular burrow *Circulichnis* (Fig. 9.5i), sinuous trails, such as *Helminthopsis*, *Nereites*, and *Scolicia* (Fig. 9.5j), various feeding burrows, including *Zoophycos*, *Lophoctenium*, and *Phycosiphon* (Fig. 9.6a), and the chevronate trail *Protovirgularia* (Fig. 9.5k)

In more proximal positions, graphoglyptid-dominated ichnofaunas also occur in levee and crevasse-splay deposits of the channel complex (e.g. McCann and Pickerill, 1988; McCann, 1993; Uchman, 1995; Wetzel and Uchman, 1997; Buatois *et al.*, 2001; Heard and Pickering, 2008; Olivero *et al.*, 2010). In addition to a wide variety of graphoglyptids (Fig. 9.7a–g)

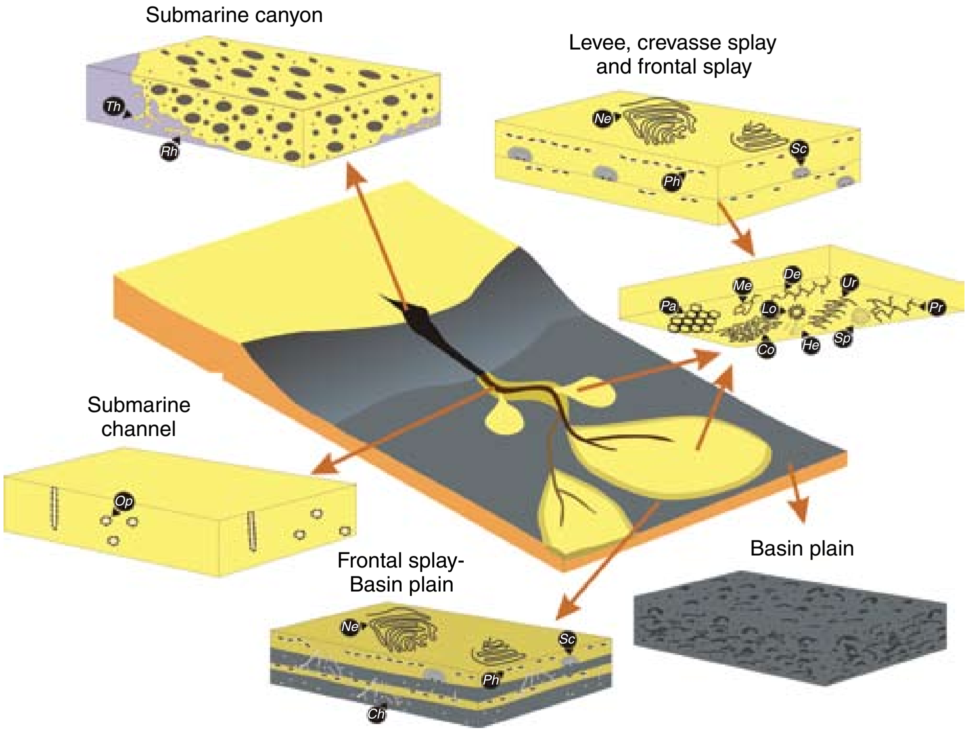


Figure 9.4 Schematic reconstruction of trace-fossil distribution in fine-grained turbidite systems. The base of the incised canyon is characterized by a firmground suite that may contain *Thalassinoides* (*Th*) and *Rhizocorallium* (*Rh*) illustrating the *Glossifungites* ichnofacies. Submarine-channel deposits typically contain *Ophiomorpha* (*Op*). Thin-bedded sandy turbidites in levee, crevasse-splay, and frontal-splay areas contain *Nereites* (*Ne*), *Scolicia* (*Sc*), and *Phycosiphon* (*Ph*) as post-depositional elements, and a wide variety of pre-depositional components, such as *Paleodictyon* (*Pa*), *Megagrapton* (*Me*), *Desmograpton* (*De*), *Lorenzinia* (*Lo*), *Cosmorhaphe* (*Co*), *Helicolithus* (*He*), *Spirorhaphe* (*Sp*), and *Protopaleodictyon* (*Pr*). Distal muddy turbidites of the transitional zone between the frontal splay and the basin plain may contain *Nereites* (*Ne*), *Scolicia* (*Sc*), *Phycosiphon* (*Ph*), and *Chondrites* (*Ch*). Basin-plain deposits are characterized by an indistinct bioturbated mottling.

such as those mentioned for the frontal-splay deposits, levee and crevasse-splay deposits also contain abundant dwelling structures (e.g. *Palaeophycus* and *Ophiomorpha*), sinuous grazing trails, such as *Gordia*, *Helminthopsis*, *Nereites*, and *Scolicia* (Fig. 9.7h), the robust spiral trace *Spirophycus* (Fig. 9.7i), the branched system *Chondrites* (Fig. 9.7j), and various spreite feeding structures, including *Zoophycos*, *Polykampton*, and *Phycosiphon* (Fig. 9.6b).

The *Nereites* ichnosubfacies tends to occur in more distal muddy turbidites, which are more typical of the distal overbank and the transition between the frontal splays and the basin plain. In these settings, various ichnospecies of *Nereites*, most commonly *N. irregularis* (Fig. 9.8a–b), and *Scolicia*, together with *Chondrites* (Fig. 9.8c–d), *Phycosiphon*, *Dictyodora* (in Paleozoic rocks), *Zoophycos*, and *Helicodromites* (Fig. 9.8c) are dominant. Formation of graphoglyptids is commonly inhibited under oxygen-deficient conditions (Leszczyński, 1991a) or high frequency of turbidity currents (D'Alessandro *et al.*, 1986). For example, Uchman (1991b, 1992) documented Cretaceous and Cenozoic turbidites emplaced in oxygen-depleted settings, having very few to almost no agrichnial structures. These ichnofaunas are also characterized by unusually low ichnodiversity and dominance of opportunistic post-turbidite trace fossils. In these distal settings, deposits showing characteristics intermediate between mud turbidites and pelagites are common. These deposits, referred to as hemiturbidites (Stow and Wetzel, 1990; Wetzel and Balson, 1992), are intensely bioturbated and accumulate slowly from a dilute suspension cloud formed beyond and above a large low-concentration turbidity current. In these outer regions of deep-sea fans, sedimentation and bioturbation are in equilibrium and, as a result, hemiturbidite mudstones are completely burrowed.

In the channels and in the most proximal areas of the sheet-sand depositional lobes, continuous erosion and high rates of sedimentation prevent development or preservation of graphoglyptid ichnofaunas and, in fact, most channelized deposits are unburrowed. However, these high-energy settings locally may host ichnofaunas that contain elements typical of shallow water (e.g. *Skolithos*, *Diplocraterion*, and *Ophiomorpha*), representing a deep-marine example of the *Skolithos* ichnofacies (Crimes, 1977; Crimes *et al.*, 1981; McCann and Pickerill, 1988). Uchman (2001, 2007, 2009) noted that some of these thick-bedded sandy turbidites are dominated by horizontal components, typically crustacean galleries (Fig. 9.9a–d), rather than vertical burrows and ascribed this association to the *Ophiomorpha rudis* ichnosubfacies. *Ophiomorpha rudis* and *O. annulata* (Fig. 9.9a–c) are typical in these deposits. Channelized areas and inner zones of depositional lobes, characterized by sandy substrates, organic particles in the water column, and good oxygenation, allow the establishment of a benthic fauna that produce trace fossils that commonly typify nearshore areas. However, shallow-water elements are not restricted to these high-energy regions of submarine fans, occurring in more distal, thin-bedded turbidites also (Uchman, 1991a; Uchman and Demircan, 1999). The crustacean producer of *Ophiomorpha rudis* may have been transported from shallower water by turbidity currents or may represent a resident fauna adapted to deep-water environments (Uchman and Demircan, 1999). These crustaceans may have penetrated into the sandy substrate in search for nutrient-rich deeply buried plant detritus (Uchman *et al.*, 2004a; López-Cabrera *et al.*, 2008).

Therefore, sandy turbidites may contain two different suites, pre- and post-turbidite, recording different times of emplacement and contrasting environmental conditions (Seilacher, 1962;

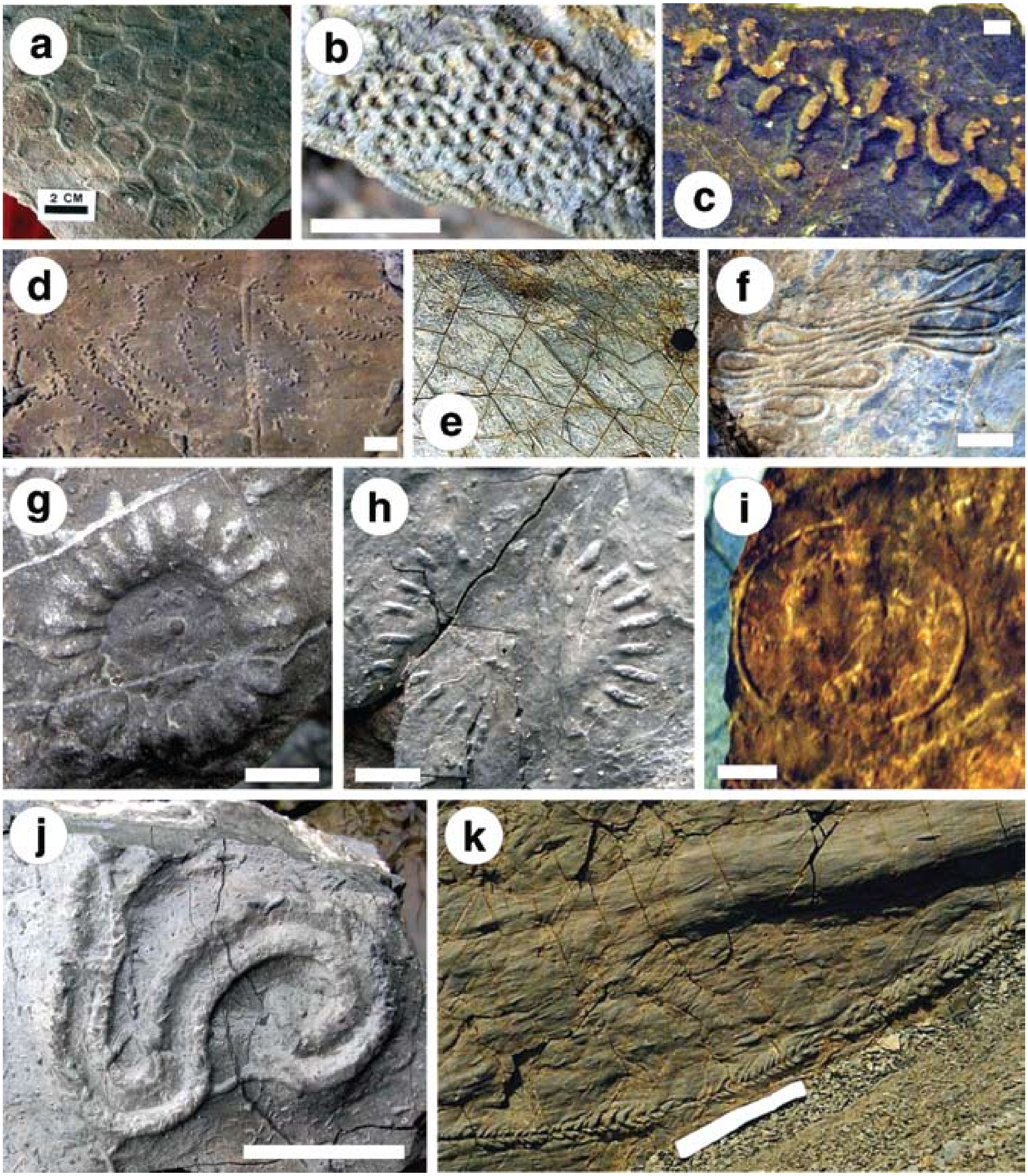


Figure 9.5 Characteristic trace fossils of turbidites in distal areas of frontal splays and fringes of fine-grained turbidite systems. (a) *Paleodictyon gomezi*. Oligocene–Miocene, Campo de Gibraltar, southern Spain. (b) *Paleodictyon minimum*. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Scale bar is 1 cm. See Macsotay (1967). (c) *Desmograpton pamiricus*. Upper Triassic, Al Ayn Formation, Oman Mountains. Scale bar is 1 cm. See Wetzel *et al*. (2007). (d) *Helicolithus sampelayoi*. Eocene, Beloveža Beds, Lipnica Mała, Outer Carpathians, Poland. Scale bar is 1 cm. (e) *Spirorhaphe involuta*. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Lens cover is 5.5 cm. See Macsotay (1967). (f) *Helminthorhaphe* isp. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Scale bar is 1 cm. See Macsotay (1967). (g) *Lorenzinia apenninica*. Upper Cretaceous–Paleocene, Ropianka Formation, Słopnice, Outer Carpathians, Poland. Scale bar is 1 cm. See Uchman (2008a). (h) *Lorenzinia carpathica*. Upper Cretaceous–Paleocene, Ropianka Formation, Słopnice, Outer Carpathians, Poland. Scale bar is 1 cm. See Uchman (2008a). (i) *Circulichnis montanus*. Upper Triassic, Al Ayn Formation, Oman Mountains. Scale bar is 1 cm. See Wetzel *et al*. (2007). (j) *Scolicia* isp. Eocene, Variegated Shale, Słopnice, Outer Carpathians, Poland. Scale bar is 5 cm. See Uchman (2008a). (k) *Protovirgularia* isp. Lower Eocene, Guárico Formation, Boca de Uchire, eastern Venezuela. Scale bar is 10 cm. See Macsotay (1967).

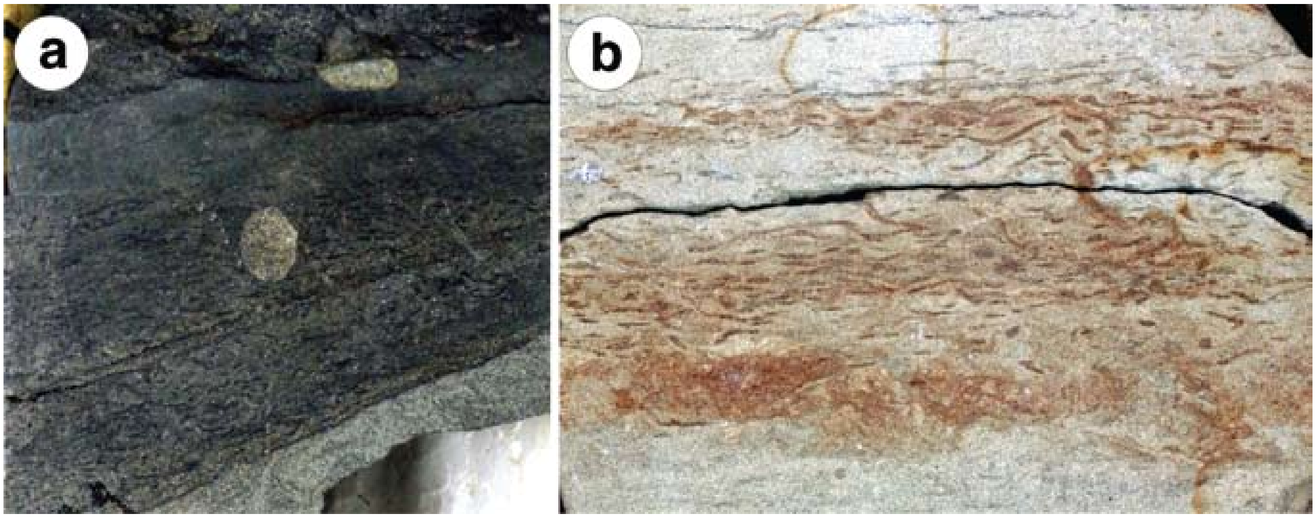


Figure 9.6 Core expression of *Phycosiphon* ichnofabrics in thin-bedded turbidites. (a) High density of *Phycosiphon incertum* at the top of a lobe-fringe turbidite sandstone and in the overlying hemipelagic mudstone. Note also associated firmground *Thalassinoides*. Lower Miocene, La Blanquilla Basin, offshore Venezuela. Core width is 7 cm. (b) Sideritized *Phycosiphon* isp. in overbank turbidite sandstone. Upper Miocene–Lower Pliocene, Carúpano Basin, offshore Venezuela. Core width is 7 cm.

Kern, 1980; Wetzel, 1991; Leszczyński, 1991b, 1992a; Uchman, 1995; Tunis and Uchman, 1996a, b; Wetzel and Uchman, 1997) (Fig. 9.10). The pre-turbidite suite is dominated by graphoglyptids and grazing trails, and is preserved as positive hyporeliefs on the turbidite soles. This suite records the activity of a diverse shallow-tier infaunal community inhabiting pelagic mud. The post-turbidite suite consists of dwelling, feeding, and grazing traces, and is preserved for the most part on the upper surface of the event beds, but also at the base or within turbidites. This suite records opportunistic colonization of the newly emplaced sandy substrate. Accordingly, the base of sandy turbidites represents a palimpsest surface that contain two suites emplaced at different times (Fig. 9.11a–c). Kern (1980) outlined a set of criteria to differentiate between post- and pre-turbidite suites at the base of sandstone. Pre-turbidite trace fossils may show evidence of erosional modification (Fig. 9.11d) and internal lamination preserved within the burrow systems. Post-turbidite trace fossils commonly cross-cut the former suite and show pristine morphologies on surfaces with abundant flute marks. In addition, emplacement of post-turbidite trace fossils may lead to modifications at the sand/mud interface. This author also noted that post-turbidite trace fossils are rare at the base of sandstone thicker than 10 cm. However, Seilacher (1962) documented spectacular specimens of *Ophiomorpha* penetrating to the base of 4 m-thick turbidites.

A number of studies have focused on the tiering structure of ichnofaunas from turbidites and related facies (e.g. Wetzel, 1984, 1991; Leszczyński and Seilacher, 1991; Leszczyński, 1991b, 1992a, b, 1993; Uchman, 1991c, 1995; Orr, 1994; Bak, 1995; Wetzel and Uchman, 1997, 1998). In the case of pre-turbidite suites, two main tiers occur: a very shallow tier consisting of graphoglyptids and a deeper tier consisting of actively filled feeding burrows (Leszczyński, 1991b) (Fig. 9.10). Due to vertical accretion of pelagic and hemipelagic sediment on the sea floor, the deeper-tier fodinichnia migrates upward obliterating the very shallow-tier agrichnia (Werner and Wetzel, 1982; Wetzel, 1991). Therefore, under conditions of suspension fallout background sedimentation, graphoglyptids are not preserved and the resultant ichnofabric is dominated by actively infilled burrows, such as *Zoophycos*, *Scolicia*, *Lophoctenium*, and *Planolites*. Graphoglyptid preservation can only take place if deposition from a turbidity current interrupts background sedimentation and associated bioturbation. Under these conditions, graphoglyptids are preserved as positive hyporelief on the bases of the sandy turbidites (Figs. 9.10). Although it has been traditionally assumed that turbidity currents erode the uppermost millimeters of the muddy substrate and cast with sand the shallow-tier biogenic structures, it has been recently suggested that preservation results from a shock wave immediately prior to deposition (Seilacher, 2007a) (see Section 4.2.5). A micro-tiering structure is developed within the pre-turbidite suite dominated by graphoglyptids. Tiny *Paleodictyon* occupy a shallower-tier position than slightly deeper *Cosmorhaphe* and *Glockerichnus* (Leszczyński and Seilacher, 1991) (Fig. 9.11c). *Spirophycus* tends to emplaced deeper into the sediment cross-cutting shallower trace fossils (Fig. 9.11e). The depth of erosion of the subsequent turbidity current controls which tier becomes preserved (Leszczyński, 1993).

Post-turbidite colonization of the event sand starts after the depositional event is complete (Leszczyński, 1991b, 1993). Some post-turbidite colonizers are adapted to specific sandy substrates, and are typically unable to migrate upward during pelagic and hemipelagic vertical accretion of the sea floor. On the other hand, those infaunal organisms that are less substrate-specific (e.g. producers of *Chondrites* and *Planolites*) may move upward into the background mud (Fig. 9.10). Penetration depth and intensity of bioturbation as a function of oxygen content, rate of

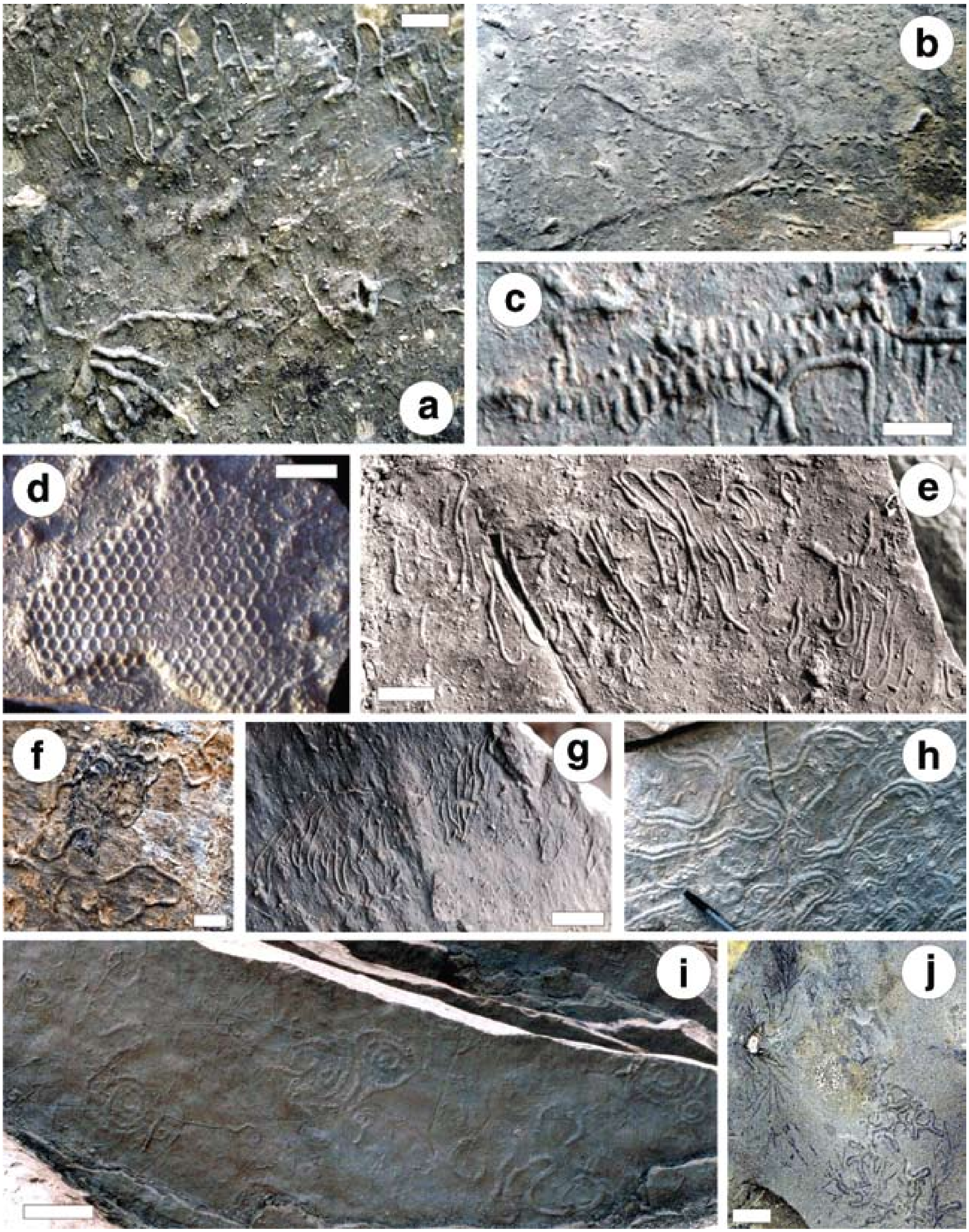


Figure 9.7 Characteristic trace fossils of overbank turbidite deposits in fine-grained turbidite systems. (a) *Helminthorhaphe* isp and *Glockerichnus* isp. Paleocene, Gurnigel Flysch, Zollhaus, Swiss Alps. Scale bar is 5 cm. See Crimes *et al*. (1981). (b) *Paleomeandron* isp. Eocene, Ganei Slates, Ganei, Swiss Alps. Scale bar is 1 cm. See Wetzel and Uchman (1997). (c) *Desmograpton pamiricus*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (d) *Paleodictyon minimum*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (e) *Helminthorhaphe flexuosa*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (f) *Megagrapton submontanum*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (g) *Urohelminthoida dertonensis*. Lower to Middle Eocene, Tarcau Sandstone, Gramaticu Valley, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 1 cm. See Buatois *et al*. (2001). (h) *Scolicia strozzi*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Pen is 15 cm. See Buatois *et al*. (2001). (i) *Spirophycus involutissimus*. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. Scale bar is 10 cm. See Buatois *et al*. (2001). (j) *Phycosiphon incertum* and *Chondrites* isp. Paleocene, Gurnigel Flysch, Zollhaus, Swiss Alps. Scale bar is 1 cm. See Crimes *et al*. (1981).

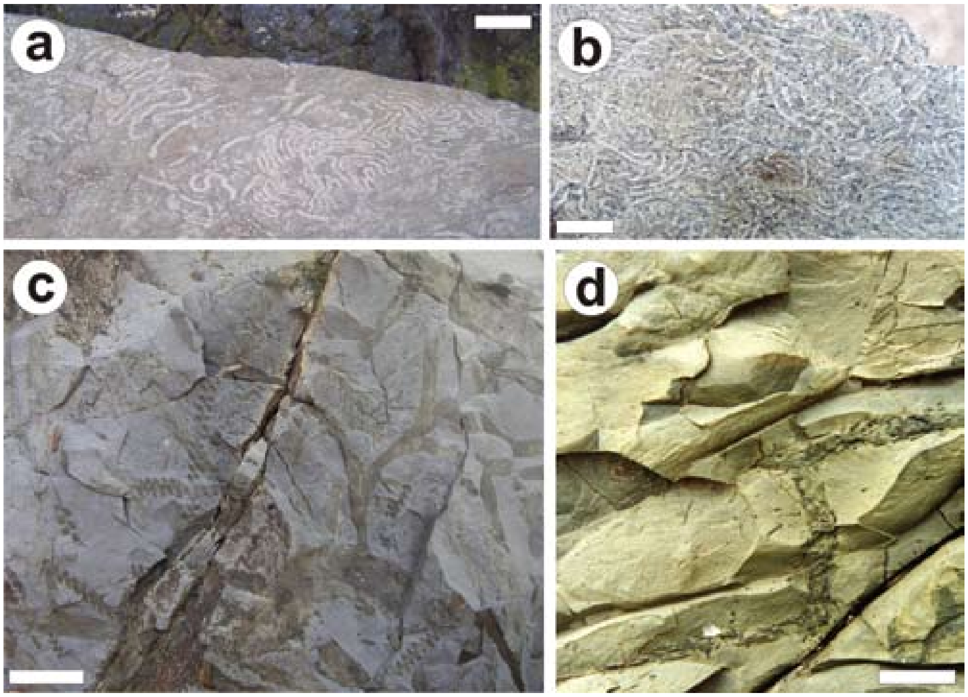


Figure 9.8 Characteristic trace fossils of distal muddy turbidites in fine-grained turbidite systems. (a) *Nereites irregularis* in distal marly turbidites. Paleocene, Głębieniec Member, Ropianka Formation, Głębieniec stream, Outer Carpathians, Poland. See Uchman and Cieszkowski (2008b). (b) *Nereites irregularis* in distal muddy turbidites. Upper Cretaceous, Helminthoid Flysch, Weissenburg Bad, Dranses Nappe, Swiss Alps. See Wetzel (2003). (c) Distal marly and silty turbidites with large and small *Chondrites* isp and *Helicodromites* isp. Eocene, Bystrica Formation, Zbludza, Outer Carpathians, Poland. See Uchman (2008b). (d) *Chondrites* isp. concentrated within "phantom burrows" and dispersed in the host rock. Upper Cretaceous, Horgazu Formation, Covasna Valley, Romania. All scale bars are 1 cm.

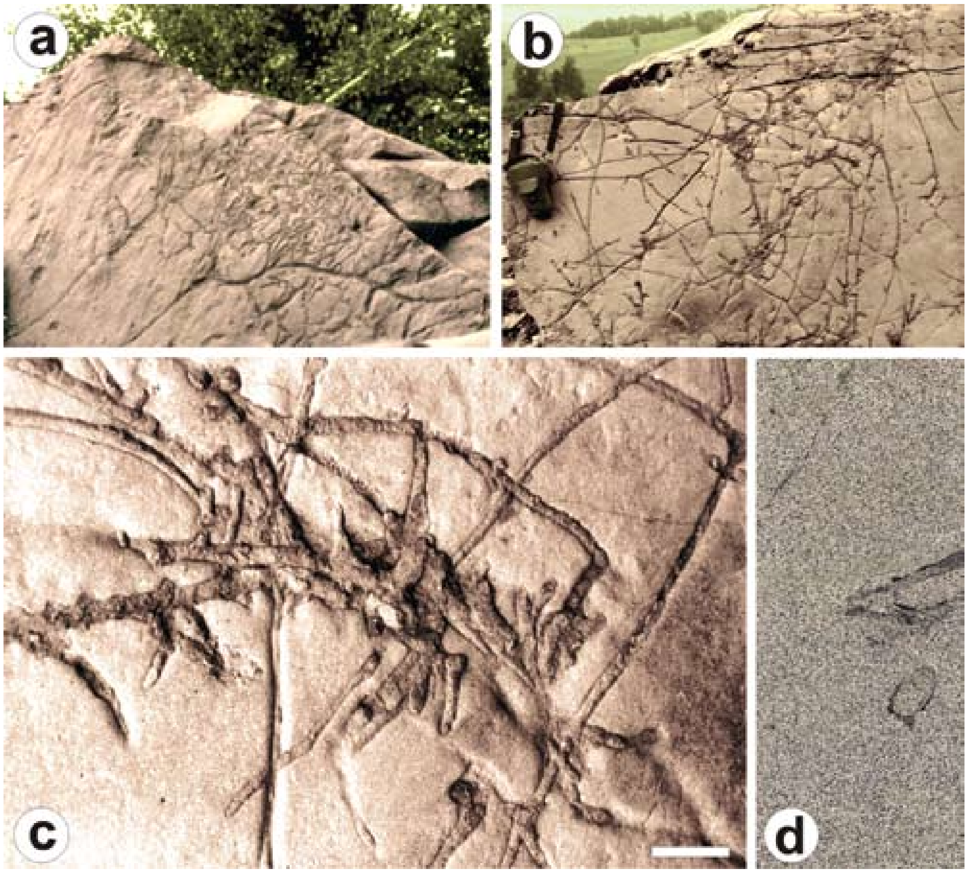


Figure 9.9 Characteristic trace fossils of turbidite-channel deposits in fine-grained turbidite systems. (a) and (b) General views of the top of a channelized sandstone unit with *Ophiomorpha annulata*. (c) Close up of burrow networks of *Ophiomorpha annulata*. Scale bar is 5 cm. (a), (b), and (c) are from outcrops of the Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al.* (2001). (d) Core expression of *Ophiomorpha* isp. in deep-marine high-energy sandstone turbidites. Lower Miocene, La Blanquilla Basin, offshore Venezuela. Core width is 7 cm.

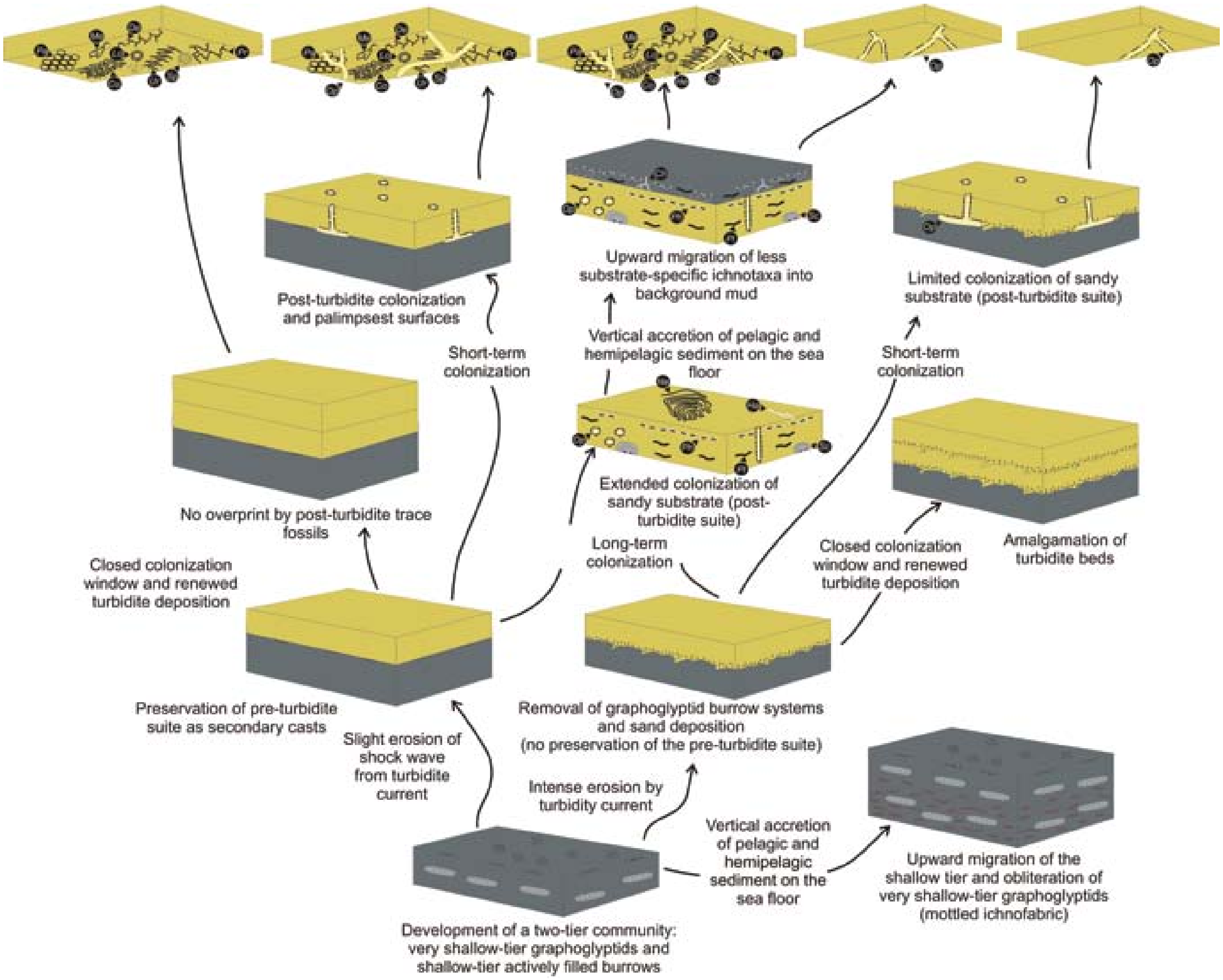


Figure 9.10 Taphonomic pathways of turbidite trace fossils. The preserved ichnofauna is the end-result of a complex array of taphonomic factors. If only hemipelagic suspension fallout takes place, no graphoglyptids are preserved and the resultant product is a mottled ichnofabric that may or may not display discrete trace fossils. If erosion by the turbidity current is too intense, graphoglyptids are not preserved either. Emplacement of post-turbidite colonizers depends on the nature of the colonization window. Under high frequency of highly erosive turbidite events, bed amalgamation occurs and sandstone units are unburrowed. If the frequency of these highly erosive events is lower, limited colonization of the sandy substrate by the post-turbidite suite may occur, being *Ophiomorpha* (*Op*) a typical component. If only slight erosion occurs, graphoglyptids are preserved as positive hyporeliefs on turbidite sandstone beds. Preservation of the graphoglyptid microtiering profile depends on the depth of erosion. Typical elements of the pre-turbidite trace-fossil suite are *Paleodictyon* (*Pa*), *Megagrapton* (*Me*), *Protopaleodictyon* (*Pr*), *Desmograpton* (*De*), *Lorenzinia* (*Lo*), *Cosmorhaphe* (*Co*), *Urohelminthoida* (*Ur*), and *Spirorhaphe* (*Sp*). Under high rates of slightly erosive turbidite events, the colonization window for post-event burrowers remains close and graphoglyptids are not overprinted by the post-turbidite trace-fossil suite. In the case of short-term colonization windows, the post-turbidite trace-fossil suite may occur, but restricted to sand-specific colonizers, typically forming *Ophiomorpha* (*Op*), overprinting the pre-turbidite trace-fossil suite. In the case of long-term colonization windows, pelagic and hemipelagic vertical accretion of the sea floor takes place and even more complex ichnofabrics develop as a result of sequential colonization. In addition to *Ophiomorpha* (*Op*), *Planolites* (*Pl*), *Scolicia* (*Sc*), and *Phycosiphon* (*Ph*) may occur. While post-turbidite sandy-specific colonizers cannot migrate upward during pelagic and hemipelagic sedimentation, less substrate-specific colonizers may move upward into the background mud.

background sedimentation, and the time to next turbidite event are the most important limiting factors (Leszczyński, 1993). Crustacean burrows (e.g. *Ophiomorpha*) are by far the deepest structures, commonly penetrating through several turbidite layers (multilayer colonizers of Uchman, 1995). In the case of muddy turbidites, observations from modern and ancient environments suggest sequential colonization and upward migration in response to geochemical conditions, particularly the re-adjustment and re-establishment of the redox boundary (Wetzel and Uchman, 2001) (Box 9.3). Passive-margin fine-grained turbidite systems tend to be affected by bottom currents (Faugères and Stow, 2008). The ichnologic signatures of contourites (i.e. bottom-current deposits) have been recently explored by Wetzel *et al.* (2008).

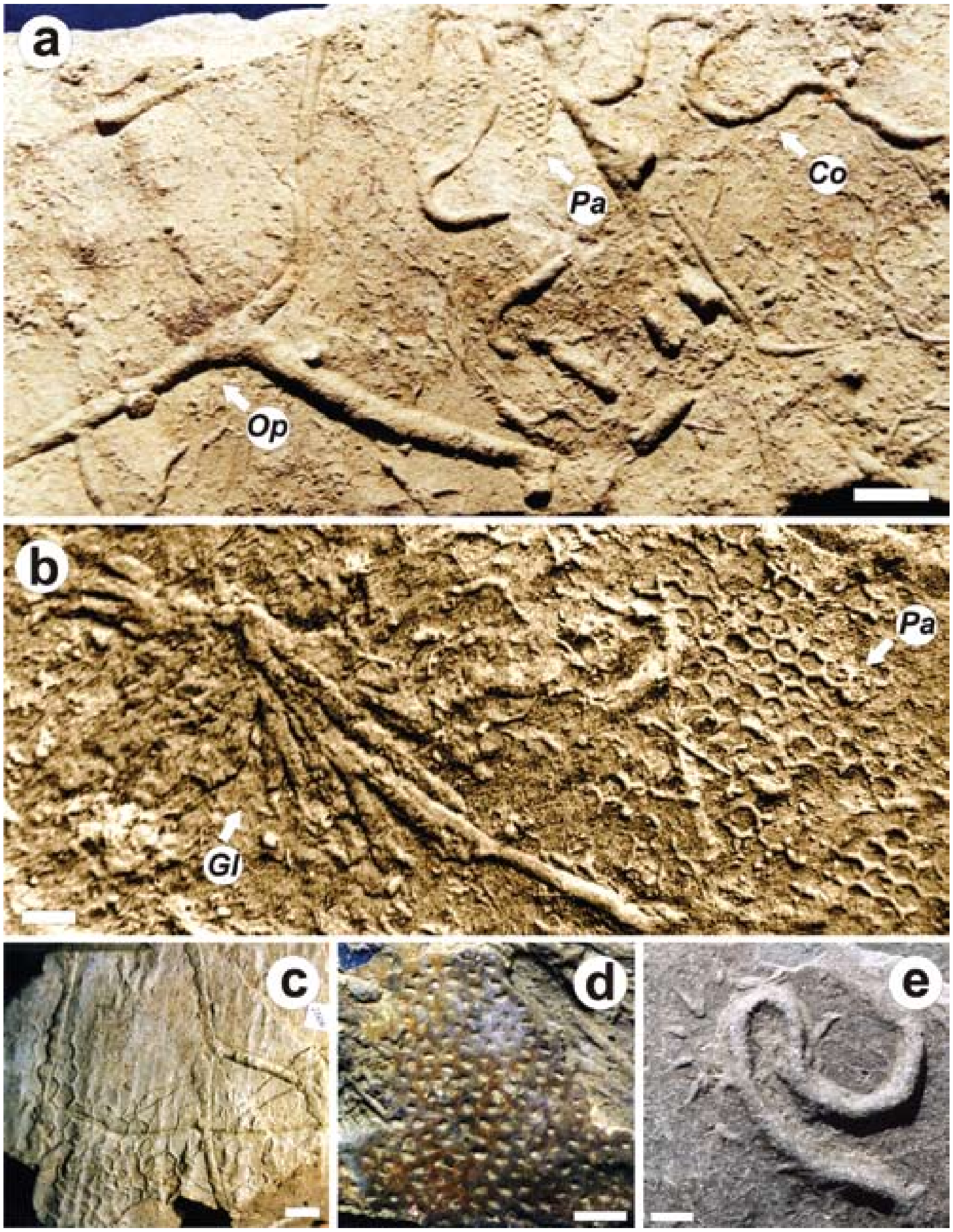


Figure 9.11 Taphonomy of thin-bedded turbidites. (a) Base of a sandstone showing juxtaposition of pre- and post-turbidite suites forming a palimpsest surface. Hexagonal networks (*Paleodictyon minimum*) (*Pa*) and meandering trace fossils (*Cosmorhaphe sinuosa*) (*Co*) belong to the pre-turbidite suite, while superimposed crustacean galleries (*Ophiomorpha annulata*) (*Op*) are part of the post-turbidite suite. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al.* (2001). (b) *Paleodictyon miocenicum* networks (*Pa*) partially modified by erosion. Minimum erosion in some areas allowed preservation of network vertical outlets. The radial trace fossil *Glockerichnus* isp. (*Gl*) occupies a deeper tier, illustrating microtiering in the pre-turbidite community. Lower to Middle Eocene, Tarcau Sandstone, Siriu Dam, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al.* (2001). (c) Hexagonal networks (*Paleodictyon maximum*) of the pre-turbidite suite cross-cut by crustacean galleries (*Ophiomorpha annulata*) of the post-turbidite suite. Lower to Middle Eocene, Tarcau Sandstone, Gramaticu Valley, Buzau Valley, Eastern Carpathians, Romania. See Buatois *et al.* (2001). (d) *Paleodictyon* cf. *nodosum* showing eroded outlines of vertical components. Lower to Middle Miocene, Shahr Pum Unit, Taherui, Makran Range, Southeastern Iran. See Crimes and McCall (1995). (e) *Spirophycus bicornis* cross-cutting *Lorenzinia pustulosa*. Eocene, Ganei Slates, Ganei, Swiss Alps. See Wetzel and Uchman (1997). All scale bars are 1 cm.

These authors contrasted the role of strong and weak bottom currents. They noted that strong currents may result in intense and deep erosion, formation of non-deposition horizons and/or deposition of sand-dominated contourites. Deep erosion and long-term non-deposition is commonly conducive to the development of the *Glossifungites* ichnofacies in compacted sediment. Sandy contourites tend to be intensely bioturbated, displaying a combination of trace fossils produced by shallow-tier ploughers and deep-tier structures, such as *Skolithos*, *Scolicia* and *Planolites*, as well as deeply emplaced crustacean domiciles (e.g. *Thalassinoides*, *Gyrolithes*).

Weak bottom currents commonly deposit fine-grained particles and abundant organic matter, resulting in the formation of mud-dominated contourites. Because these sediments commonly have anoxic pore waters at very shallow depths, ichnodiversity tend to be low and trace fossils are typically small. *Chondrites* is commonly dominant, and *Nereites* may form along the redox boundary. Low sedimentation rates may be conducive to intense bioturbation, particularly if bottom currents supply additional food. In these cases, distinction from silty/muddy turbidites and hemipelagites may be complicated.

9.2.2 COARSE-GRAINED TURBIDITE SYSTEMS

Coarse-grained turbidite systems are characterized by (1) very high sandstone/shale ratio, including the interchannel areas; (2) medium- and coarse-grained sands with little or no clay minerals; and (3) gradual progradation into the

Box 9.3 Colonization of Eocene muddy turbidites in the Polish Carpathians

Detailed ichnofabric analysis in muddy turbidites of the Eocene Beloveža Formation of the Polish Carpathians allows the reconstruction of the colonization of event beds in the deep sea. Evaluation of cross-cutting relationships demonstrates that colonization was sequential and most likely controlled by changes in geochemical conditions, particularly re-adjustment and re-establishment of the redox boundary. The makers of *Phycosiphon* and *Halopoa* were the first to exploit the newly emplaced substrate. The former is suited to colonize well-oxygenated muds, while the later displayed a preference for sandy substrates. After re-establishment of the redox boundary, *Nereites* was emplaced probably exploiting microbial organic matter right above the redox discontinuity. Next in the sequence was *Chondrites*, which was able to penetrate below the redox boundary, even reaching below the previously emplaced turbidite layer. *Ophiomorpha* and *Scolicia* represent the deepest tier and most likely record permanent bioturbation that was unaffected by the deposition of new turbidites. Both reflect adaptations to burrowing though sand and mud, and to coping with oxygen-restricted conditions. This model is consistent with observations from the modern deep-sea floor that suggest that newly emplaced turbidites contain abundant organic matter and are fully oxygenated. However, because oxygen consumption exceeds oxygen production, the lower part of the turbidite and the buried hemipelagic layer become rapidly depleted in oxygen.

Reference: Wetzel and Uchman (2001).

basin (Bouma, 2000a, b, 2004). Because of the scarcity of very fine-grained sediment, coarse-grained turbidite systems are poorly efficient (Mutti, 1979). These systems are more typical of active margins, and tend to occur in basins with narrow shelves and coastal plains. Submarine channels form at the base of the slope and are typically of a low sinuosity, braided-type. Because of their poor efficiency, lobe deposits are formed relatively close to the base of slope (Fig. 9.12).

As in the case of fine-grained turbidite systems, high-energy channelized areas and the most proximal zones of sheet-sand depositional lobes are typically unbioturbated or may contain trace fossils that are usually common in shallow water, illustrating the *Skolithos* ichnofacies in a deep-marine context (e.g. Kern and Warme, 1974; Buatois and López Angriman, 1992b). However, and in contrast to fine-grained turbidite systems, the *Nereites* ichnofacies (in particular, the *Paleodictyon* ichnosubfacies) is rare to absent in coarse-grained deep-marine systems. The absence or scarcity of graphoglyptids is not a direct result of grain size because off-channel and lobe thin-bedded turbidites of the same grain size occur in both fine-grained and coarse-grained turbidite systems. Rather, the ichnofauna of thin-bedded turbidites in coarse-grained turbidite systems tends to be dominated by feeding traces of deposit feeders, such as *Phycosiphon*, *Chondrites*, *Planolites*, and *Zoophycos*, suggesting affinities with the *Zoophycos* ichnofacies (Buatois and López Angriman, 1992b) (Fig. 9.12) (Box 9.4). The replacement of the *Nereites* ichnofacies by the *Zoophycos* ichnofacies is most likely due to the associated narrow shelf and the close proximity of frontal splays to the base of the slope. This may have promoted a high frequency of sediment gravity flows supplying significant amounts of organic matter to the system, precluding the need for the sophisticated farming strategies that characterize agrichnial structures (Buatois and López Angriman, 1992b). In some cases, it is even possible that the post-turbidite suite displays higher diversity than the pre-turbidite suite (e.g. W. Miller, 1991b). These post-turbidite trace fossils may have exploited abundant plant detritus accumulated within the event-flow sand.

9.3 HYPERPYCNAL SYSTEMS

In recent years, a number of studies have underscored the importance of sustained turbidity currents or hyperpycnal flows as opposed to more classic episodic turbidity currents (Mulder and Syvitski, 1995; Mutti *et al.*, 1996; Plink-Björklund and Steel, 2004; Zavala *et al.*, 2011). Even more recently, ichnological studies started to focus on the trace-fossil signatures of both modern and ancient deep-marine hyperpycnites (Ponce *et al.*, 2007; Wetzel, 2008; Olivero *et al.*, 2010; Carmona and Ponce, 2011). Studies from modern deep-sea bottoms indicated that hyperpycnal-flow deposits provide a more appropriate substrate for rapid colonization, particularly in comparison with volcanic ash (Wetzel, 2008). Hyperpycnal flows typically transport larvae, juvenile, and adult organisms, together with benthic food to the deep sea, resulting in deposits commonly containing abundant organic matter. Analysis of Upper Eocene–Lower Oligocene hyperpycnal-flow deposits of Tierra del Fuego, southern Argentina, indicates that bioturbation typically occurs in connection with pause horizons (Ponce *et al.*, 2007). This ichnofauna is dominated by *Phymatoderma* (Fig. 9.14a–b) with *Chondrites* (Fig. 9.14c), *Zoophycos* (Fig. 9.14b), *Tasselia* (Fig. 9.14d), and *Paradictyodora* (Fig. 9.14b) also being common. The bioturbated deposits correspond to mudstone accumulated during the backstepping stage of the flow, overlying forestepping-stage unbioturbated sandy-channel and lobe deposits.

Proximal–distal trends in trace-fossil distribution with respect to both the paleoshoreline and the axis of the channel in a deep-marine system dominated by hyperpycnal flows have been evaluated in Miocene deposits of the same region (Carmona and Ponce, 2011). Hyperpycnal-channel and inner-levee deposits

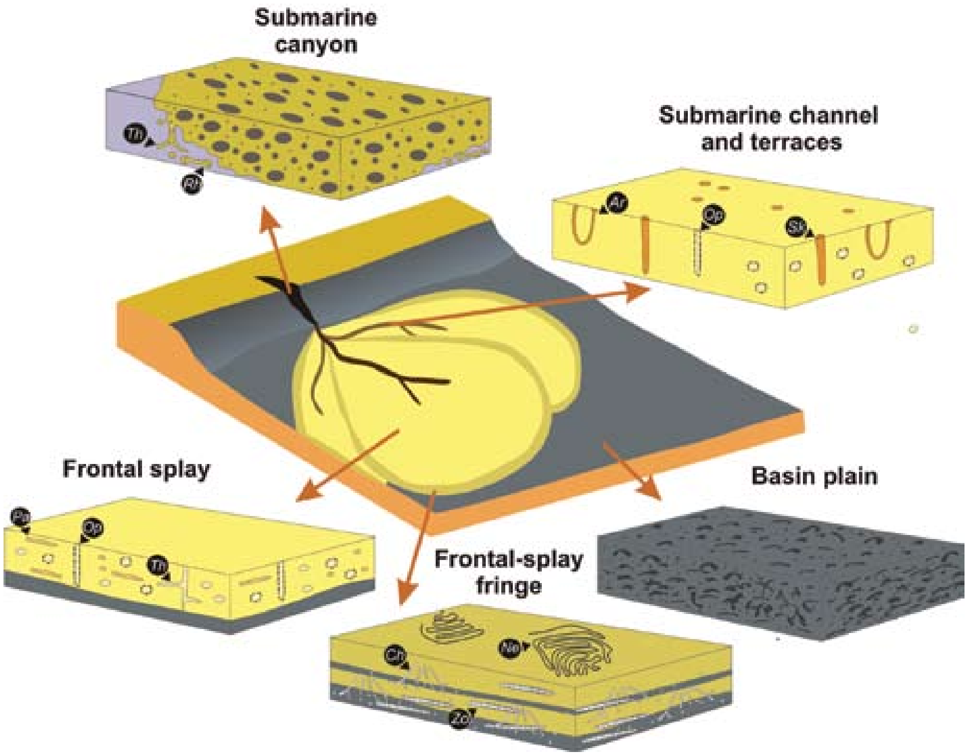


Figure 9.12 Schematic reconstruction of trace-fossil distribution in coarse-grained turbidite systems. As in the case of fine-grained turbidite systems, the base of the incised canyon is characterized by a firmground suite that may contain *Thalassinoides* (*Th*) and *Rhizocorallium* (*Rh*) illustrating the *Glossifungites* ichnofacies. Submarine-channel and terrace deposits typically contain *Ophiomorpha* (*Op*), *Skolithos* (*Sk*), and *Arenicolites* (*Ar*). Frontal-splay deposits may exhibit *Palaeophycus* (*Pa*), *Ophiomorpha* (*Op*), and *Thalassinoides* (*Th*). Frontal-splay fringe deposits may contain *Nereites* (*Ne*), *Zoophycos* (*Zo*), and *Chondrites* (*Ch*). Basin-plain deposits are characterized by an indistinct bioturbated mottling.

Box 9.4 Ichnology of a Cretaceous coarse-grained turbidite system of Antarctica

The Cretaceous Whisky Bay Formation of the James Ross Island, Antarctica, represents part of the infill of a back-arc basin. Deposition occurs in a submarine braided-channel complex comprising a wide variety of subenvironments, including main and secondary braided channels, adjacent marginal terraces and sandy plains, and muddy and sandy interchannel areas. The main braided channel deposits are unburrowed, but two main ichnocoenoses have been recognized in the other subenvironments. The first ichnocoenose occurs in conglomerate and pebbly sandstone which accumulated in minor braided channels, marginal terraces, and sandy plains. It consists of *Arenicolites*, *Diplocraterion* (Fig. 9.13a), *Skolithos*, *Thalassinoides* (Fig. 9.13b), *Palaeophycus*, and *Planolites*. It is essentially dominated by dwelling trace fossils of suspension feeders, illustrating the *Skolithos* ichnofacies. The second ichnocoenose is present in sandstone and mudstone of the interchannel areas. It consists of *Zoophycos*, *Chondrites*, and *Cylindrichnus*. It is dominated by feeding traces of deposit feeders, representing the *Zoophycos* ichnofacies. The absence of graphoglyptids is attributed to a high frequency of sediment gravity flows that introduced abundant organic material, inhibiting the establishment of complex farming strategies. The Whisky Bay Formation provides a good example of the most relevant ichnological features of a coarse-grained turbidite system.

Reference: Buatois and López Angriman (1992b).

tend to contain dwelling trace fossils of suspension feeders, such as *Diplocraterion*. Outer-levee deposits tend to be dominated by opportunistic grazing and locomotion structures (e.g. *Protovirgularia*, *Gordia*, and *Scolicia*) and concentrically laminated burrows. In the middle positions of the system, at the base of the depositional slope, bivalve escape structures occur in sandstone bodies. High sedimentation rates and fluctuating salinity, together with energy fluctuations and high food supply, may have been the most important limiting factors. The importance of salinity fluctuations is also supported by the presence of synaeresis cracks in levee deposits (Carmona and Ponce, 2011; Ponce and Carmona, 2011). A higher intensity of bioturbation was recorded in distal hyperpycnal-lobe deposits, but ichnodiversity is low to moderate. The distal assemblage is dominated by deposit-feeder structures, such as *Scolicia* and *Nereites*. Salinity fluctuations were apparently less intense than in the more proximal positions (Carmona and Ponce, 2011). Graphoglyptids are virtually absent in these hyperpycnal-flow deposits.

Also in Tierra del Fuego, Olivero *et al*. (2010) analyzed the ichnology of an Eocene channel-levee complex containing both hyperpycnal-flow and turbidity-current deposits. Channel-fill to proximal-levee thick-bedded sandstone is dominated by *Ophiomorpha rudis*. Proximal to distal-levee thinner-bedded

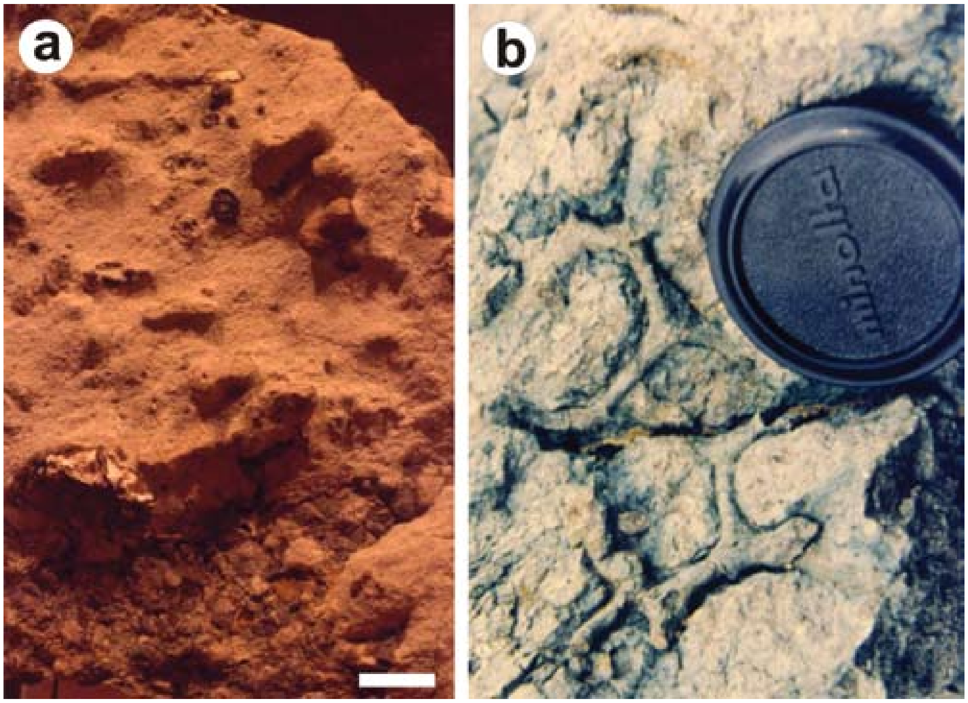


Figure 9.13 Trace fossils from coarse-grained turbidite system deposits in the Lower Cretaceous Whisky Bay formation of James Ross Island, Antarctica. (a) *Diplocraterion* isp. penetrating into an abandoned-channel pebble conglomerate from a mudstone layer mantling the coarse-grained deposit. Scale bar is 1 cm. (b) *Thalassinoides suevicus* in marginal-terrace pebbly sandstone. Lens cover is 5.5 cm. See Buatois and López Angriman (1992b).

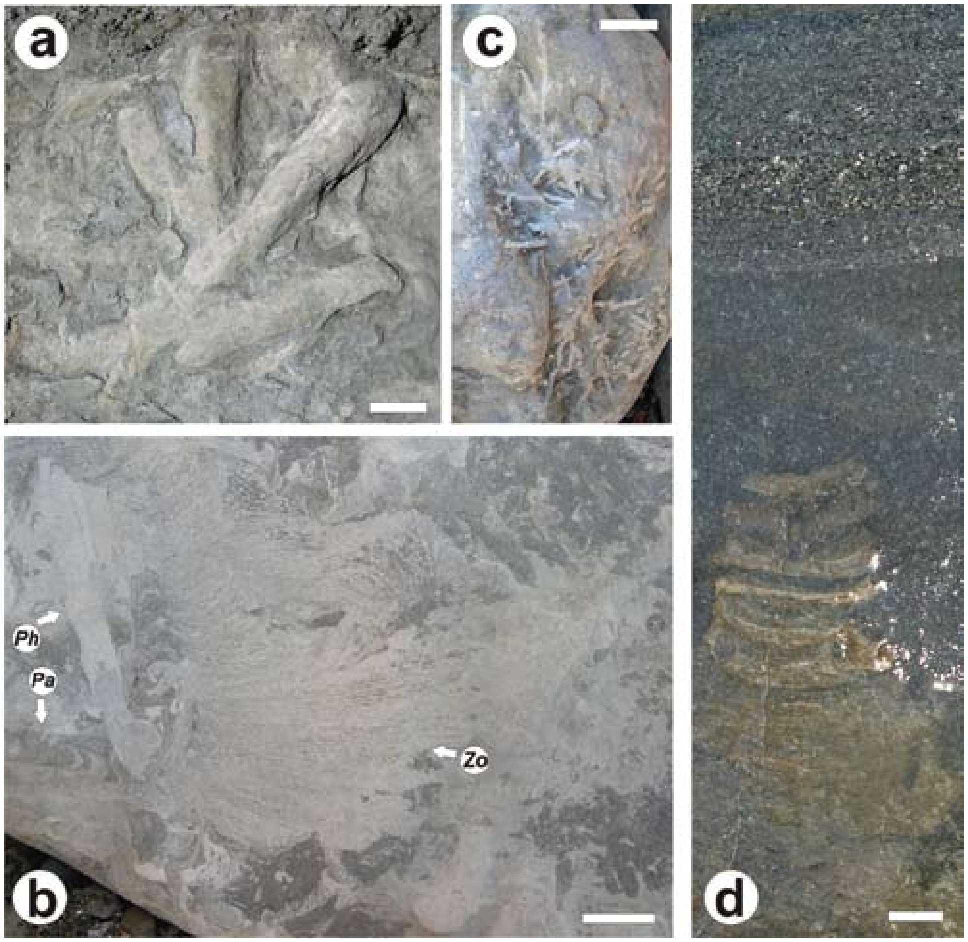


Figure 9.14 Trace fossils from deep-marine hyperpycnal deposits in the Upper Eocene to Lower Oligocene Punta Gruesa Beds, Tierra del Fuego, southern Patagonia, Argentina. (a) *Phymatoderma granulata*. (b) *Phymatoderma granulata* (*Ph*), *Zoophycos* isp. with pelletoidal infill (*Zo*), and *Paradictyodora antarctica* (*Pa*). (c) *Chondrites* isp. (d) *Tasselia* isp. Note overlying erosive surface. All bars are 1 cm. See Ponce *et al*. (2007).

Box 9.5 Biogenic structures in modern deep-sea floors off New Caledonia, southwestern Pacific

Bottom photographs taken in modern deep-sea floors off New Caledonia from water depths of 800 to more than 3000 m documented the presence of a wide variety and complexity of biogenic structures. Most biogenic structures occur over a rather large depth range. Simple holes and mounds are ubiquitous, being abundant along the whole bathymetric range analyzed. However, two main associations were recognized. The deep-slope association is dominated by composite craters having actinarian and enteropneust traces, and horseshoe-shaped traces of an unknown maker. The basin-plain association is dominated by incipient *Asteriacites* and linear grooves. In addition, although other traces show wider bathymetric ranges, they tend to be more abundant at certain water depth ranges. For example incipient *Lorenzinia* is common at 2100–2300 m deep and *Scolicia* at 1600–2200 m. Incipient *Paleodictyon* is apparently present only at water depths below 1700 m and incipient *Urohelminthoida* seems to occur between 1700–2150 m. Overall, holothurians and echinoderms are the most important tracemakers. This study reinforces the idea that deep-tier bioturbation and erosion are detrimental to the preservation of graphoglyptids, underscoring the role of slightly erosive turbidity currents in the preservation of agrichnial structures.

Reference: Gaillard (1991).

turbidites and hyperpycnites contain various ichnotaxa, such as *Nereites*, *Phycosiphon*, *Tasselia*, *Diplocraterion*, and several graphoglyptids, including *Cosmorhaphe*, *Desmograpton*, *Glockerichnus*, *Paleodictyon*, and *Helicolithus*, among other ichnogenera. Some of these deposits display a high content of plant debris. The presence of graphoglyptids in organic-rich deposits that accumulated in an overall high-energy setting is apparently rather unusual, but, in fact, underscores the role of taphonomic controls and times of oligotrophy in graphoglyptid distribution (see Section 9.2.1).

9.4 BASIN PLAINS

The basin plain corresponds to flat and deep areas of the sea bottom (Stow *et al*., 1996). Here, we specifically address those areas of the basin plain that are removed from turbidity-current or bottom-current supply, and that are dominated by hemipelagic and pelagic sedimentation. Evaluating the role of the fossilization barrier is essential in characterizing the ichnology of basin-plain environments. Complex grazing trails and graphoglyptids have been observed and photographed on modern basin plains during exploration of the deep sea (Ewing and Davis, 1967; Heezen and Hollister, 1971; Hollister *et al*., 1975; Kitchell *et al*., 1978a, b; Ekdale and Berger, 1978; Kitchell, 1979; Ekdale, 1980; Gaillard, 1991) (Box 9.5). However, the fossilization potential of these structures is virtually zero because the absence of sand emplaced by turbidity currents precludes their preservation along lithological interfaces. Continuous vertical accretion of the deep-sea floor is conducive to intense reworking of the sediment and destruction of shallow-tier representatives of the *Nereites* ichnofacies by deep-infaunal bioturbators (Ekdale and Berger, 1978; Wetzel, 1983, 1984). Pelagic deposits contain deep-tier dwelling and feeding structures, such as *Zoophycos*, *Thalassinoides*, *Teichichnus*, and *Planolites*. In the distal-most settings, the extremely low sedimentation rates allows complete homogenization of the substrate, and only a mottled texture attributed to *Planolites* is observed (Bromley, 1990, 1996).

10 Ichnology of continental environments

The prevalent notion that trace fossils are comparatively rare in nonmarine facies is more a reflection of insufficient reconnaissance than of a true dearth of specimens.

Robert Frey and George Pemberton
"The *Psilonichnus* ichnocoenose, and its relationship to adjacent marine and
nonmarine ichnocoenoses along the Georgia coast" (1987)

Vemos las cosas según como las interpretamos. Lo llamamos previsión: saber de antemano, estar prevenidos. Usted en el campo sigue el rastro de un ternero, ve huellas en la tierra seca, sabe que el animal está cansado porque las marcas son livianas y se orienta porque los pájaros bajan a picotear en el rastro. No puede buscar huellas al voleo, el rastreador debe primero saber lo que persigue: hombre, perro, puma. Y después ver. Lo mismo yo. Hay que tener una base y luego hay que inferir y deducir. Entonces – concluyó – uno ve lo que sabe y no puede ver si no sabe…Descubrir es ver de otro modo lo que nadie ha percibido. Ése es el asunto.. – Es raro, pensó Renzi, pero tiene razón –.

Ricardo Piglia
Blanco Nocturno (2010)

Historically invertebrate ichnology has focused on marine ichnofaunas. However, studies have gradually moved into freshwater and, more recently, terrestrial environments. As a result, continental ichnology has experienced a remarkable development during the last 15 years, and our perspective on this topic has changed dramatically. Earlier case studies started to show that continental invertebrate ichnofaunas were more varied and abundant than originally envisaged (e.g. Bromley and Asgaard, 1979; Bown, 1982; Pollard *et al*., 1982; Frey *et al*., 1984b; Walker, 1985; Ekdale and Picard, 1985; D'Alessandro *et al*., 1987; Gierlowski-Kordesch, 1991; Pickerill, 1992). It rapidly became clear that continental environments were as numerous and diverse as marine settings, and that such variability was indeed reflected in the ichnological record (Frey and Pemberton, 1987). Subsequent work focused on the expansion of the continental dataset, but more significantly in the proposal of archetypal ichnofacies in addition to the *Scoyenia* ichnofacies (Smith *et al*., 1993; Buatois and Mángano, 1995b, 2004a, 2007; Bromley, 1996; Genise *et al*., 2000, 2004b, 2010a). Also, the potential and limitations of the ichnofabric approach to the study of freshwater and terrestrial ichnofaunas have been addressed in a number of studies (e.g. Buatois and Mángano, 1998, 2007; Genise *et al*., 2004a; Buatois *et al*., 2007a). More recently, proposals have been made to define continental ichnofacies based on vertebrate trace fossils (Lockley *et al*., 1994; Hunt and Lucas, 2006a, 2007). There has also been a recent revival of continental neoichnology (e.g. Scott *et al*., 2007b; Smith and Hasiotis, 2008; Hembree, 2009; Genise *et al*., 2009). The fields of invertebrate and vertebrate ichnology have evolved independently, and research involves two separate scientific communities to a great extent (Lockley, 2007). This is certainly not a significant problem in marine ichnology, but it has had a negative impact on continental ichnology. The need to integrate vertebrate and invertebrate datasets has long been recognized (e.g. Buatois and Mángano, 1995b, 1996), but little progress has been attained. However, a series of recent papers seem to show that a better articulation between invertebrate and vertebrate ichnology is possible (e.g. Melchor *et al*., 2006; Lockley, 2007; Hunt and Lucas, 2007; Minter *et al*., 2007b; Scott *et al*., 2007b; Krapovickas *et al*., 2009). Integration of both datasets will be essential to produce more robust depositional models of continental environments.

While most, if not all, of the ichnotaxa from the various terrestrial ichnofacies are produced by insects, and are restricted to continental environments (e.g. *Coprinisphaera*, *Termitichnus*, *Celliforma*, *Eatonichnus*), this is not entirely the case with the ichnogenera commonly recorded from the freshwater *Mermia* and *Scoyenia* ichnofacies (Buatois and Mángano, 2007). With the exception of *Scoyenia*, *Mermia*, *Camborygma*, and some arthropod trackways (e.g. *Stiaria*, *Stiallia*, *Hexapodichnus*), the other components of these ichnofacies are facies-crossing ichnotaxa known from both the continental and marine realm (e.g. *Taenidium*, *Palaeophycus*, *Planolites*, *Gordia*, *Helminthopsis*, *Helminthoidichnites*, *Cochlichnus*, *Treptichnus*). Meniscate trace fossils informally referred to by some authors as "adhesive meniscate burrows" (e.g. Hasiotis, 2004) were subsequently included in a new ichnogenus, *Naktodemasis*, based on meniscate packaging (Smith *et al*., 2008a). Although this ichnotaxon seems to be exclusive of continental environments, it clearly falls within the diagnosis of *Taenidium* and it is better regarded as a separate ichnospecies, *T. bowni*, rather than a new ichnogenus (Krapovickas *et al*., 2009). The eolian *Octopodichnus–Entradichnus* ichnofacies contain some forms exclusive to continental environments (e.g. *Octopodichnus, Paleohelcura*) associated with other facies-crossing ichnotaxa (e.g. *Palaeophycus*, *Planolites*) (Hunt and Lucas, 2007; Ekdale *et al*., 2007). *Entradichnus* has also only been recorded in continental environments, but its distinction from *Taenidium* is still unclear (Keighley and Pickerill, 1994; Ekdale *et al*., 2007).

While subaerial ichnofaunas are overwhelmingly dominated by terrestrial insects and, to a lesser extent, arachnids, freshwater ichnofaunas mostly reveal behavioral convergence of many different groups, including aquatic insects, but also crustaceans and mollusks, to name a few. As a result, freshwater ichnofaunas more closely resemble marine associations than their terrestrial counterparts. Undoubtedly, it is the whole assemblage that should be analyzed in order to distinguish between marine and freshwater ichnofaunas.

Conversely, there is a large number of ichnotaxa that are exclusive of marine settings. These include all the typical elements of the *Nereites* and *Zoophycos* ichnofacies, and most of the ichnotaxa of the *Cruziana* ichnofacies (e.g. *Asterosoma*, *Rosselia*, *Dactyloidites*, *Arthrophycus*, *Asteriacites*, *Curvolithus*, *Psammichnites*, *Teichichnus*). These trace fossils reflect specific behavioral patterns that are exclusive of marine organisms. Some typical marine ichnogenera (e.g. *Paleodictyon*, *Nereites*, *Scolicia*, *Chondrites*) have occasionally been mentioned in continental deposits (e.g. Smith *et al.*, 1982; Archer and Maples, 1984; Pickerill, 1990; Hu *et al.*, 1998; Hasiotis, 2002, 2004; Kim *et al.*, 2005), but they have been misidentified. Re-examination invariably indicates that the forms reported in freshwater settings are much simpler than the marine ichnotaxa, and that they do not display the diagnostic features of those ichnogenera (Buatois and Mángano, 2007). In this chapter, we review the ichnology of different continental environments, from alluvial fans and fluvial systems to lakes and deserts, as well as paleosols.

10.1 ALLUVIAL FANS

Alluvial fans occur where a channel emerges from a mountainous upland to an adjoining valley depositing coarse-grained material at a marked break in the slope, forming a sedimentary body with a form that resembles the segment of a cone radiating downslope (Bull, 1977; Blair and McPherson, 1994; Harvey *et al.*, 2005). Alluvial fans typically contain coarse-grained sediment, particularly at their mouths, but display a decrease in grain size towards their edges. Ichnological studies of alluvial-fan successions are virtually non-existent. Rapid rates of sedimentation, high energy and coarse-grained sediments, commonly of gravel-size, make alluvial-fan environments extremely harsh for animal life. As a result, colonization by invertebrate and vertebrate burrowers is unusual, and typically associated with pauses in sedimentation. In addition, the preservation potential of almost any structure produced in alluvial-fan sediments is low because of the strongly erosive nature of depositional events, particularly in the most proximal zones of the systems.

The few studies documenting alluvial-fan ichnofaunas in the fossil record deal with biogenic structures produced in the most distal zones of these systems, particularly in the areas that are transitional with braided-river systems, where both invertebrate (e.g. MacNaughton and Pickerill, 1995; Neef, 2004a; Krapovickas *et al.*, 2008), and vertebrate (e.g. García-Ramos and Valenzuela, 1979; Carvalho *et al.*, 1995; Carvalho, 1996) trace fossils are preserved in sandstone beds. Invertebrate trace fossils in distal alluvial-fan deposits are remarkably simple, and consist of a few facies-crossing ichnotaxa, such as *Palaeophycus* and *Skolithos*, which commonly reflect progressive consolidation of the substrate due to desiccation (Krapovickas *et al.*, 2008). Slightly more diverse ichnofaunas, dominated by arthropod locomotion trace fossils, such as *Cruziana*, *Diplichnites*, *Diplopodichnus*, *Merostomichnites*, and *Palmichnium*, occur in ponded areas where fine-grained sedimentation may be locally important (Neef, 2004a). Vertebrate ichnofaunas recorded in alluvial-fan deposits are scarce, and mostly consist of poorly preserved dinosaur trackways in Mesozoic strata (e.g. García-Ramos and Valenzuela, 1979; Carvalho *et al.*, 1995; Carvalho, 1996). In addition, the ichnogenus *Ichniotherium*, probably produced by reptilomorph amphibians (Voight *et al.*, 2007), is common in Permian distal alluvial-fan deposits (Hunt and Lucas, 2006a).

In terms of archetypal ichnofacies, alluvial-fan systems display a transition from the *Skolithos* to the *Scoyenia* ichnofacies. The *Skolithos* ichnofacies tends to occur at the top of channel sandstones, reflecting rapid colonization during short breaks in sedimentation. The *Scoyenia* ichnofacies is extremely impoverished, commonly containing one or two ichnotaxa, but a diversity increase may occur in associated ponds. With respect to vertebrates, the so-called *Ichniotherium* sub-ichnocoenosis of the *Batrachichnus* ichnofacies typically occurs in alluvial-fan settings from the Devonian to the Middle Triassic (Hunt and Lucas, 2006a, 2007).

10.2 RIVERS

Fluvial systems include a wide range of lithofacies and architectural elements, representing a complex mosaic of subenvironments, such as channels of variable sinuosity, containing different types of bars, and overbank settings displaying levees, crevasse splays, and floodplains (Miall, 1996). Modern rivers are inhabited by a wide variety of vertebrates (e.g. fish, amphibians, and reptiles) and invertebrates, including aquatic to semiaquatic insects (e.g. ephemeropterans, trichopterans, dipterans, coleopterans, hemipterans); several groups of crustaceans, such as ostracodes, branchiopods (e.g. conchostracans), and malacostracans (e.g. amphipods, decapods), as well as oligochaete annelids, nematodes, nematomorphs, and mollusks (Chamberlain, 1975; Ratcliffe and Fagerstrom, 1980; Hasiotis and Bown, 1992; Giller and Malmqvist, 1998; Cushing and Allan, 2001). Many of these organisms are able to produce a relatively wide variety of biogenic structures. However, trace fossils are not abundant in fluvial successions. In a classic study, Ratcliffe and Fagerstrom (1980) demonstrated that modern floodplains are very rich in invertebrate structures, although relatively few of the forms documented by these authors have been reported from the fossil record. This fact suggests that the problem of scarcity of trace fossils in continental successions is, at least in part, one of preservation potential.

Although it is sometimes assumed that fluvial ichnofaunas have not been frequently reported from the fossil record,

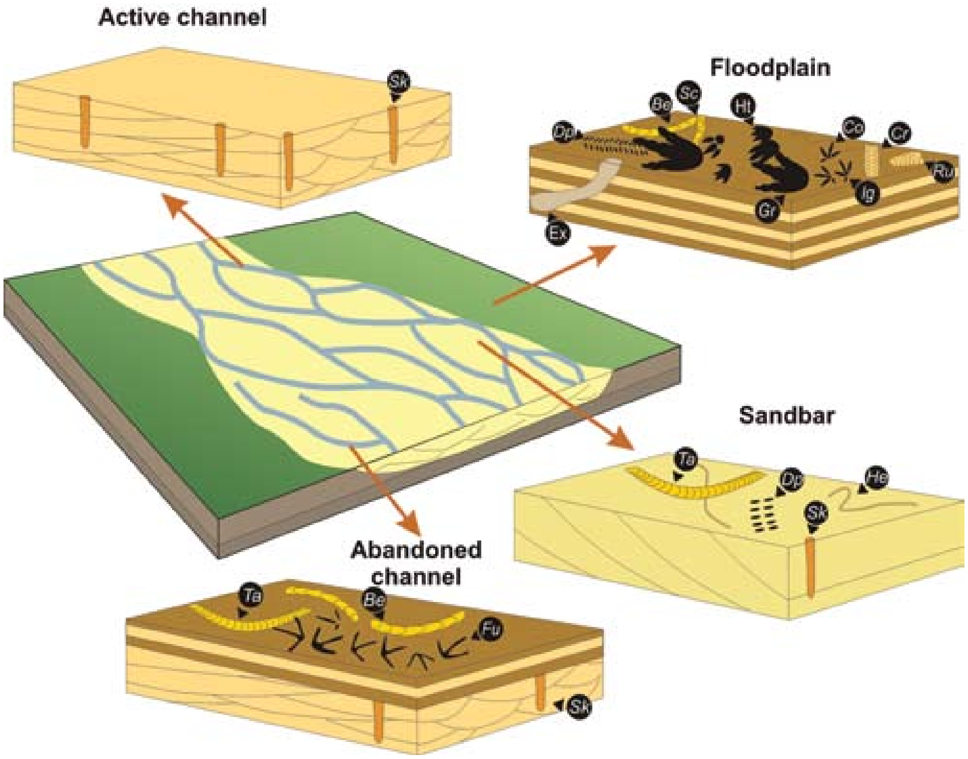


Figure 10.1 Schematic reconstruction of trace-fossil distribution in braided river systems. Composition of vertebrate ichnofaunas is highly variable according to geological age. Active-channel deposits contain *Skolithos* (*Sk*). Abandoned-channel deposits may display the meniscate trace fossils *Taenidium* (*Ta*) and *Beaconites* (*Be*), as well as vertebrate trace fossils such as the bird trackway *Fuscinapeda* (*Fu*). Sandbar deposits may exhibit *Skolithos* (*Sk*), *Taenidium* (*Ta*), *Helminthopsis* (*He*), and *Diplichnites* (*Dp*). Floodplain deposits typically host *Scoyenia* (*Sc*), *Beaconites* (*Be*), *Cochlichnus* (*Co*), *Diplichnites* (*Dp*), *Cruziana* (*Cr*), and *Rusophycus* (*Ru*). Vertebrate trackways and excavations (Ex) are typically abundant and diverse in floodplain deposits. Examples include the theropod ichnogenera *Grallator* (*Gr*) and the shorebird ichnotaxa *Ignotornis* (*Ig*) in the Mesozoic. Various types of heteropod trackways (Ht) are common in the Cenozoic. Vertebrate and invertebrate trace fossils not to scale.

recent compilations have shown that several examples have been documented (Buatois and Mángano, 2007; Minter *et al.*, 2007b). Abundance and diversity of trace fossils in fluvial successions are highly variable from one subenvironment to the other. Thick successions of fluvial deposits are commonly unburrowed or display trace fossils only in discrete beds. Suites are typically monospecific or contain few ichnotaxa. In contrast, the density of biogenic structures may be quite high locally. Ichnofossil distribution in fluvial environments largely depends on the variability in stream discharge and the amount of time between depositional episodes (D'Alessandro *et al.*, 1987). Recent work indicates that ichnofossils have been recorded more commonly in meandering rather than in braided deposits (Buatois and Mángano, 2007). Only a few examples are known in anastomosing and ephemeral deposits, but this sparse record probably reflects lack of studies rather than true absence. Overall, more favorable preservational conditions occur in abandoned channels and associated floodplain settings, instead of active channels (Figs. 10.1 and 10.2). The *Scoyenia* ichnofacies occurs in deposits of any fluvial style, but the *Mermia* ichnofacies is more common in floodplain deposits of meandering systems (Buatois and Mángano, 2007). The *Skolithos* ichnofacies seems to be more common in channel sandstones of braided rivers (e.g. Fitzgerald and Barrett, 1986; Zawiskie *et al.*, 1983), but has also been recorded in ephemeral systems (Sarkar and Chaudhuri, 1992). Buatois and Mángano (2004a) distinguished between ichnofaunas from channel and overbank deposits, a classification framework that is followed here. The ichnology of the subaerial portion of the alluvial plain characterized by soil development is discussed elsewhere (see Section 10.5).

10.2.1 CHANNELS

Fluvial channels display high to relatively high energy, rapid fluctuations in flow velocity and rates of sedimentation and erosion, unstable banks and floors, and coarser-grain sizes than associated overbank environments. Running water or lotic habitats represent stressful and unstable environments for colonization by a benthic fauna. Accordingly, production and/or preservation of biogenic structures are commonly inhibited. Buatois and Mángano (2004a, 2007) noted that some fluvial-channel ichnofaunas seem to have been emplaced when the channel is still active, while others reflect colonization after channel diversion ("abandonment"), or during periods of low discharge characterized by non-deposition ("inactive").

Active-channel deposits tend to have a meager trace-fossil record (Fig. 10.3). These deposits are characterized by low-diversity suites (typically monospecific), and dominance of simple vertical burrows and escape traces (e.g. Bradshaw, 1981; Zawiskie *et al.*, 1983; Fitzgerald and Barrett, 1986; Woolfe, 1990; Sarkar and Chaudhuri, 1992). The degree of bioturbation is commonly low, although dense assemblages of moderately deep to deep *Skolithos* are known (e.g. Fitzgerald and Barrett, 1986) (Figs. 10.1 and 10.2). Affinities with the *Skolithos* ichnofacies are consistent with the associated environmental scenario, although the identity of the tracemakers and the functional significance of these vertical structures are poorly understood (Buatois and

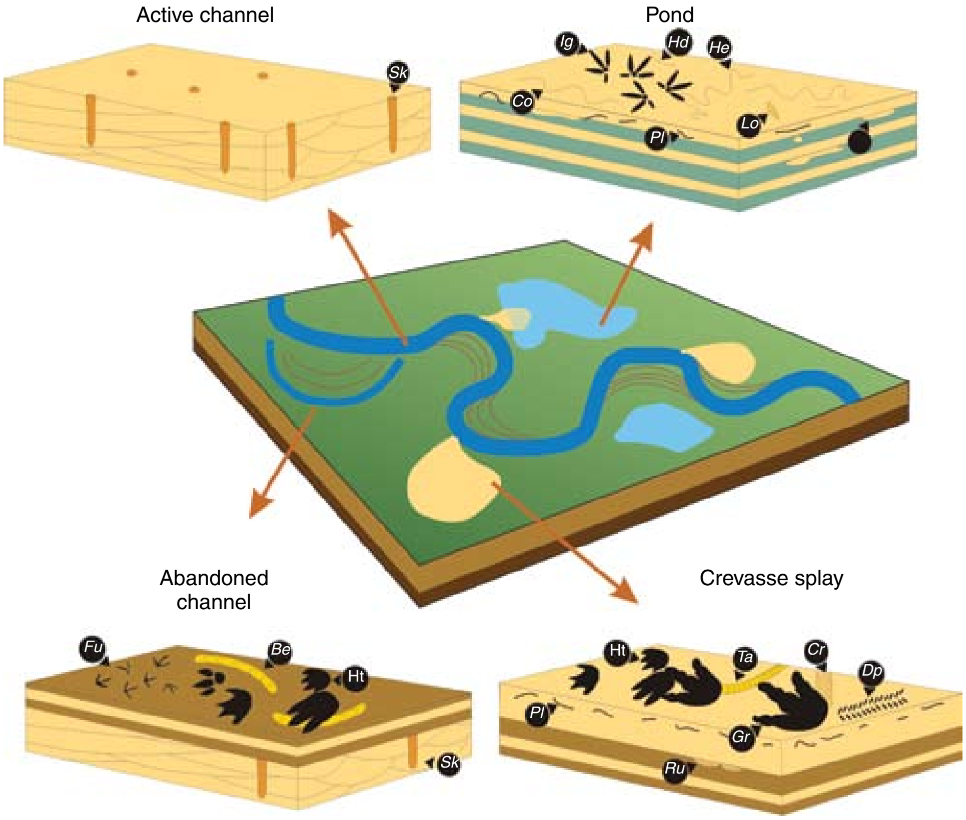


Figure 10.2 Schematic reconstruction of trace-fossil distribution in meandering river systems. Composition of vertebrate ichnofaunas is highly variable according to geological age. As in the case of braided rivers, active-channel deposits contain *Skolithos* (*Sk*). Abandoned-channel deposits commonly display *Beaconites* (*Be*), as well as vertebrate trace fossils such as the bird trackway *Fuscinapeda* (*Fu*) and a variety of heteropod trackways (Ht). Crevasse-splay deposits may exhibit *Taenidium* (*Ta*), *Planolites* (*Pl*), *Cruziana* (*Cr*), *Rusophycus* (*Ru*), and *Diplichnites* (*Dp*). Examples of vertebrate trace fossils in crevasse-splay deposits include the theropod ichnogenera *Grallator* (*Gr*) in Mesozoic strata and various types of heteropod trackways (Ht) in Cenozoic strata. Pond deposits may host *Cochlichnus* (*Co*), *Planolites* (*Pl*), *Lockeia* (*Lo*), *Palaeophycus* (*Pa*), *Helminthopsis* (*He*), and *Helminthoidichnites* (*Hd*). Vertebrate trackways are abundant and diverse in pond deposits including, for example, the shorebird ichnogenus *Ignotornis* (*Ig*) in Mesozoic strata. Vertebrate and invertebrate trace fossils not to scale.

Mángano, 1998, 2004a, 2007; White and Miller, 2008). In other situations, colonization of omission surfaces may have occurred (Netto *et al.*, 2007). More rarely, vertebrate swim tracks, such as those produced by turtles (e.g. *Chelonipus*), are preserved in channel deposits (Lockley and Foster, 2006).

Abandoned- or inactive-channel deposits contain meniscate trace fossils (*Beaconites* and *Taenidium*), vertical to inclined burrows (*Skolithos* and *Cylindricum*), arthropod trackways (*Diplichnites*), and simple horizontal burrows (*Palaeophycus*) (e.g. Allen and Williams, 1981; Graham and Pollard, 1982; Bamford *et al.*, 1986; Sarkar and Chaudhuri 1992; Miller and Collinson, 1994; Miller, 2000; Keighley and Pickerill, 2003; Morrissey and Braddy, 2004; Lucas *et al.*, 2006a; Buatois *et al.*, 2007a) (Fig. 10.3). Vertebrate (e.g. dinosaur and bird) tracks may occur locally in profuse densities at the top of abandoned-channel deposits (e.g. Lockley *et al.*, 2003, Falcon-Lang *et al.*, 2007) (Figs. 10.1 and 10.2). Ichnodiversity is typically low, but relatively high when compared to active channels. The degree of bioturbation is highly variable. Low to moderate intensities of bioturbation are common, but high bioturbation indexes are locally measured, more commonly at the top of channel-sandstone units (e.g. Buatois *et al.*, 2007a). Meniscate trace fossils reflect the activity of vagile organisms that excavate while searching for food, most likely revealing a combination of bypassing and ingestion. Vertical to inclined burrows may serve several functions, such as permanent domiciles, semi-permanent shelters, nests, and passageways (Stanley and Fagerstrom, 1974). Insect nesting trace fossils may also be present, reflecting the ability of these organisms to colonize various types of substrates (Genise *et al.*, 2000) (see Section 10.5). Tracemakers that colonize abandoned or inactive channels are regarded as behavioral generalists that record an opportunistic strategy (Miller and Collinson, 1994). Ichnofaunas of abandoned- or inactive-channel deposits are similar in taxonomic composition to those from overbank deposits, because abandoned channels lead to the formation of ponded areas (Fig. 10.3). In terms of archetypal ichnofacies, abandoned- or inactive-channel ichnofaunas belong to the *Scoyenia* ichnofacies. If channels are reactivated, the *Skolithos* ichnofacies is re-established.

10.2.2 OVERBANK

Overbank settings encompass a wide variety of subenvironments, including floodplains, crevasse splays and levees, which comprise complex riparian ecosystems (Naiman *et al.*, 2005). These represent quite unique habitats in which a link is established between aquatic and terrestrial realms (Malanson, 1993). Ecological studies suggest that the lateral water flow that characterizes these settings near river channels ranks among one of the most important controlling factors in riparian ecology (e.g. Brown *et al.*, 1979; Malanson, 1993). Overbank flooding helps to define terrestrial–aquatic gradients, from perennially inundated wetlands through frequently inundated wetlands to occasionally and infrequently flooded areas.

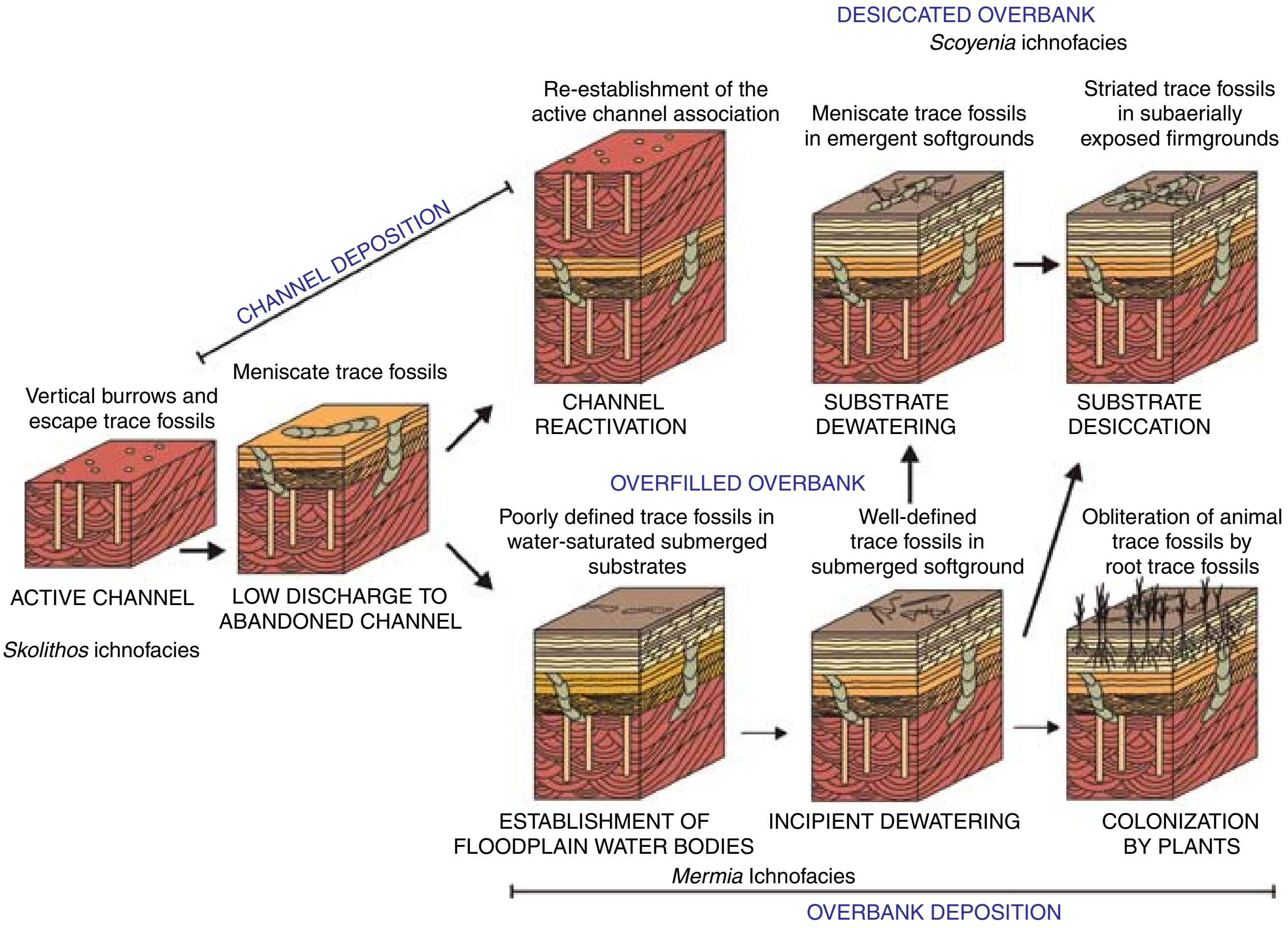


Figure 10.3 Taphonomic pathways of fluvial ichnofaunas showing transitions between different channel and overbank trace-fossil suites. Substrate consolidation plays a major role in controlling ichnofacies occurrence (after Buatois and Mángano 2004a, 2007).

Box 10.1 Ichnology of Miocene fluvial deposits of the Sub-Andean region of Bolivia

Cenozoic deposits with thicknesses up to 7.5 km accumulated in the Chaco foreland basin of the Sub-Andean region of Bolivia, mostly recording sedimentation in fluvial environments. Bioturbation is widespread in anastomosed fluvial deposits of the Upper Miocene Tariquia Formation. This unit is dominated by *Taenidium barretti*, illustrating the *Scoyenia* ichnofacies. Ichnodiversity is remarkably low and trace-fossil composition does not change significantly throughout the succession, but ichnofabric analysis reveals some degree of variability as a result of various taphonomic pathways (Fig. 10.4). Abandoned main-channel deposits are sparsely bioturbated, while medium- to very fine-grained crevasse sandstone and overbank mudstone display intense and deep bioturbation (bi = 6), showing complete destruction of the primary sedimentary fabric. Main-channel and crevasse-splay sandstones both display upward increases in degree of bioturbation. The tops of the channel and crevasse-splay sandstones represent colonization surfaces, therefore, allowing direct measurements of maximum burrowing depth. Some specimens of *Taenidium barretti* may extend up to 2.2 m into the crevasse sand sheets. Depth and intensity of bioturbation of the main-channel and crevasse sandstones are a reflection of the colonization window (i.e. time between depositional events). Main-channel and crevasse sandstones that underlie thick packages of bioturbated overbank mudstones are intensely bioturbated, as a result of prolonged periods of low-energy sediment fall-out between crevassing events. Conversely, the lowest degree of bioturbation occurs in amalgamated channel sandstone units underlying thin intervals of overbank mudstones, reflecting high-frequency depositional episodes.

Reference: Buatois *et al.* (2007a).

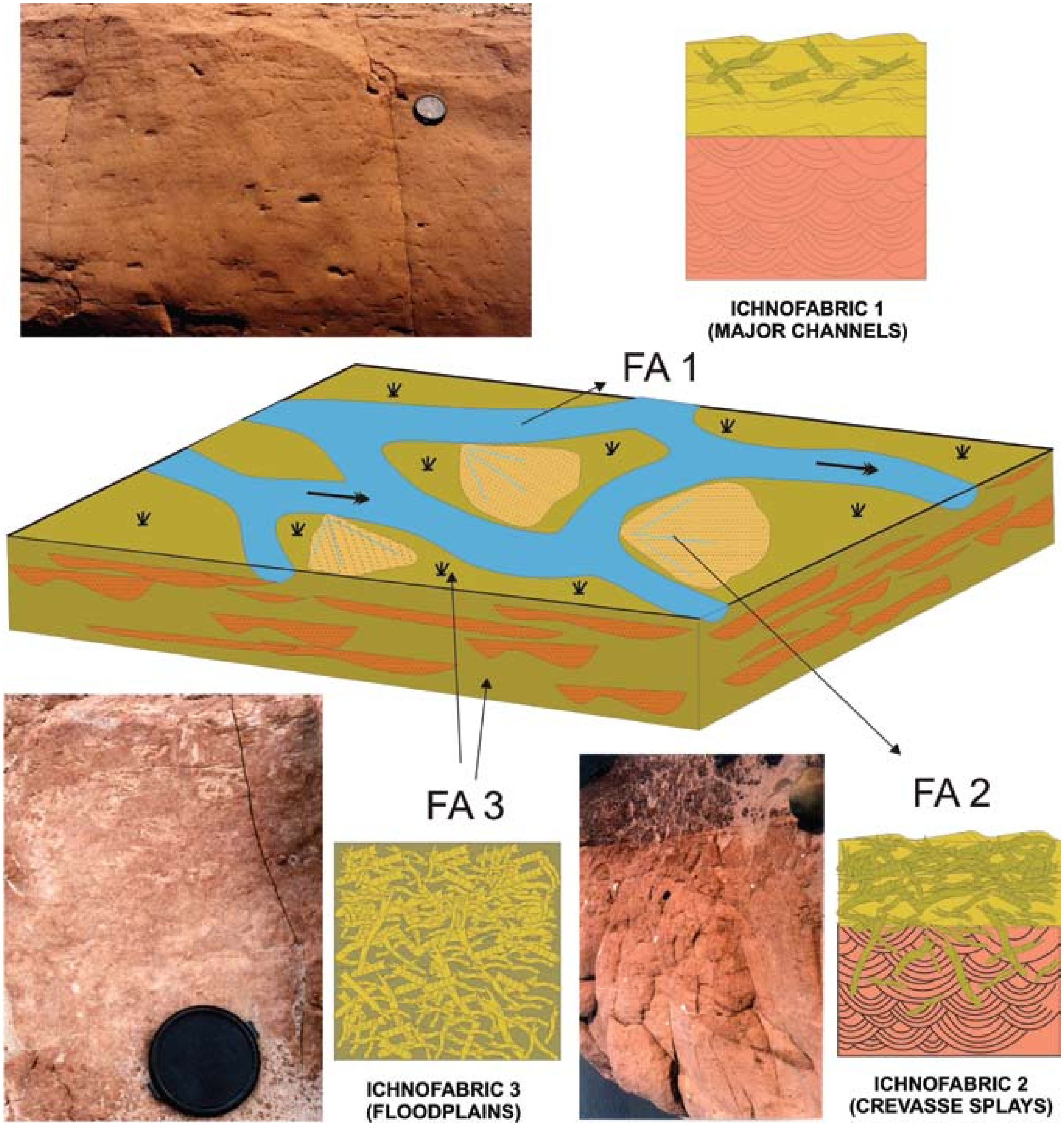


Figure 10.4 Ichnofabric distribution in anastomosed fluvial systems from the Upper Miocene Tariquia Formation of Bolivia (modified from Buatois *et al.*, 2007a).

Trace fossils are more abundant and varied in overbank deposits, particularly where standing bodies of water are established (e.g. Fordyce, 1980; D'Alessandro *et al.*, 1987; Buatois *et al.*, 1997a; Buatois and Mángano, 2002, 2004a; Keighley and Pickerill, 2003). Although in some cases no increase in ichnodiversity is observed, overbank deposits are more intensely bioturbated than their associated channel deposits (Buatois *et al.*, 2007a) (Box 10.1). In many cases, the only trace fossils present in a fluvial succession are found in fine-grained overbank intervals interbedded with unbioturbated, coarser-grained stacked-channel deposits, recording taphonomic and colonization windows (Buatois *et al.*, 1997a).

Maples and Archer (1989) outlined a number of conditions that enhance the preservation potential of biogenic structures in overbank settings, namely: (1) deposition of fine-grained heterogeneous sediment; (2) little or no reworking; and (3) enough time between depositional events to allow colonization, but not so much time that plant colonization obliterates

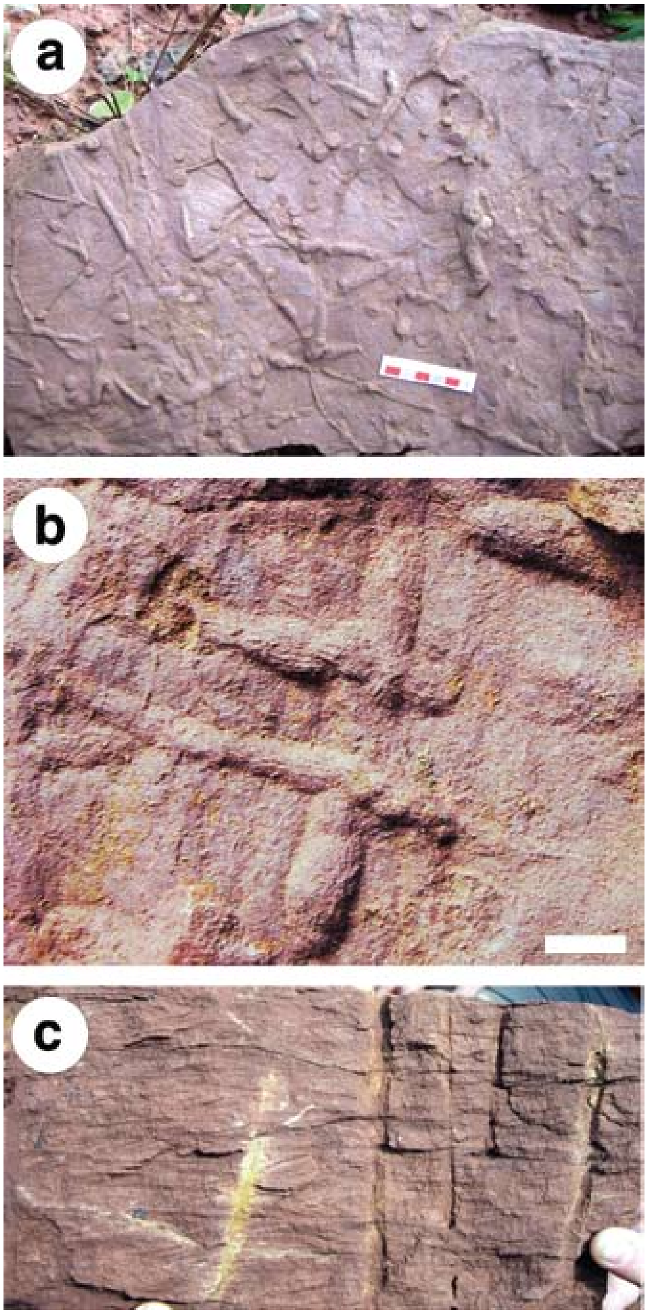


Figure 10.5 Invertebrate and plant trace fossils in crevasse-splay deposits of braided rivers Lower Triassic, Baranów Formation, Baranów Quarry, Holy Cross Mountains, Poland. (a) General view of bedding plane with *Scoyenia gracilis*, displaying both horizontal and vertical components and desiccation cracks. Scale bar is 5 cm. (b) Close-up of *Scoyenia gracilis* with well-developed scratch marks. Scale bar is 1 cm. (c) Vertical root trace fossil. See Bujok *et al.* (2008).

animal traces. These conditions allow the preservation of delicate biogenic structures in protected ponded areas. Buatois and Mángano (2004a, 2007) noted that some overbank ichnofaunas are emplaced in water bodies that have been progressively desiccated (desiccated overbank), while others record subaqueous colonization in water bodies filled by the vertical accretion of overbank deposits without experiencing desiccation (overfilled overbank). These two ichnofaunas commonly display contrasting characteristics and are discussed separately.

Desiccated-overbank deposits contain arthropod trackways (*Diplichnites*, *Protichnites*, *Hexapodichnus*, *Trachomatichnus*), meniscate trace fossils (*Scoyenia*, *Taenidium*, *Beaconites*) (Fig. 10.5a–b), ornamented burrows (*Spongeliomorpha*, *Tambia*), and bilobate trace fossils with scratch marks (*Cruziana*, *Rusophycus*) (e.g. Bromley and Asgaard, 1979; Bracken and Picard, 1984; Squires and Advocate, 1984; D'Alessandro *et al.*, 1987; Debriette and Gand, 1990; Sarkar and Chaudhuri, 1992; Smith, 1993; Kim and Paik, 1997; Gand *et al.*, 1997; Eberth *et al.*, 2000; Savrda *et al.*, 2000; Gierliński *et al.*, 2004; Buatois *et al.*, 2007a; Lucas *et al.*, 2010a). Vertical burrows (*Skolithos*, *Cylindricum*) and insect and arachnid nesting structures may also be present (Figs. 10.1 and 10.2).

Desiccated-overbank deposits commonly contain superbly preserved vertebrate trackways. Late Paleozoic floodplain deposits may host abundant basal amniote trackways including a variety of sauropsids and synapsids (e.g. Smith, 1993). Mesozoic examples are dominated by dinosaur (e.g. theropods, ornithopods, sauropods), amphibian (e.g. temnospondyls), reptile (e.g. archosaurs, lepidosaurs), and bird trackways (e.g. Calafat *et al.*, 1986; Lockley and Conrad, 1989; Fuglewicz *et al.*, 1990; Currie *et al.*, 2003; Gierliński *et al.*, 2004; Gangloff *et al.*, 2004; Foster and Lockley, 2006; Hunt and Lucas, 2006b; Zhang *et al.*, 2006; Smith *et al.*, 2009) (Figs. 10.1 and 10.2). Formation of densely crowded tracked surfaces by chiroteriids and rhychosauroids resulted from a complex taphonomic history in which flooding may have led to the concentration of reptiles on narrow land patches (Fuglewicz *et al.*, 1990) (Fig. 10.6a–d). During low water levels, footprints were impressed on muddy substrate and subsequently cast by sand during the next flooding event. Wide varieties of bird (e.g. ciconiiforms, charadiiforms), reptile (e.g. turtles), and mammal (e.g. artiodactyls, perissodactyls, proboscideans, liptoterns, megatheriids, carnivores,) trackways occur in Cenozoic river-margin deposits (Aramayo and Manera de Bianco, 1996; Mustoe, 2002; Krapovickas *et al.*, 2009).

In addition to trackways, floodplain deposits may contain tetrapod burrows (Fig. 10.1). Permian–Triassic examples were produced by therapsids, such as *Diictodon* (Fig. 10.7a–c), *Trirachodon*, and *Thrinaxodon* (Smith, 1987; Groenewald *et al.*, 2001; Damiani *et al.*, 2003; Sidor *et al.*, 2008), while similar structures in the Neogene are attributed to medium to small mammals, such as the primitive beaver *Paleocastor* (Martin and Bennet, 1977). Helicoidal burrows have been commonly placed in the ichnogenus *Daimonelix*, while other tetrapod burrows have not received formal ichnotaxonomic assignation. Amphibian burrows attributed to the lysorophid *Brachydectes elongates* were produced in Permian pond deposits, probably during episodic droughts (Hembree *et al.*, 2004). Also, the finding of dinosaur skeletal remains in the expanded distal chamber of a burrow suggests that some dinosaurs were able to excavate (Varricchio *et al.*, 2007).

Invertebrate ichnodiversity is low to rarely moderate in desiccated-overbank deposits, but vertebrate trace fossils may be relatively diverse. The degree of bioturbation is highly variable, ranging from low to intense; some floodplain deposits may

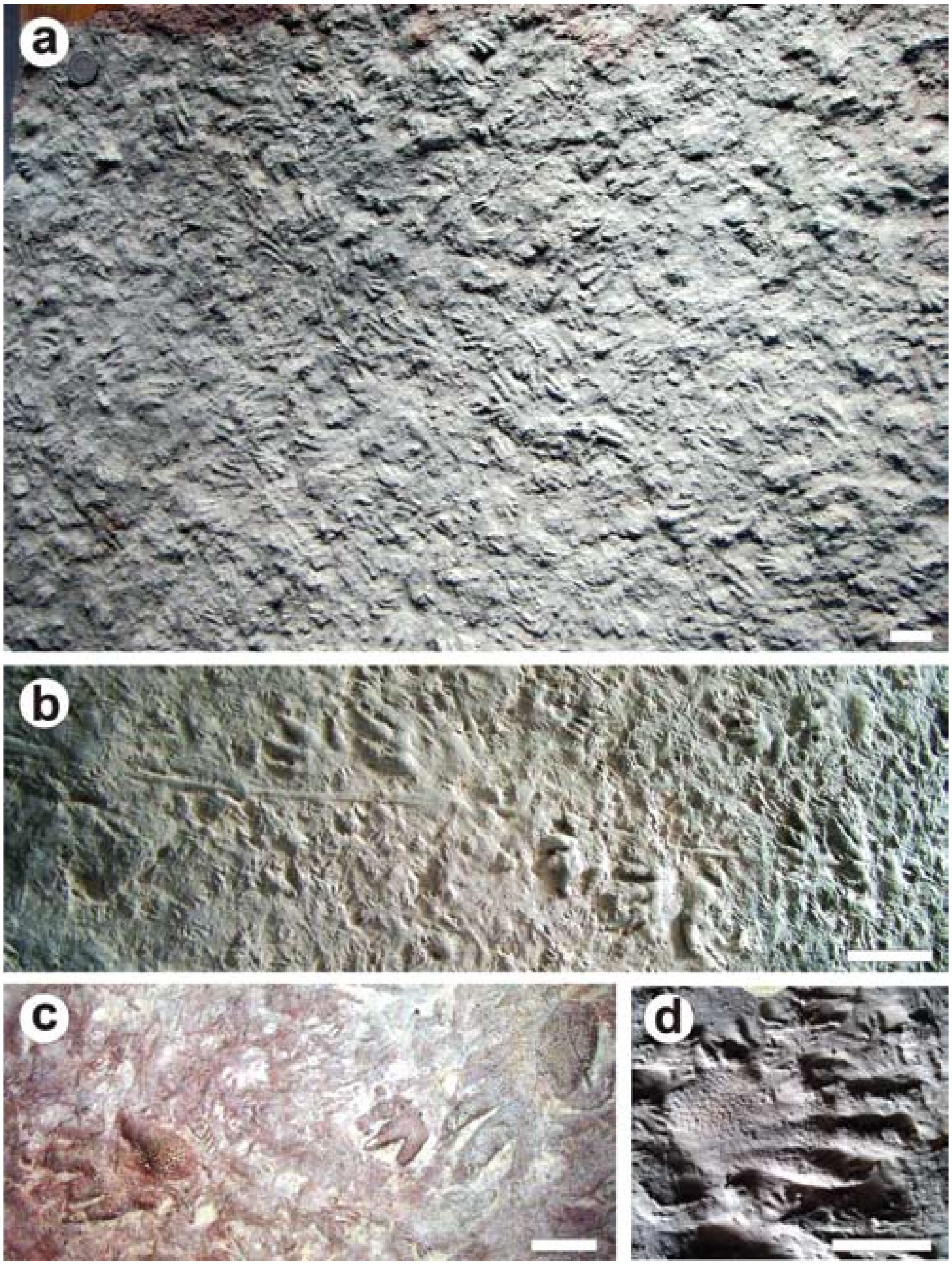


Figure 10.6 Vertebrate trackways in crevasse-splay deposits of braided rivers. Lower Triassic, Wióry Formation, Wióry site, Holy Cross Mountains. (a) General view of a surface having a large density of labyrinthodontid trackways, including both *Isochirotherium* and *Rhynsochauroides*. Scale bar is 10 cm. (b) Surface with *Isochirotherium* (large tracks) and *Rhynsochauroides* (small tracks). Tail marks are associated with *Isochirotherium* tracks. Scale bar is 10 cm. (c) Close-up of *Isochirotherium* trackway. Scale bar is 5 cm. (d) Skin textures preserved in *Isochirotherium* track. Scale bar is 5 cm. See Fuglewicz *et al.* (1990).

be totally bioturbated (e.g. Buatois *et al.*, 2007a). Ichnofossils are associated with physical structures that indicate periodic subaerial exposure (e.g. desiccation cracks, raindrop imprints) (Fig. 10.5a). Root trace fossils occur locally (Fig. 10.5c). Depths of bioturbation up to 2.2 m have been measured for *Taenidium barretti* from colonization surfaces at the top of crevasse-splay sandstones (Buatois *et al.*, 2007a). Deep bioturbation may reveal avoidance of stressful conditions caused by extreme desiccation. Morrissey and Braddy (2004) suggested that the *Beaconites* producer, most likely a myriapod, burrowed to the water table in search of moisture during the dry season. In terms of archetypal ichnofacies, desiccated-overbank suites illustrate the *Scoyenia* ichnofacies (Buatois and Mángano, 2002, 2004a, 2007). With respect to vertebrate ichnofacies, these fluvial deposits contain examples of the so-called *Amphisauropus* sub-ichnocoenosis of the *Batrachichnus* ichnofacies from the Devonian to the Middle Triassic (Hunt and Lucas, 2006a, 2007).

Trace-fossil morphology and burrow-wall characteristics suggest common emplacement in firm substrates (Fig. 10.3). For example, striated walls in *Scoyenia* (Fig. 10.5a–b) and *Spongeliomorpha*, sharp scratch marks in *Tambia*, *Cruziana*, and *Rusophycus* and well-defined appendage imprints in arthropod trackways all indicate a cohesive substrate that has experienced desiccation due to subaerial exposure. This “desiccation suite” commonly cross-cuts an earlier, “pre-desiccation suite”,

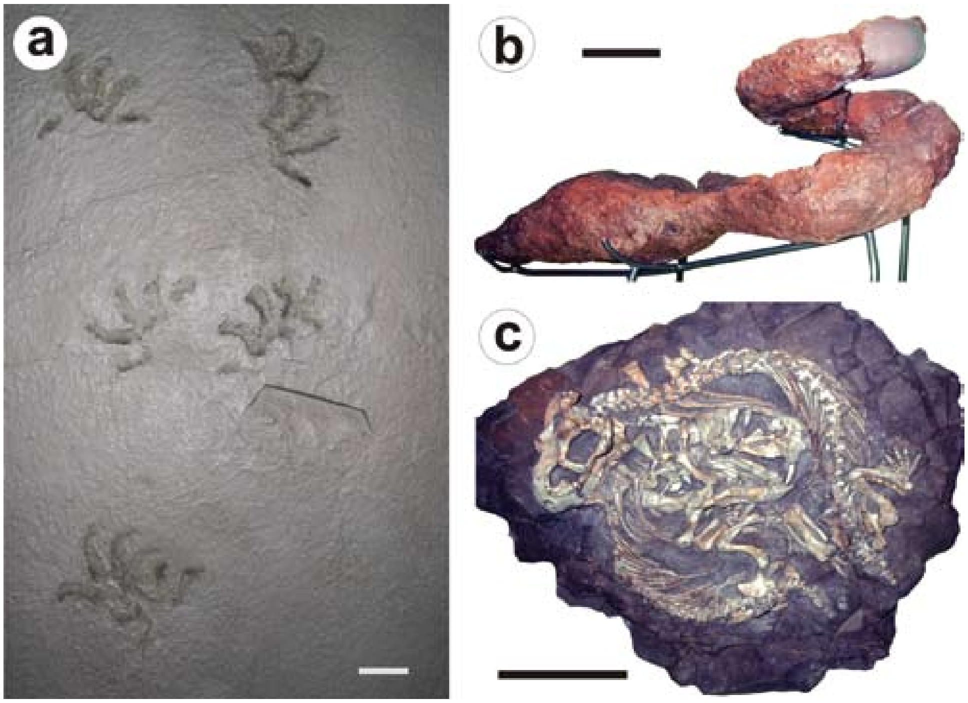


Figure 10.7 The small dicynodont *Diictodon* and its ichnological record. Upper Permian, Teekloof Formation, Beaufort Group, southwestern Karoo basin, South Africa. (a) Trackways formed along the shoreline of a floodplain water body. Scale bar is 3 cm. (b) Sand-filled helicoidal burrows containing at the base a terminal chamber. Scale bar is 10 cm. (c) Articulated skeletons found within the terminal chambers and spirals of burrows. Scale bar is 10 cm. Specimens exhibited at the South African Museum, in Cape Town. See Smith (1987).

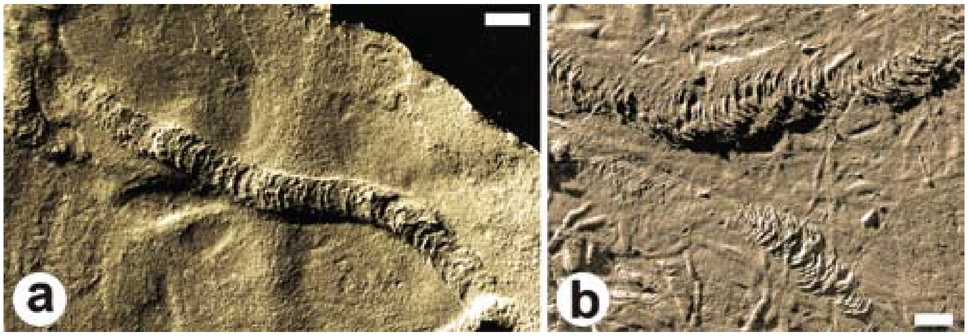


Figure 10.8 Two suites of the *Scoyenia* ichnofacies in desiccated overbank deposits. Lower Permian, La Colina Formation, Los Colorados de Patquia, western Argentina. (a) *Beaconites barretti*. Meniscate backfilled trace fossils lacking striated walls, suggesting emplacement in a softground. (b) Firmground meniscate striated trace fossils cross-cutting the softground suite. See Buatois *et al.* (1996a). Scale bars are 1 cm.

which is typically characterized by meniscate, backfilled structures without ornamentation (e.g. *Taenidium* and *Beaconites*) developed in soft substrates (Buatois *et al*., 1996a; Savrda *et al*., 2000; Buatois and Mángano, 2002, 2004a) (Fig. 10.8a–b). Both suites belong to the *Scoyenia* ichnofacies, which in desiccated-overbank deposits may form palimpsest surfaces or composite ichnofabrics that record taphonomic pathways showing progressive desiccation of floodplain sediments (see Section 6.2). Desiccated-overbank ichnofaunas are common in distal zones (comprising occasionally to infrequently flooded areas) and/or arid to semiarid settings.

Overfilled-overbank deposits contain simple grazing trails (*Helminthopsis*, *Helminthoidichnites*), locomotion trails (*Cochlichnus*), horizontal dwelling burrows (*Palaeophycus*), dwelling burrow systems (*Ctenopholeus*), and bivalve resting (*Lockeia*) and equilibrium (*Calceoformites*) traces (e.g. Turner, 1978; Fordyce, 1980; Miller, 1986; Pollard and Hardy, 1991; Gluszek, 1995; Buatois *et al*., 1997a; Buatois and Mángano, 2002; Keighley and Pickerill, 2003; Uchman *et al*., 2004b; Pieńkowski and Niedźwiedzki, 2009) (Fig. 10.9a–c). Fish trails (*Undichna*) may be preserved in floodplain bodies of water (e.g. Morrissey *et al*., 2004; Wisshak *et al*., 2004). Arthropod and tetrapod trackways, meniscate trace fossils, and bilobate structures with scratch marks are typically absent; where present, they are subordinate elements (Buatois and Mángano, 2002, 2004a, 2007). Ichnodiversity is low to rarely moderate. With rare exceptions (e.g. *Ctenopholeus*), most of the ichnofossils are oriented parallel to the bedding plane, and reflect very shallow-tier emplacement, so intensity of bioturbation is low. Physical structures indicating subaerial exposure are absent, reflecting overbank vertical accretion rather than desiccation of the water body. Root trace fossils may be common in associated waterlogged paleosols (Fig. 10.10a–d).

In these settings, morphological details of the trace fossils are commonly very poorly preserved, suggesting that they were formed in a water-saturated substrate (e.g. Buatois *et al*., 1997a). Overall features of these overbank ichnofaunas indicate subaqueous emplacement (Fig. 10.3). Poorly preserved trace

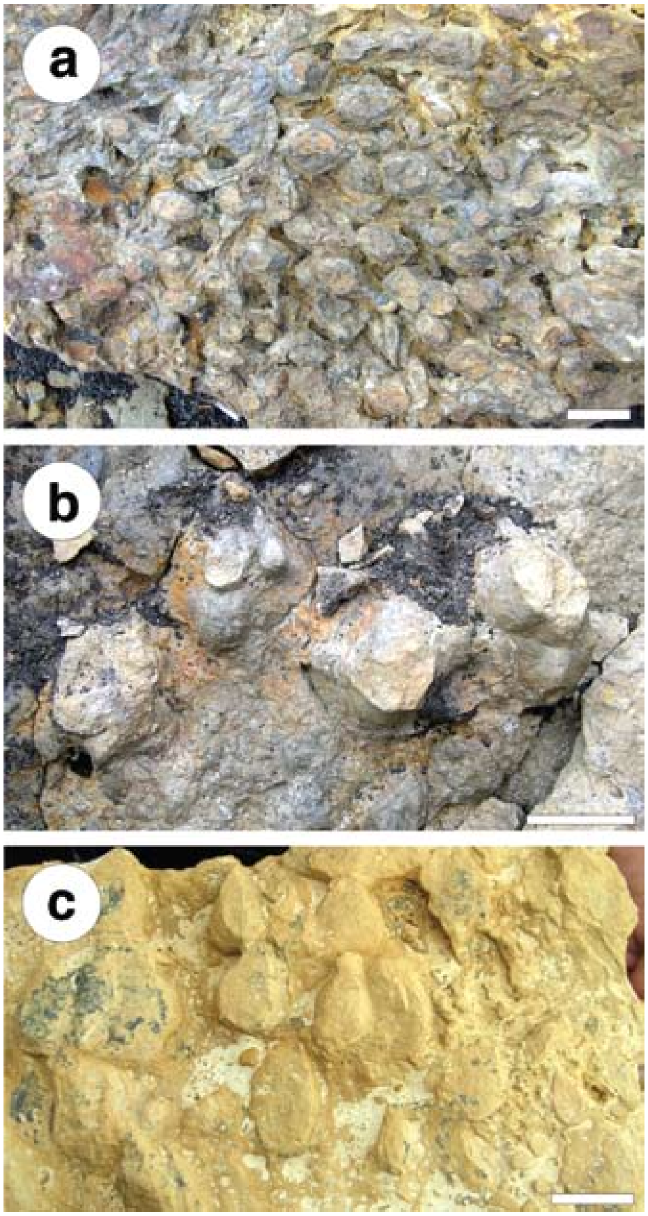


Figure 10.9 Bivalve trace fossils in crevasse-splay deposits of meandering rivers. Lower Jurassic, Zagaje Formation, Sołtyków Nature Reserve, Holy Cross Mountains, Poland. (a) General view of a sandstone base showing high density of the equilibrium structure *Calceoformites uchmani*. Scale bar is 3 cm. (b) Close-up of *Calceoformites uchmani*. Note spreite in the specimen on the right revealing re-positioning of the bivalve in response to sedimentation. Scale bar is 2 cm. (c) The dwelling/resting trace *Lockeia*. Scale bar is 2 cm. See Pieńkowski and Niedźwiedzki (2009).

fossils may be cross-cut by better-defined softground ichnofossils reflecting improving taphonomic conditions due to increasing consolidation of the substrate. In any case, burrow walls are unornamented indicating that substrates never attained firmground stage. These ichnofaunas lack most of the diagnostic features of the *Scoyenia* ichnofacies and are regarded as examples of the impoverished *Mermia* ichnofacies (Buatois and Mángano, 2002, 2004a, 2007). The lower ichnodiversity of the *Mermia* ichnofacies in these overbank deposits in comparison with their equivalents from lakes results from the temporary nature of floodplain bodies of water and their less-stable conditions. Overfilled-overbank ichnofaunas are dominant in the proximal-overbank settings of meandering systems (comprising perennially to frequently inundated wetlands) and/or temperate and humid settings (Buatois and Mángano, 2004a, 2007).

10.3 LAKES

Modern lake systems contain a wide variety of benthic organisms that produce biogenic structures, including annelids (e.g. oligochaetes, leeches), aquatic to semiaquatic insects (e.g. dipterans and coleopterans), crustaceans (e.g. ostracodes), and mollusks (e.g. bivalves, gastropods) (Cohen, 2003; White and Miller, 2008). Some vertebrates, mostly fish, amphibians, and aquatic reptiles, although nektonic, may occasionally interact with the substrate to produce biogenic structures. Biogenic structures emplaced in lacustrine sediments have the highest preservation potential of all continental ichnofossils. Unsurprisingly, recent compilations demonstrated that there is a large volume of literature documenting examples of lacustrine ichnofaunas (Buatois and Mángano, 2007; Minter *et al.*, 2007b). Cohen (2003) listed a number of abiotic and biotic factors that control animal distribution in lakes. Abiotic factors include energy, light, oxygen, temperature, salinity, substrate, and nutrients, while biotic factors, such as competition, grazing, predation, and symbiosis, have complex feedback loops and are difficult to interpret (see also Miller and White, 2007).

Species diversity results from a complex interplay of these different factors. Overall, larger lakes contain more species than small ones, because they are more persistent, encompass a great variety of habitats, and are located closer to centers of species origin (Cohen, 2003). As a general trend, ichnofaunas from large lakes are typically more diverse than those in small lakes or fluvial ponds (Buatois and Mángano, 2007). The density and diversity of benthic fauna usually reach a maximum in the oxygenated sublittoral zone (the concentration zone of Mackie, 2001). In most lakes, this zone occurs between 2 and 4 m deep, but it may as deep as 18 m in large oligotrophic lakes (Mackie, 2001, Martin *et al.*, 2005; White and Miller, 2008).

Taphonomic factors also play a major role in controlling ichnodiversity. The highest preservation potential of biogenic structures is in low-energy areas of lacustrine systems. Low-energy conditions may occur both in the deep zones of the lake, and in shoreline areas in systems that are weakly affected by wave action. In deep-lake environments, alternation of very fine-grained sandstone and mudstone deposited from underflow or turbidity currents promotes the preservation of delicate and tiny surface trails, as well as very shallow trace fossils (Buatois and Mángano, 1995c, 1998, 2007). In low-energy shoreline areas, preservation of biogenic structures commonly results from rapid influx of sand via non-erosive sheet floods (e.g. Zhang *et al.*, 1998; Minter *et al.*, 2007b). Although monospecific trace-fossil assemblages are present, moderately

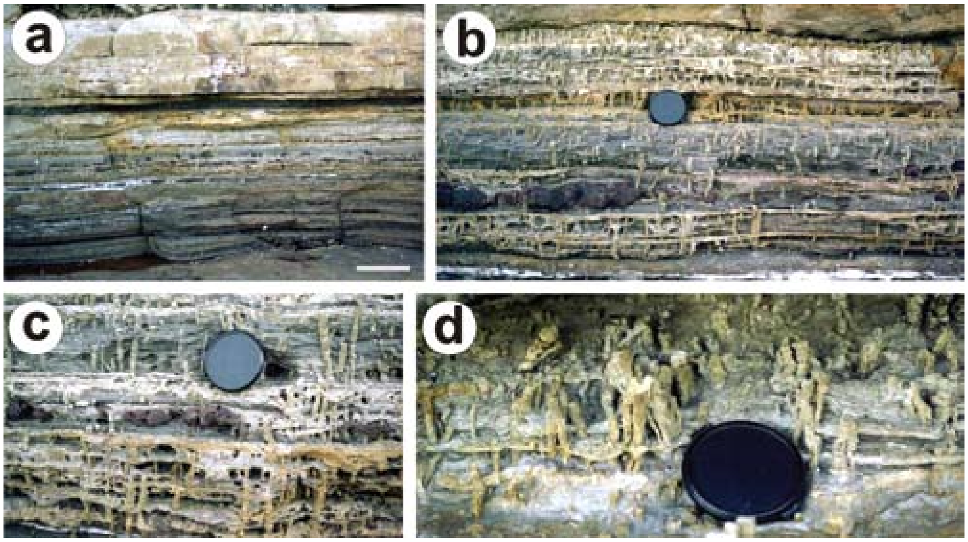


Figure 10.10 Plant trace fossils from floodplain deposits of meandering rivers. Lower Triassic, Newport Formation, St. Michaels Cave, Sydney Basin, eastern Australia. (a) General view of intensely rooted deposits. Scale bar is 50 cm. (b) Close-up showing dominance of vertically oriented root trace fossils. Lens cap is 5.5 cm. (c) and (d) Close-ups of root trace fossils. Note that the root trace fossils are filled with sand, and no carbonaceous wall or infill is present.

Box 10.2 Ichnology Oligocene fluvial-fan-lacustrine systems of Spain

The Ebro Basin of northeastern Spain was characterized by fluvial fans attached to the basin margins grading towards the central-basin areas into hydrologically closed, shallow lakes. Trace fossils have been recorded in one such complex, the Oligocene Solsona–Sanaüja Fluvial Fan and the Noguera Lacustrine System. Bioturbation is absent in the lacustrine deposits, most likely as a reflection of the closed hydrology that may have caused hypersalinity. Fluvial-fan terminal-lobe deposits formed in low wetland areas around the lake contain a moderately diverse trace-fossil assemblage dominated by *Taenidium barretti*, *Cochlichnus anguineus*, and the bird footprint *Gruipeda* isp. Medial fluvial-fan areas include crevasse-splay deposits, which contain most of the ichnotaxa present in the terminal lobes, except for the bird tracks, plus abundant vertical burrows (*Taenidium barretti* and ornamented burrows). The presence of deep-tier traces in this assemblage was linked to the greater relief and lower mean groundwater position in the more proximal fan with respect to the lowland areas. Fluvial-channel deposits only contain irregularly clustered tunnels of unknown affinity formed after abandonment of the channel. The distribution of trace-fossil assemblages was essentially controlled by the position and fluctuations of water tables, which also promoted their composite nature.

Reference: Gibert and Sáez (2009).

diverse ichnofaunas are common in lacustrine deposits. Gore (1989) subdivided lacustrine systems into hydrologically open and hydrologically closed. Buatois and Mángano (1998, 2004a, 2007) used this scheme to frame ichnological observations and, accordingly, this classification is used here.

10.3.1 CLOSED LAKES

Hydrologically closed lakes lack an outlet, and are characterized by high salinity and rapidly fluctuating shorelines (Gore, 1989). As a result, they represent extremely stressful ecosystems, in which faunal diversity is very low. Trace fossils formed under permanent subaqueous conditions are scarce or absent because of hypersalinity (e.g. Price and McCann, 1990; Uchman and Álvaro, 2000). However, moderately diverse ichnofaunas, both produced by invertebrates and vertebrates, may occur at the lake margins, in subaerially exposed littoral to mud-flat environments, recording the activity of terrestrial rather than aquatic faunas (e.g. Zhang *et al.*, 1998; Minter *et al.*, 2007b; Scott *et al.*, 2007b; Gibert and Sáez, 2009) (Boxes 10.2 and 10.3) (Fig. 10.11). Species diversity increase is most evident at the lake margins due to rising lake levels and the associated decrease in salinity, while low diversity levels are maintained in the central part of the lake due to continuous accumulation of saline groundwater and chemical stratification (Cohen, 2003). Ichnofaunas from hydrologically closed lakes mostly consist of plant traces, arthropod trackways (*Diplichnites*, *Umfolozia*, *Lithographus*), meniscate trace fossils (*Scoyenia*, *Taenidium*), bilobate structures (*Cruziana*, *Rusophycus*), chironomid, coleopteran, and annelid dwelling and feeding traces (*Fuersichnus*, *Labyrintichnus*, and *Beaconites filiformis*), and vertebrate traces (e.g. Bromley and Asgaard, 1979; Gierlowski-Kordesch, 1991; Dam and Stemmerik, 1994; Kozur and Lemone, 1995; Rodríguez-Aranda and Calvo, 1998; Zhang *et al.*, 1998; Clemmensen *et al.*, 1998; Uchman and Álvaro, 2000; Schlirf *et al.*, 2001; Lucas *et al.*, 2002; Melchor and Sarjeant, 2004; Minter *et al.*, 2007b; Scott *et al.*, 2007b). Chironomid (Diptera) larvae are highly tolerant to saline conditions, and are regarded

Box 10.3 Ichnology of Triassic lacustrine deposits of western Argentina

Spectacular outcrops of the continental Middle to Upper Triassic Agua de la Peña Group of the Ischigualasto-Villa Unión Basin of western Argentina allow careful analysis of trace-fossil distribution in lacustrine systems of contrasting characteristics. The Chañares Formation and the lowermost part of the Ischichuca Formation represent deposition in mildly saline to playa lakes surrounded by mud flats. Tetrapod trackways occur in the mud-flat deposits associated with desiccation cracks. These units reveal the stressful conditions dominant in hydrologically closed lakes, but also highlight the potential for trackway preservation in lake-margin areas. However, most of the Ischichuca Formation represents deposition in alternating shallow- and deep-water conditions, fluctuating from hydrologically open to closed. Lacustrine strata are stacked forming coarsening-upward parasequences due to progradation of wave- and river-dominated deltas. Offshore underflow current deposits do not contain trace fossils, most likely as a result of anoxia in the hypolimnion of freshwater stratified lakes. However, delta-plain channel deposits contain escape trace fossils, recording rapid sedimentation in a river-dominated context. Lower delta-plain deposits contain a moderately diverse ichnofauna dominated by locomotion trace fossils (*Cruziana problematica*, *Undichna britannica*, *Diplichnites* isp., *Stiaria* isp.), together with resting (*Rusophycus stromnessi*) and grazing (*Cochlichnus anguineus*) trace fossils. The pattern of trace-fossil distribution in the succession reveals the complex interplay of environmental conditions in lakes of fluctuating hydrological regime. The most diverse ichnological record is present in the Los Rastros Formation, with coarsening-upward parasequences as a result of deltaic progradation. Upper delta-plain deposits contain simple dwelling trace fossils (e.g. *Palaeophycus striatus*) and vertebrate trackways (*Rhynchosauroides* isp.). Upper delta-front to lower delta-plain deposits are sparsely bioturbated and only contain a few ichnotaxa, mostly dwelling trace fossils (*Palaeophycus tubularis*, *Skolithos* isp.), although *Cochlichnus anguineus* is also present. Some of the delta-front trace fossils are present in hummocky cross-stratified sandstone, recording opportunistic colonization after storm events. Middle delta-front deposits display a relatively diverse association dominated by simple grazing trails (*Helminthoidichnites tenuis*, *Helminthopsis abeli*, *Gordia indianaensis*, *Archaeonassa fossulata*, *Cochlichnus anguineus*), with fish locomotion trails (*Undichna britannica*) and simple facies-crossing dwelling trace fossils (*Palaeophycus tubularis*) as subordinate components. Underflow-current deposits of the distal delta front are the most diverse in terms of trace-fossil content, hosting a wide variety of simple grazing trails (*Helminthoidichnites tenuis*, *Gordia marina*, *Archaeonassa fossulata*, *Cochlichnus anguineus*) and fish trails (*Undichna britannica*, *U. bina*, *U.* cf. *insolentia*), with subordinate occurrences of feeding structures (*Treptichnus pollardi*), horizontal dwelling structures (*Palaeophycus tubularis*), and arthropod trails (*Cruziana problematica*, *Diplopodichnus biformis*, *Didymaulichnus lyelli*), resting traces (*Rusophycus stromnessi*, *Avolatichnium* isp.) and trackways (*Bifurculapes* isp., *Diplichnites* isp., *Protichnites* isp.). The Los Rastros Formation is an excellent example illustrating patterns of trace-fossil distribution in a hydrologically open lake affected by wave-dominated deltaic progradation.

References: Melchor (2001, 2004, 2007); Melchor *et al.* (2003).

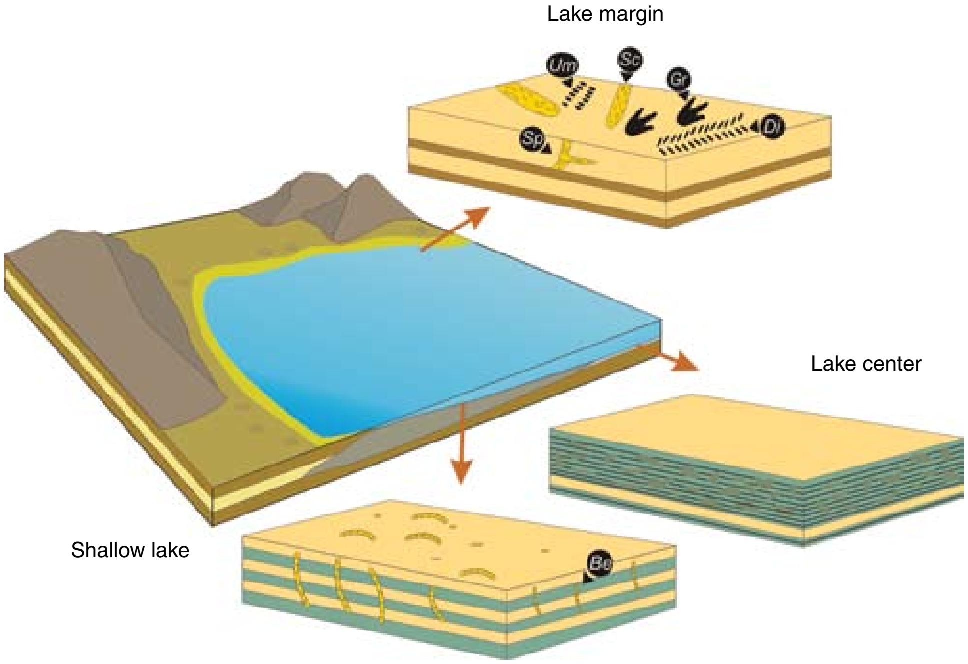


Figure 10.11 Schematic reconstruction of trace-fossil distribution in hydrologically closed lakes. Composition of vertebrate ichnofaunas is highly variable according to geological age. This type of lake typically displays sparse bioturbation, particularly in subaqueous settings. Lake-margin deposits tend to have the highest diversity and density of trace fossils, including the striated burrow system *Spongeliomorpha* (*Sp*), the striated meniscate trace fossil *Scoyenia* (*Sc*), arthropod trackways, such as *Umfolozia* (*Um*) and *Diplichnites* (*Di*), and a wide variety of vertebrate trackways, such as *Grallator* (*Gr*) in Mesozoic examples. The salinity-tolerant ichnotaxon *Beaconites filiformis* (*Be*) may be present in shallow-lake areas, while lake-center deposits are commonly unburrowed or may show local bioturbation in gypsum deposits. Desiccation cracks, and vertebrate and invertebrate trace fossils not to scale.

as the producer of *Beaconites filiformis* in saline lacustrine deposits (Uchman and Álvaro, 2000). However, large meniscate trace fossils filled with gypsum and micrite may occur in relatively high densities in some saline lake deposits (Rodríguez-Aranda and Calvo, 1998; Ortí *et al*., 2003).

Basal amniote trace fossils, particularly sauropsid trackways (*Erpetopus*, *Dromopus*, *Varanopus*, *Hyloidichnus*) and, to a lesser extent, "amphibian" trackways (*Amphisauropus*) may be particularly common in late Paleozoic ephemeral lake deposits (Haubold and Lucas, 2003; Melchor and Sarjeant, 2004; Minter *et al*., 2007b) (Fig. 10.11). Mesozoic vertebrate tracksites are typically dominated by dinosaur trackways, which have high preservation potential around ephemeral- and playa-lake environments (Lockley and Hunt, 1995). The theropod ichnogenera *Eubrontes*, *Anchisauripus*, *Grallator* are typical components (e.g. Lockley and Hunt, 1995; Getty, 2005). Cenozoic lake margins of closed lakes may contain abundant bird and mammal tracks (e.g. Scrivner and Bottjer, 1986; Cohen *et al*., 1991, 1993; Lockley and Hunt, 1995; Lockley and Meyer, 2000; Lucas *et al*., 2002).

Associated physical structures (e.g. desiccation cracks, raindrop imprints) indicate subaerial exposure. Under appropriate taphonomic conditions, omission surfaces totally covered by trackways may be preserved (Zhang *et al*., 1998) (Fig. 10.12a–b). Due to the progressive desiccation of the substrate, better-defined trackways emplaced in compacted sediment commonly cross-cut those with less-defined imprints that were formed in less-firm substrates (Uchman and Álvaro, 2000; Buatois and Mángano, 2004a, 2007; Scott *et al*., 2009).

The distribution and preservation of biogenic structures in saline lakes is controlled by a series of factors, some of which are related to the evolved fluid compositions resulting from evaporation (Cohen *et al*., 1991; Scott *et al*., 2010), and in many saline lakes, by the presence of thermal springs (Scott *et al*., 2007a, b). Relatively fresh areas of lake margins, such as springs and ephemeral streams, favor the concentration of many species of insects, mammals, birds, and reptiles that may contribute to the ichnological record. In addition, local development of microbial mats, associated with hypersaline conditions and/or hot springs, may favor burrowing by certain insects (e.g. staphylinid, heterocerid beetles). In turn, matgrounds help to stabilize the substrate or contribute to its early cementation, increasing the preservation potential of biogenic structures produced by both vertebrates and invertebrates (Scott *et al*., 2007b). Lake-margin trace-fossil assemblages of closed lakes are typical examples of the *Scoyenia* ichnofacies. No examples of the *Mermia* ichnofacies have been documented in closed-lake deposits. In terms of vertebrate ichnofacies, lake-margin trackway suites commonly belong to the *Grallator* ichnofacies from the Late Triassic to the Recent (Hunt and Lucas, 2007).

10.3.2 OPEN LAKES

Hydrologically open lakes have an outlet, and are characterized by low salinity and relatively stable shorelines (Gore, 1989). Accordingly, they represent less stressful ecosystems than closed lakes. Open lakes contain more varied ichnofaunas, and a distinction can be made between those established along the lake margin and those formed subaqueously further into the lake (Buatois and Mángano, 2004a, 2007) (Fig. 10.13; Box 10.3).

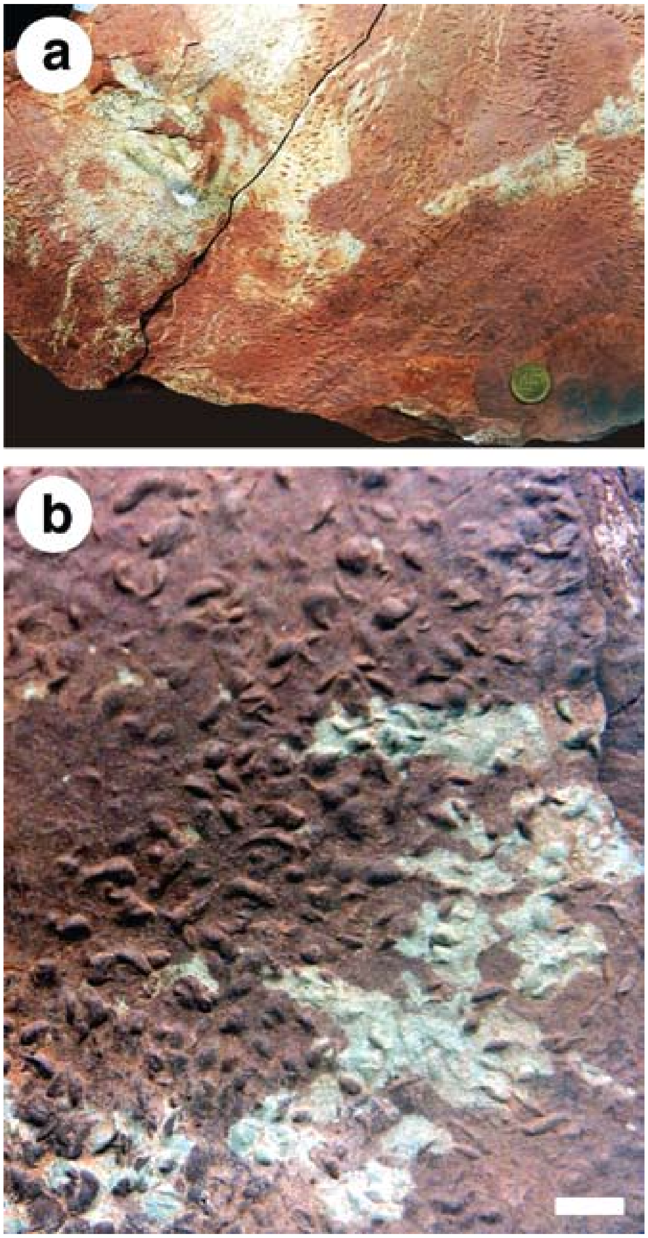


Figure 10.12 Trackway overlap in marginal deposits of playa lakes. Lower Permian, Patquía Formation, Bordo Atravesado, western Argentina. See Zhang *et al*. (1998). (a) General view of a sandstone top exhibiting high density of arthropod trackways. Coin is 1.6 cm. (b) Close-up of the tracked surface. Scale bar is 1 cm.

Lake-margin ichnofaunas of hydrologically open lakes can be in turn subdivided into two main environmental settings: those of protected, low-energy sites under weak wave action and those in comparatively higher-energy environments either due to wave action or influence of distributary channels. Low-energy

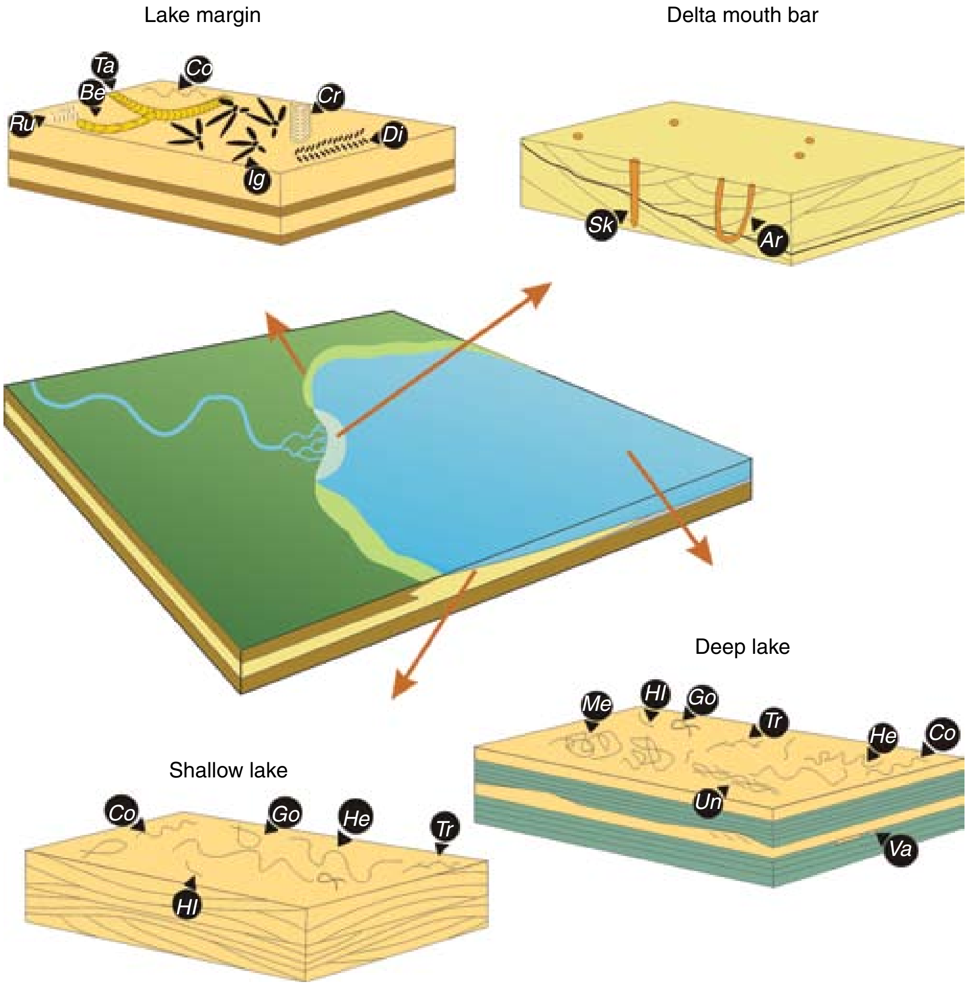


Figure 10.13 Schematic reconstruction of trace-fossil distribution in hydrologically open lakes. Composition of vertebrate ichnofaunas is highly variable according to geological age. This type of lake typically contains more diverse ichnofaunas. Protected lake-margin deposits are characterized by meniscate trace fossils, namely *Beaconites* (*Be*) and *Taenidium* (*Ta*), bilobate trace fossils, such as *Cruziana* (*Cr*) and *Rusophycus* (*Ru*), arthropod trackways, such as *Diplichnites* (*Di*), and the sinusoidal trail *Cochlichnus* (*Co*). Vertebrate trackways are abundant and diverse in the subaerial portion of the lake margin. In particular, shorebird tracks are common, including the ichnogenus *Ignotornis* (*Ig*) in Mesozoic strata. Vertical burrows, including *Skolithos* (*Sk*) and *Arenicolites* (*Ar*), tend to dominate in high-energy shoreline areas, such as mouth bars. Shallow- and deep-lake areas are very similar in taxonomic composition. Both are dominated by grazing trails, such as *Gordia* (*Go*), *Cochlichnus* (*Co*), *Helminthopsis* (*He*), and *Helminthoidichnites* (*Hl*). The simple burrow system *Treptichnus* (*Tr*) is also common. The grazing trail *Mermia* (*Me*) and the fish trail *Undichna* (*Un*) are more common in deep-lake deposits. *Vagorichnus* (*Va*) may occur in deep-lake turbidites. Vertebrate and invertebrate trace fossils not to scale.

conditions tend to predominate in sheltered shorelines or in small lakes. Ichnofaunas from low-energy lake margins consist of meniscate trace fossils (*Scoyenia*, *Taenidium*), arthropod trackways (e.g. *Diplichnites*, *Kouphichnium*), simple horizontal burrows (*Palaeophycus*), bivalve resting structures (*Lockeia*), and bilobate trails (*Cruziana*, *Rusophycus*) (e.g. Daley, 1968; Pollard *et al*., 1982; Smith *et al*., 1982; Pollard and Walker, 1984; Walker, 1985; Cook and Bann, 2000; Hester and Lucas, 2001; Kim *et al*., 2005; Lucas and Lerner, 2006; Lucas *et al*., 2006b). Associations dominated by *Lockeia* seem to be common in carbonate lake shorelines (Lucas *et al*., 2010a).

Vertebrate trackways are also extremely common in low-energy marginal-lake deposits, including traces produced by amphibians, reptiles, dinosaurs, mammals, and birds (e.g. Olsen *et al*., 1978; Alonso, 1985; Lockley *et al*., 1986; Lim *et al*., 1989; Prince and Lockley, 1989; Abbassi and Lockley, 2004; Kim *et al*., 2006; Lockley *et al*., 2006). Shorebird tracks are particularly common in lake-margin deposits, with *Ignotornis*, *Jindongornipes*, *Koreanaornis*, and *Aquatilavipes* the most commonly ichnogenera preserved (Fig. 10.13). In fact, dinosaur and bird tracks have been used to recognize paleoshorelines in lacustrine successions; tracked horizons typically occur at the top of shallowing-upward successions (e.g. Olsen *et al*., 1978; Alonso, 1985; Lockley *et al*., 1986; Prince and Lockley, 1989). Multiple horizons with dinosaur tracks allowed delineation of cycles of expansion and contraction of the water body (Lockley, 1986, 1989). Fossil human footprints have also been documented in lake-margin deposits (Zavala *et al*., 1992; Bayón and Politis, 1996). Other vertebrate trace fossils include lungfish burrows, which may have served as aestivation chambers and breeding tunnels (e.g. Gobetz *et al*., 2006).

Even freshwater, open lakes can experience periods of relatively low lake levels, with exposure of littoral deposits and desiccation of lake-margin areas. Accordingly, trace fossils are commonly associated with physical structures that indicate subaerial exposure. These ichnofaunas are examples of the *Scoyenia* ichnofacies, which occurs in low-energy, lake-margin areas, and records adaptations of a benthos to either very slightly submerged sediments that are periodically desiccated or to waterside subaerial substrates that are periodically submerged (Frey and Pemberton, 1987). Because of desiccation of lake-margin deposits, firmground ichnofaunas dominated by striated meniscate trace fossils (*Scoyenia*) and burrow galleries (*Spongeliomorpha*) may be present (e.g. Metz, 1993). Bioerosion

Figure 10.14 Vertebrate trace fossils in lacustrine deposits. Upper Carboniferous, Radnice Member, Kladno Formation, Bohemia, Czech Republic. See Turek (1989). (a) The fish trail *Undichna britannica*. (b) The amphibian trackway *Gracilichnium* (?) *chlupaci*. Scale bars are 1 cm.

in stromatolites has been recorded also, but it is relatively rare (Ekdale *et al*., 1989). Vertebrate ichnofacies in these low-energy shorelines typically represent the *Grallator* ichnofacies from the Late Triassic to the Recent (Hunt and Lucas, 2007).

Moderate- to high-energy conditions are more common in large lakes affected by strong waves or near the mouth of distributary channels. These zones are characterized by strong turbulence and a mobile substrate, complicating colonization by the macrobenthos (Cohen, 2003). The ichnofauna of these lakes is dominated by simple vertical burrows (*Skolithos*), U-shaped vertical burrows (*Arenicolites*), and escape structures (e.g. Mángano *et al*., 1994; Melchor *et al*., 2003; Buatois and Mángano, 1998, 2004a, 2007) (Fig. 10.13). These trace-fossil assemblages show affinities with the *Skolithos* ichnofacies (Buatois and Mángano, 1998, 2004a; Melchor *et al*., 2003) (see Section 10.2.1). Overall, ichnofaunas dominated by vertical burrows are less common than the typical lake-margin *Scoyenia* assemblages.

The subaqueous zones of hydrologically open lakes are characterized by low energy and relative environmental stability. The most important controls on trace-fossil distribution in these areas are oxygen content, energy, food supply, and substrate (Buatois and Mángano, 2007). Oxygenation is a first-order limiting factor because in lakes with thermal stratification, the hypolimnion becomes anoxic/dysoxic and bioturbation is commonly suppressed. Turbidity and underflow currents may provide oxygen to lake bottoms, favoring the establishment of benthic faunas. In addition, episodic or sustained flows help to increase food supply by transporting organic detritus from adjacent alluvial plains and lacustrine-shoreline areas. On the other hand, in areas strongly affected by high-energy sediment gravity flows, bioturbation may be inhibited. The degree of consolidation of the substrate also plays a role because trace-fossil preservation is precluded in soupy substrates.

Feeding (*Treptichnus*, *Vagorichnus*, and *Tuberculichnus*) and grazing traces (e.g. *Mermia*, *Gordia*, *Helminthopsis*, and *Helminthoidichnites*) of detritus and deposit feeders are commonly dominant in subaqueous zones of open lakes (Fig. 10.13), most commonly in siliciclastic (e.g. Walter, 1985; Pickerill, 1992; Buatois and Mángano, 1993a; Miller *et al*., 1991; Buatois *et al*., 1996b; Walter and Suhr, 1998; Melchor *et al*., 2003; Melchor, 2004), but also in carbonate deposits (e.g. Buatois *et al*., 2000; Gibert *et al*., 2000). Although arthropod trackways may occur, they are comparatively rare. Vertebrate trace fossils are represented by the fish trail *Undichna* and the amphibian trackways *Lunichnium* and *Gracilichnium* (Higgs, 1988; Turek, 1989; Gibert *et al*., 1999; Trewin, 2000; Minter and Braddy, 2006b) (Figs. 10.13 and 10.14a–b).

Pleistocene varves seem to contain a very distinctive ichnofauna (e.g. Gibbard and Stuart, 1974; Gibbard, 1977; Gibbard and Dreimanis, 1978; Walter and Suhr, 1998; Gaigalas and Uchman, 2004; Uchman *et al*., 2009; Benner *et al*., 2009; Knecht *et al*., 2009). Glacial varves contain not only simple grazing trails (e.g. *Gordia*, *Cochlichnus*, and *Helminthoidichnites*) and fish traces (e.g. *Undichna*, *Pisichnus*, and *Broomichnium*), but also arthropod trackways (e.g. *Glacichnium* and *Warvichnium*).

Ichnological evidence is useful to distinguish between deposits from sustained density underflows and episodic turbidity currents (Buatois and Mángano, 1998, 2004). Both processes commonly operate in open lakes and are difficult to differentiate based on physical sedimentary structures alone. As discussed by Pharo and Carmack (1979), turbidites are deposited by episodic currents that involve redeposition of sediment initially emplaced under unstable conditions, while underflow currents are relatively continuous and represent the uninterrupted transport of river-borne sediment into the lake. Turbidites commonly display ichnofossils at the top of layers or, more rarely, at the base of layers. In both cases, the trace-fossil suite records colonization of opportunistic organisms after episodic emplacement of the event bed (Buatois and Mángano, 1998) (Fig. 10.15). Where preserved at the base, a post-depositional origin is indicated by the presence of trace fossils cross-cutting inorganic sole marks (e.g. Buatois *et al*., 1996b). Almost invariably pre-depositional suites are more diverse than post-depositional suites. Underflow-current deposits contain distinctive suites of ichnofossils in each lamina or lamina set (e.g. Buatois and Mángano, 1993a; 1998; Melchor *et al*., 2003), reflecting that they were produced contemporaneously with sedimentation, rather than after a major break in deposition as is typical of turbidites (Fig. 10.16).

Trace fossils also help to distinguish between marine and lacustrine turbidites, which are identical in terms of physical sedimentary structures (Buatois and Mángano, 1998, 2004a). Deep-marine turbidites display diverse ichnofaunas dominated by ornate grazing trace fossils and graphoglyptids that reflect highly specialized feeding strategies recorded by the *Nereites* ichnofacies (see Section 4.3.5). In contrast, lacustrine turbidites are characterized by non-specialized grazing and feeding trace fossils (Buatois and Mángano 1998, 2004a) (Fig. 10.17a–e). These

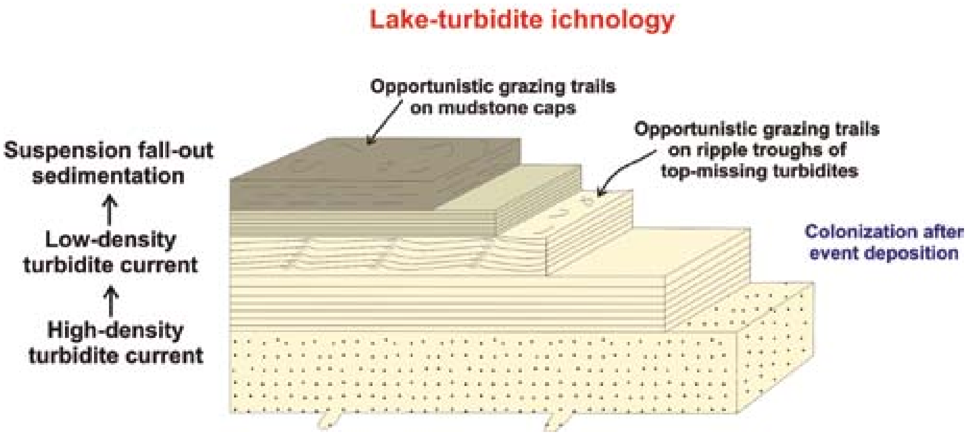


Figure 10.15 Ichnology of lacustrine turbidites. Ichnofossils typically occur at the top of turbidite layers (e.g. simple grazing trails) or, more rarely, at the base of layers (e.g. *Vagorichnus*), recording opportunistic colonization after episodic emplacement of the event bed. Modified from Buatois and Mángano (1998).

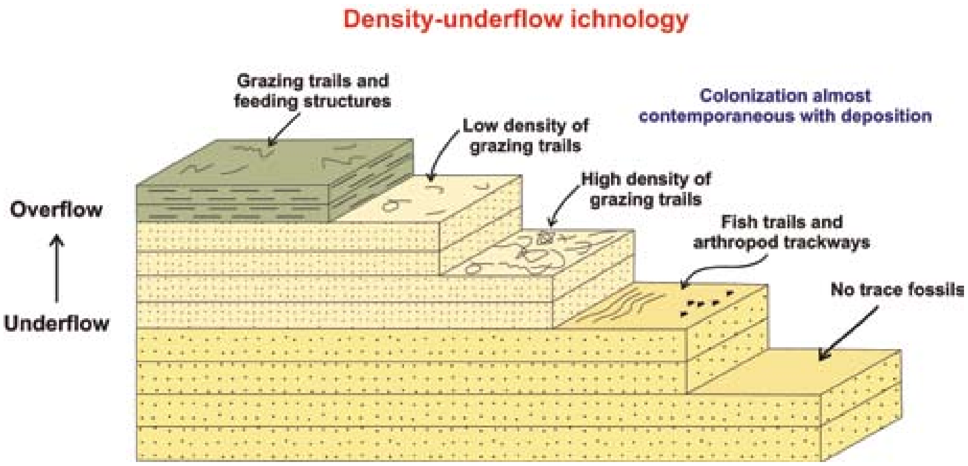


Figure 10.16 Ichnology of underflow-current deposits. These deposits may contain distinctive suites of ichnofossils in each lamina or lamina-set, recording animal activity contemporaneous with sedimentation. Modified from Buatois and Mángano (1998).

non-specialized feeding patterns are illustrated by the ichnogenus *Mermia*, which shows looping and a high level of self-overcrossing, revealing the repeated passage of the tracemaker across the same portion of sediment. Other examples of unsophisticated feeding strategies are the simple grazing trails *Helminthopsis* and *Helminthoidichnites*. Such non-specialized feeding strategies most likely reflect the abundance and accessibility of food in lacustrine systems (Buatois and Mángano, 2004a). The comparatively lower ichnodiversity of lakes in comparison with deep-marine environments results from the more ephemeral nature of the continental bodies of water (Buatois and Mángano, 1998).

Although oxygen-depleted lacustrine sediments are commonly unbioturbated, some organisms have developed adaptations to deal with dysaerobic to anoxic settings (Cohen, 2003). In modern lakes, chironomid larvae construct oxygen-mining burrows similar to *Polykladichnus* and *Thalassinoides* to exploit food in suboxic and anoxic sediment (Gingras *et al.*, 2007). Similar structures have been rarely documented in the fossil record (e.g. Smith *et al.*, 1982).

Permanent subaqueous lacustrine zones of hydrologically open lakes are characterized by the *Mermia* ichnofacies, which extends from shallow to deep areas of the lake (Buatois and Mángano, 1995a, 1998). No archetypal trace-fossil associations can be defined at present to distinguish between shallow-and deep-lacustrine subenvironments. Virtually all of the same assemblages that occur in shallow areas of some lakes (e.g. Pickerill, 1992) occur in the deep areas of others (e.g. Buatois and Mángano, 1993a; Buatois *et al.*, 1996b). Both examples belong to the same archetypal ichnofacies, the *Mermia* ichnofacies. These variations in ichnofossil content from one lake to the other probably reflect the wide variability of lacustrine basins. Although there are no recurrent ichnofacies that distinguish shallow-versus deep-lacustrine subenvironments, zonations can be made at the scale of individual lacustrine basins (e.g. Metz, 1996; Walter and Suhr, 1998; Melchor *et al.*, 2003; Melchor, 2004) (Box 10.3). In general, traces of deposit and detritus feeders dominate in deeper areas of the lake, while suspension-feeder traces may occur in littoral zones, a pattern consistent with distribution of these trophic types in modern lakes (Cohen, 2003).

10.4 DESERTS

Deserts develop in areas where rainfall rarely exceeds evaporation and, as such, impart significant stress on their biotas. In

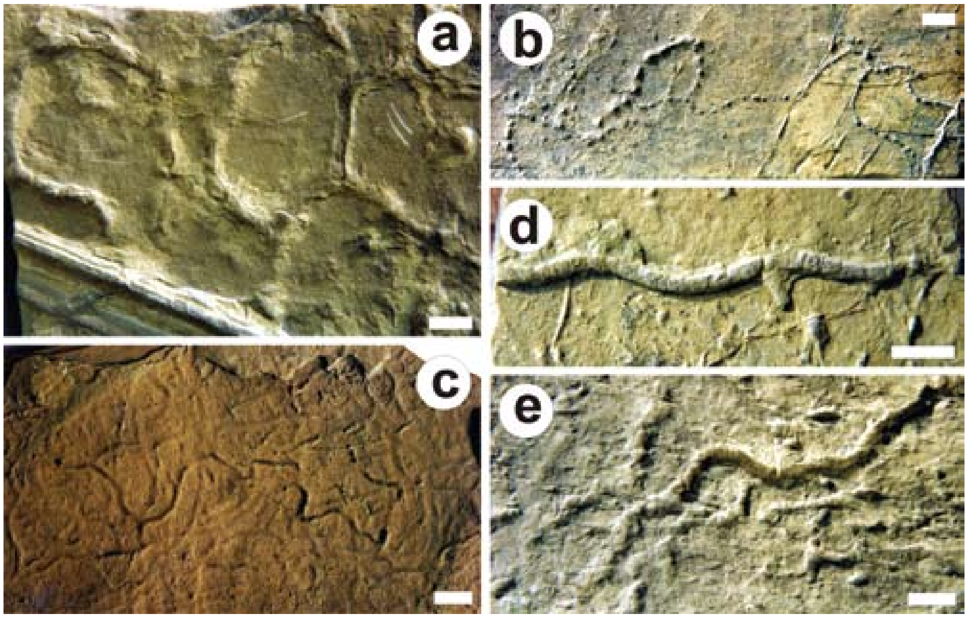


Figure 10.17 Trace fossils preserved at the base of lacustrine turbidites. Lower Jurassic, Anyao Formation, Jiyuan–Yima Basin, central China. (a) *Vagorichnus anyao* cross-cutting sole mark. (b) *Tuberculichnus vagans*. (c) *Paracanthorhaphe togwunia*. (d) *Cochlichnus anguineus*. (e) *Helminthopsis abeli*. Scale bars are 1 cm. See Buatois *et al*. (1996b).

particular, the interaction between rainfall and nutrient availability is essential in controlling desert dynamics and ecology (Whitford, 2002). Episodic events, such as flash floods and wind storms, also have a huge impact in desert ecosystems. Animals inhabiting deserts have a series of adaptive physiological traits and behavioral mechanisms that allow them to maintain a survivable thermal energy balance and water balance (Whitford, 2002). In this regard, the role of benign microclimates within desert areas is of paramount importance.

In contrast with other continental environments, the ichnology of eolian systems is less well understood. However, in recent years there has been a renewed interest in eolian trace fossils (e.g. Fornós *et al*., 2002; Hunt and Lucas, 2007; Ekdale *et al*., 2007; Loope, 2008). Available information derives from both modern environments and some case studies from the fossil record. In modern eolian systems, a moderate diversity of biogenic structures, mostly produced by arthropods (in particular arachnids and insects), has been documented (e.g. Ahlbrandt *et al*., 1978). More specifically, tracemakers in inland dunes and interdune areas include burrowing wasps, crickets, beetles, spiders, scorpions, millipedes, termites, and ants. In the case of coastal eolian dunes, dwelling burrows of the crab *Ocypode quadrata*, producer of *Psilonichnus* in the fossil record, are common (Frey *et al*., 1984a; Curran, 1992, 1994).

Burrowing commonly represents an efficient strategy to escape from the harsh conditions at the surface. In hot deserts most arthropods live underground during the day and leave their burrows at night, while under warmer conditions some may be diurnal (Cloudsey-Thompson, 1991). However, some arthropods (e.g. millipedes, mites) lack morphological and physiological water-conservation adaptations, and are only able to live at the surface after rainfall events (Tevis and Newell, 1962; Whitford, 2002). Termites and ants live mainly in underground nests and galleries that may extend up to 2–3 m below the surface (Whitford, 2002). Burrows not only offer protection from high temperatures and desiccation, but they are also an integral part of the feeding strategies of passive predators, such as spiders, scorpions, and tiger beetle larvae, which prey on different insects and even small vertebrates, adopting a "sit and wait" strategy (Main, 1982; Pearson, 1988; Whitford, 2002). Many insects (e.g. crickets, most beetles) are detritus and deposit feeders that exploit sites of preferential accumulation of wind-blown detritus (Crawford, 1988). Overall, desert ichnofaunas reflect the activity of feeding generalists.

In addition, a number of vertebrates, mostly mammals and reptiles, inhabit desert systems, and may produce biogenic structures. The majority of small mammals (e.g. squirrels, kangaroo rats) live in their own burrows during the day, where they experience more favorable microclimates. Intermediate-size mammals (e.g. rabbits, foxes) either construct their own burrows, or enlarge those constructed by other animals (Whitford, 2002). Reptiles also burrow into the sediment, although their efficient thermoregulatory behavior allows them to experience less stress due to high temperatures (Whitford, 2002). Experiments with sand-swimming snakes (the Kenyan sand boa *Eryx colubrinus*) indicate that these organisms produce a wide variety of biogenic structures (Hembree and Hasiotis, 2007). Amphibians are rare, but they may occur in ephemeral water bodies, which serve as breeding sites (Whitford, 2002). They typically burrow into the sediment to absorb moisture from the soil and avoid the desiccating environment of the surface. Although vegetation is typically sparse to non-existent, plant traces may occur around water bodies.

Ahlbrandt *et al*. (1978) noted that the preservation potential of most eolian biogenic structures is low. Wind erosion is pervasive and detrimental for preservation of plant or animal structures. Most of the traces seen in modern environments occur in the erosional stoss side of dunes and, therefore, have very low preservational potential (Ekdale *et al*., 2007). The presence of temporarily wetted and cohesive substrates, rapid burial, emplacement in the depositional slip phase, lined burrow walls, preferential cementation, and stabilization by biological crusts are among the factors that promote preservation of biogenic structures. In particular, Seilacher (2008) emphasized the importance of microbial participation (bioglues) in the preservation of delicate arthropod and vertebrate trackways in eolian-dune deposits. Animal burrowing removes and disaggregates large volumes of sediment, contributing to its deflation by wind (Whitford and Kay, 1999; Whitford, 2002).

Eolian ichnofaunas typically show low diversity in the fossil record, mainly because of their low preservation potential (Fig. 10.18). In general, trace-fossil diversity is directly linked to the position of the water table and the predominant climatic conditions. In hyper-arid climatic settings, the regional water table lies well below the accumulation surface in most areas of the desert (Mountney, 2004). Under these conditions, dry eolian systems, characterized by large and extensive dunes are formed. Associated dry interdunes are characterized by accelerating airflow and are subject to intense erosion. As a consequence, dunes grow and expand at the expense of the interdune flats (Mountney, 2006). Typically, dry eolian systems are sparsely vegetated at best, and contain few or no trace fossils due to the absence of near-surface moisture. However, trace-fossil suites may occur in grain-flow layers of the dune slip faces, reflecting preferential preservation in damp sand during rainy seasons (Sadler, 1993; Loope, 2006; Ekdale *et al*., 2007).

Under arid climates, wet eolian systems tend to dominate (Mountney, 2004). In these systems the water table or its capillary fringe is in contact with the accumulation surface and, therefore, moisture influences sedimentation (Mountney, 2006). The presence of damp sand restricts sediment availability for transport. Complex patterns of dunes and wet and damp interdunes are common. Vegetated zones may occur along interdunes corridors, leading to the local formation of rooted layers. Elevated water tables result in local concentrations of track, trails, and burrows in interdune settings. In addition, the preservation potential of biogenic structures is enhanced particularly in wet interdunes. Large burrows probably formed by insectivorous vertebrates have been documented on the flanks of actively migrating, compound dunes, in moist sand that most likely formed due to seasonal rainfall (Loope, 2008).

In semiarid climatic settings, large parts of deserts become stabilized (Mountney, 2004). In stabilized eolian systems, vegetation and surface cementation play a major role in accumulation by restricting sediment availability (Mountney, 2006). Due to extended vegetation cover, root traces may be abundant and incipient paleosols may develop. Water tables are typically high, promoting the formation and preservation of invertebrate and vertebrate structures. Rooted and burrowed horizons commonly occur at several stratigraphic levels. These horizons reflect bypass supersurfaces that form where the water table remains static (Mountney, 2004).

Interestingly, Paleozoic and post-Paleozoic eolian ichnofaunas are remarkably different (see Sections 4.5.4 and 14.2.6). Trackways produced by scorpions (*Octopodichnus*, *Paleohelcura*) are particularly common in Paleozoic eolianites (e.g. Brady, 1947; Sadler, 1993; Hunt and Lucas, 2007). Although ichnodiversity may reach moderate levels particularly in post-Paleozoic eolian deposits, many ichnotaxa (e.g. *Arenicolites*, *Palaeophycus*, *Skolithos*) may have been produced by the same burrower (Ekdale *et al*., 2007). During the Permian, the fossil track record is dominated by different ichnospecies of *Chelichnus* (Fig. 10.18), possibly produced by non-mammalian synapsids (McKeever and Haubold, 1996). Mesozoic eolianites contain carnivore dinosaur trackways (e.g. *Grallator*) rather than those produced by herbivore dinosaurs, suggesting that carnivorous dinosaurs fed on smaller carnivores, mammals and invertebrates (Leonardi, 1989; Lockley, 1991). In addition, some of these trackways are of small size, which may indicate dwarfism in response to the harsh conditions of deserts (Leonardi, 1989). In addition to trackways, vertebrate burrows attributed to tritylodontid cynodonts have been recorded in interdune deposits (Fig. 10.18), probably reflecting colonization during periods of high rainfall (Lucas *et al*., 2006c). Preferential preservation of trackways has been noted in certain eolian settings, such as cliff-front coastal echo dunes (Fornós *et al*., 2002). The preservation potential of biogenic structures is enhanced in echo dunes because deflation erosion is reduced against the cliff. Extensively trampled horizons may alternate with intervals preserving the primary sedimentary fabric. Associated biogenic structures include root traces at the margins of dune deposits and horizontal insect galleries similar to the ichnospecies *Gracilichnus sinualis* (Fornós *et al*., 2002).

Eolian dune ichnofaunas are attributed to the recently introduced *Octopodichnus–Entradichnus* ichnofacies (Hunt and Lucas, 2007; Ekdale *et al*., 2007). In terms of vertebrate ichnofacies, they belong to the *Chelichnus* ichnofacies (Hunt and Lucas, 2007). Vegetated dunes may contain the *Coprinisphaera* or the *Celliforma* ichnofacies in connection to incipient paleosols, while the *Scoyenia* ichnofacies typically occur in wet and, less commonly, damp interdunes (Buatois and Mángano, 1996; Genise *et al*., 2000).

10.5 PALEOSOLS

Paleosols represent an important element of alluvial successions and its associated ichnofaunas have received significant attention during the last decade (e.g. Bown and Laza, 1990; Hasiotis *et al*., 1993b; Genise and Bown, 1994b; Smith *et al*., 2008b; Genise *et al*., 2000, 2004b, 2010a) (Box 10.4). The nature of paleosol ichnofaunas is shaped by a number of factors, such as the intensity of soil processes, the position of the water table, climate, the duration of subaerial exposure, and the evolution of bioturbating insects (Genise *et al*., 2000, 2004b). Needless to say, most of these factors are not independent, but are closely interrelated.

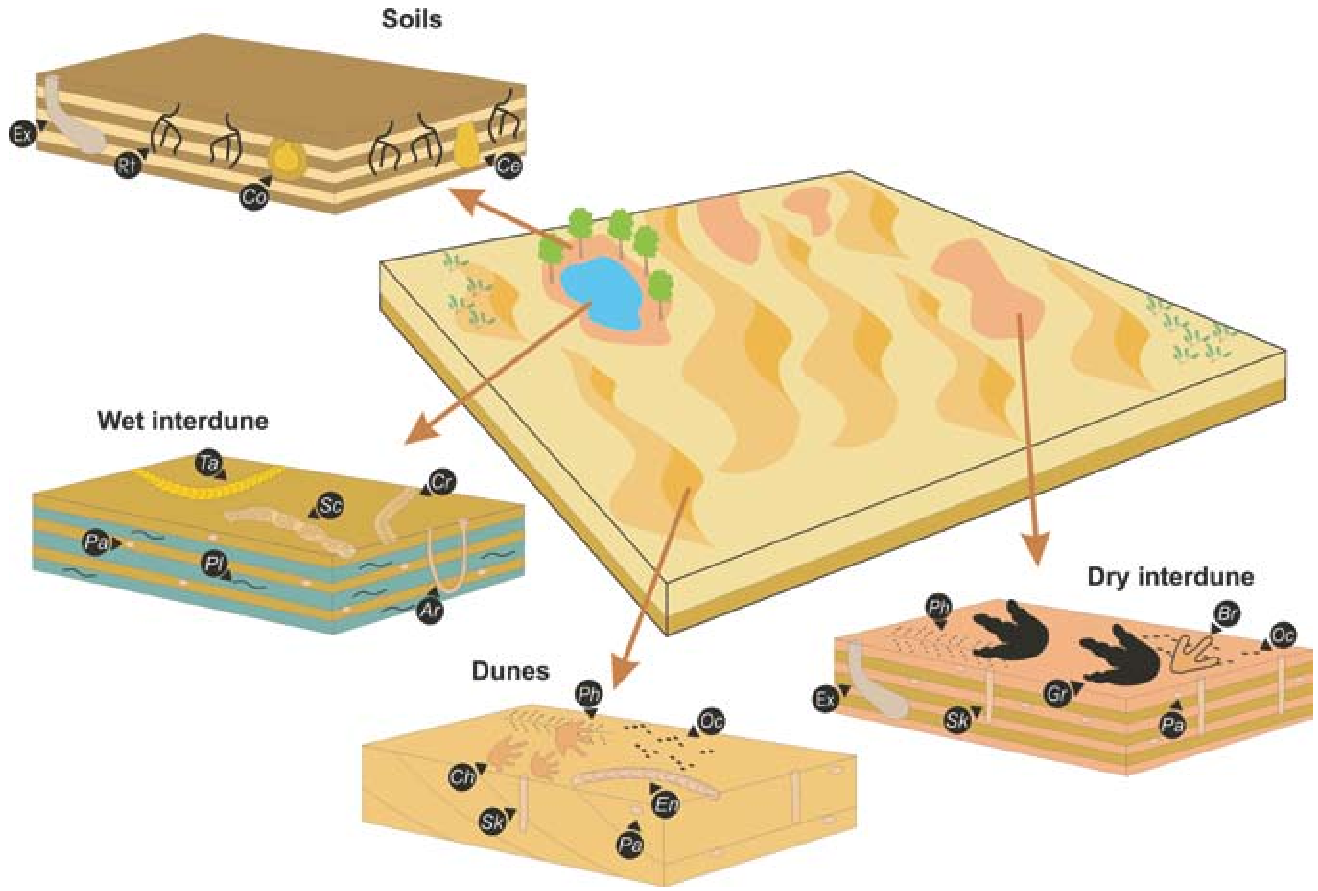


Figure 10.18 Schematic reconstruction of trace-fossil distribution in deserts. Composition of vertebrate ichnofaunas is highly variable according to geological age. Dune areas display a low diversity and density of trace fossils, including scorpion trackways, such as *Octopodichnus* (*Oc*) and *Paleohelcura* (*Ph*), meniscate trace fossils, such as *Entradichnus* (*En*), simple vertical and horizontal burrows, such as *Skolithos* (*Sk*) and *Palaeophycus* (*Pa*), and various vertebrate trackways, including *Chelichnus* (*Ch*) in Permian examples. Dry-interdune deposits commonly contain a few trace fossils, such as *Octopodichnus* (*Oc*), *Paleohelcura* (*Ph*), *Skolithos* (*Sk*), and *Palaeophycus* (*Pa*) and tetrapod excavations (Ex). In Mesozoic assemblages dune and dry-interdune deposits may contain trackways produced by theropod dinosaurs (e.g. *Grallator* (*Ga*)) and synapsids (e.g. *Brasilichnium* (*Br*)). Wet-interdune deposits may contain slightly more diverse ichnofaunas, including the ichnogenera *Taenidium* (*Ta*), *Scoyenia* (*Sc*), *Cruziana* (*Cr*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*) and *Arenicolites* (*Ar*). Some areas may be vegetated with moderate soil development. Trace fossils in these soils may include *Coprinisphaera* (*Co*), *Celliforma* (*Ce*), tetrapod excavations (Ex), and root traces (Rt). Vertebrate and invertebrate trace fossils not to scale.

Box 10.4 Ichnology of Lower-Middle Miocene paleosols of Patagonia, Argentina

Mesozoic and Cenozoic paleosols preserved in Patagonia, southern Argentina, have become a natural laboratory from which some of the most comprehensive studies of terrestrial ichnology have resulted. These studies include the detailed characterization of a large number of ichnotaxa, careful analysis of their producers, and evaluation of the resulting ichnofabrics. In particular, the Lower to Middle Pinturas Formation has been the subject of a number of studies. This pyroclastic unit contains abundant fossil mammals (including platyrrhine primates) and trace fossils of insects and rodents. Analysis of its insect trace fossils has provided valuable information to explain changes in paleoenvironmental conditions during deposition of this unit. Mature paleosols from the lower part of the Pinturas Formation contain the termite nest *Syntermesichnus fontanae*, which is locally associated with the scarabid beetle nest *Coprinisphaera frenguellii*. These paleosols were formed in a marginal habitat between forested areas and more open country. Associated primate body fossils also point towards the presence of nearby forested areas. These mature paleosols alternate with immature ones containing the bee cells *Celliforma rosellii* and *Celliforma pinturensis*, together with *Coprinisphaera frenguellii*. While primate body fossils are absent, skeletons of large herbivorous mammals (e.g. *Astrapotherium* and *Astrapothericulus*) are abundant. Large herbivores most likely provided the dung that was exploited by the scarabid beetles. The presence of burrowing bees is consistent with arid conditions and moderate plant growth. Integration of sedimentological, ichnological, and paleontological evidence suggests that the Pinturas Formation reveals a succession of ash-fall events, deforestation, drying, and establishment of eolian-dune fields, followed by the return of humid conditions, forest development, and the formation of mature paleosols.

References: Bown and Laza (1990); Genise and Bown (1994a).

Soil processes affect the primary sedimentary fabric and may also disrupt biogenic structures. For example, laterization may strongly affect paleosol ichnofabrics, only allowing preservation of insect nests with thick constructed walls (Genise *et al.*, 2004b). In addition, laterization disrupts ichnofabrics by randomly reorienting insect nests. These authors noted that soil features that disrupt the primary fabric of terrestrial deposits are in some cases independent of bioturbation and, therefore, proposed that the pedofabric should be evaluated independently from the ichnofabric (see Section 5.5).

The position of the water table strongly controls the type of trace fossils present in soils (e.g. Hasiotis *et al.*, 1993b; Genise *et al.*, 2004b). While bee and dung beetle nests commonly occur in environments characterized by low water tables, ant and termite nests are present in well-drained to seasonally flooded soils, and earthworms typically burrow in moist substrates, such as gleyed paleosols (Genise *et al.*, 2004b) (see Section 6.1.10). The water table preferences of coleopteran pupal chambers are less understood, although available information indicates that they occur above the water table (Genise *et al.*, 2002). Waterlogged soils are commonly reducing, precluding insect nesting (Retallack, 1990).

Climate ranks as one of the most significant controls in paleosol ichnofaunas, and this is clearly reflected in recently developed models of paleosol ichnofacies (Genise *et al.*, 2000, 2004a, 2010a). As a result, ichnofacies show a close correspondence with the plant formations identified by Mueller-Dombois and Ellenberg (1980). In particular, the *Coprinisphaera* ichnofacies occurs in paleosols developed in paleoecosystems of herbaceous communities, ranging from dry and cold to humid and warm conditions, while the *Termitichnus* ichnofacies is present in paleosols formed in closed forests with plant growth under warm and humid conditions and the *Celliforma* ichnofacies typifies carbonate-rich paleosols (see Sections 4.4.3, 4.4.5, and 4.4.6).

The importance of climate as a limiting factor on paleosol ichnofaunas is due to their overwhelming dominance by insect nests, which contain larvae provisioned with organic matter. Larvae and provisions are strongly sensitive to microclimatic conditions (e.g. moisture and soil temperature) because an excess of moisture inside cells leads to decay of provisions and insufficient moisture is conducive to larval dehydration (see Section 6.1.9). Overall, dung beetles, bees and, to a lesser extent, ants nest in bare soil exposed to sun rather than in humid tropical areas (Batra, 1984; Michener, 1979; Genise and Bown, 1994a). In contrast, most termite nests typically characterize more humid soils (Grassé, 1984). Some termites (e.g. Macrotermitinae), however, exhibit a wider range and are able to live from tropical rain forests to semiarid steppes.

Duration of subaerial exposure strongly impacts soil maturity and trace-fossil diversity. Extended periods of subaerial exposure are commonly associated with mature soils that contain abundant and diverse insect nests. Termite colony growth by apposition of chambers and contemporaneous formation of new colonies reflect long periods of subaerial exposure (Genise and Bown, 1994b). In contrast, nests of solitary insects require shorter periods of subaerial exposure. Finally, soils formed around water bodies or in swamps lack insect nests and contain only root traces.

11 Ichnology of carbonate environments, rocky shorelines, and volcanic terrains

> The pillars are forty-two feet in height; their surface is smooth and uninjured to the height of about twelve feet above their pedestals. Above this, is a zone, twelve feet in height, where the marble has been pierced by a species of marine perforating bivalve – *Lithodomus*, Cuv. The holes of these animals are pear-shaped, the external opening being minute, and gradually increasing downwards. At the bottom of the cavities, many shells are still found, notwithstanding the great numbers that have been taken by the visitors. The perforations are so considerable in depth and size, that they manifest a long continued abode of the Lithodomi in the columns; for, as the inhabitant grows older and increases in size, it bores a larger cavity, to correspond with the increasing magnitude of its shell. We must, consequently, infer a long continued immersion of the pillars in sea-water, at a time when the lower part was covered up and protected by strata of tuff and the rubbish of buildings, the highest part at the same time projecting above the waters, and being consequently weathered, but not materially injured.
>
> Charles Lyell
> *Principles of Geology* (1830)

> Estoy sentado aquí en el atolón. Estoy sentado y plantado aquí en el atolón.
>
> Luis Alberto Spinetta
> *Holanda* (1996)

As mentioned in previous chapters, our ichnological knowledge of the different depositional environments is highly variable. For example, carbonates have received less attention than siliciclastics. Also, volcanic terrains have been little explored from an ichnological perspective. On the other hand, rocky shorelines, which fall within the realm of bioerosion, have been the focus of a number of detailed ichnological studies, both on modern and ancient shorelines. In fact, the study of bioerosion has a long history, starting with Lyell's (1830) observation of borings produced by the lithophagid bivalve *Lithodomus*, which actually belongs in the ichnogenus *Gastrochaenolites*, pervasively bioeroding the marble pillars of the Temple of Serapis. In this chapter, we will explore the ichnology of this last set of environments. First, we will focus on carbonate rocks, addressing shallow-marine tropical carbonates, reefs, shelf and deep-sea chalk, and carbonate turbidites. Second, we will review our present knowledge of rocky shorelines. Finally, we will explore the ichnology of environments strongly affected by volcanism.

11.1 CARBONATE SYSTEMS

Notwithstanding some exceptions (e.g. fluvial and glacial), almost all siliciclastic environments have carbonate counterparts (Kennedy, 1975). Carbonates have certain peculiarities that distinguish them from siliciclastics, and impact on production and preservation of biogenic structures. Among these peculiarities, the role of early cementation (leading to ample development of firm and hard substrates), the influence of organisms on early diagenesis, the role of color contrast, and the heterogeneity in sediment composition and texture rank among the most important (Kennedy, 1975; Ekdale *et al*., 1984; Curran, 1994, 2007). Early cementation is widespread in carbonate substrates (e.g. Wilson, 1975). In fact, lithification can take place even before burrow abandonment by the producers, or after abandonment but before infill of the structures (Shinn, 1968; Kennedy, 1975). Early cementation is conducive to the establishment of hardgrounds, and is the driving force behind development of substrate-controlled ichnofacies and associated bioerosion (e.g. Bromley, 1967, 1975; Goldring and Kaźmierczak, 1974; Palmer, 1978; Gruszczynski, 1979; Bottjer, 1985; Landing and Brett, 1987; Mángano and Buatois, 1991; Bromley and Allouc, 1992) (Fig. 11.1a–b). In turn, early diagenesis is influenced by burrowing activities, and diagenesis influences preservation of biogenic structures (e.g. Mason, 1980; Archer, 1984; Narbonne, 1984; Fillion *et al*., 1990). For example, diagenesis may lead to the formation of dolomite haloes surrounding burrow systems contributing to the formation of mottling textures (e.g. Pak and Pemberton, 2003; Pemberton and Gingras, 2005) (Fig. 11.2a–b). Carbonate sediment Eh/pH is strongly affected by the activity of deposit and detritus feeders. For example, Taylor (1964) demonstrated that between 80 and 90% of carbonate sands at a study area in the Bahamas have passed through the digestive tract of echinoderms. Virtually every single chalk particle is thought to have been ingested by organisms (Ekdale and Bromley, 1991). In addition, pellet production plays a major role in substrate consistency, sometimes reducing substrate stability (Pryor, 1975; Ekdale *et al*., 1984). Several factors contribute to the somewhat decreased preservation potential of biogenic structures in carbonates. Although common in siliciclastics, contrasts between trace fossils and the host sediment are rare in carbonates, complicating visualization of ichnofossil forms (Curran, 1994, 2007). Furthermore, the degree of heterogeneity in composition and texture also impacts on preservation potential. Carbonates with high textural and compositional contrasts tend to favor preservation of discrete biogenic structures (Archer, 1984; Maples and Archer, 1986).

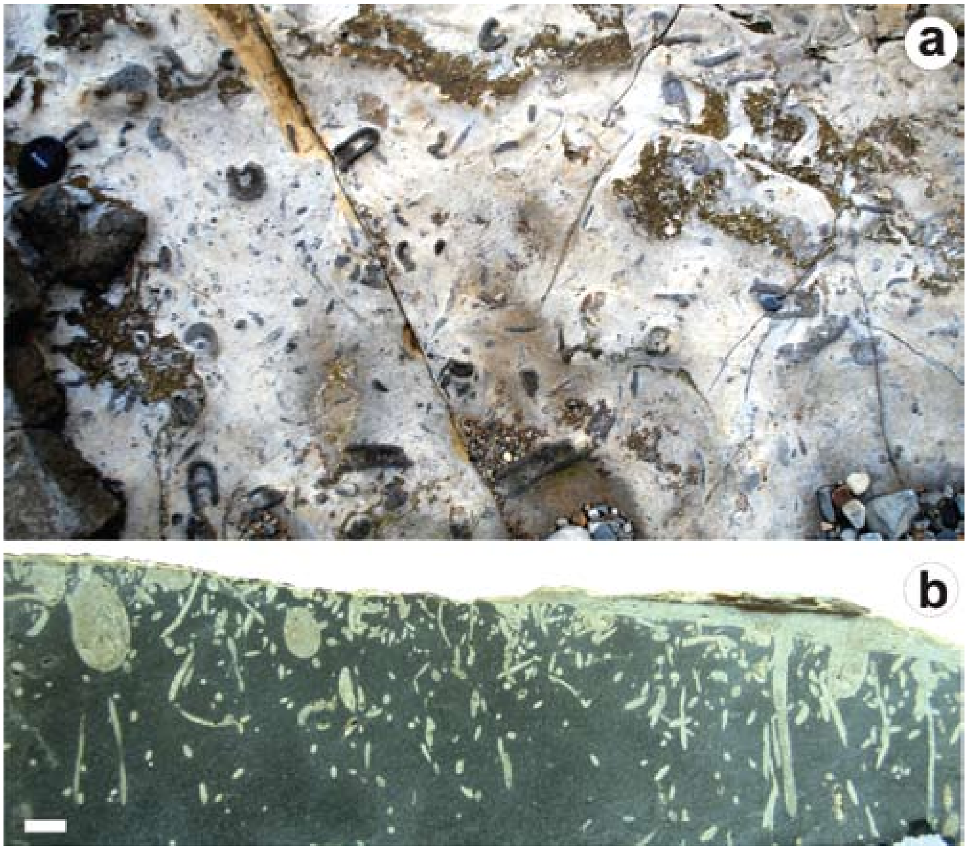


Figure 11.1 Substrate-controlled ichnofaunas in carbonate rocks. (a) High density of firmground *Rhizocorallium* isp. Upper Jurassic, Rodiles Formation, El Puntal Cliffs, San Martín del Mar, Villaviciosa, Asturias, northern Spain. Lens cap is 5.5 cm. (b) *Trypanites* isp. and *Gastrochaenolites* isp. in a hardground. Contact between the Middle Jurassic Upper Inferior Oolite and underlying Carboniferous limestone. Nunney Quarry, Somerset, England. Scale bar is 1 cm. See Bromley (1975).

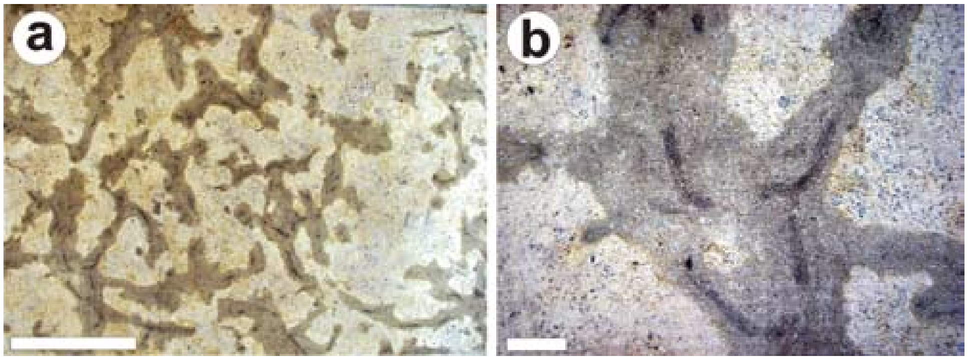


Figure 11.2 *Thalassinoides*-like burrow systems in a mottled limestone, Upper Ordovician, Red River Formation of Manitoba, Canada. This limestone is known as Tyndall stone. Wall at the entrance to the Department of Geological Sciences of the University of Saskatchewan. (a) General view of branching burrow systems. Scale bar is 10 cm. (b) Close-up showing branching and dolomitic halo surrounding the burrow; only the darker inner core is the actual burrow. Scale bar is 1 cm. See Pak and Pemberton (2003).

However, Pemberton and Jones (1988) indicated that differences between carbonate and siliciclastic ichnology have been overstated. These authors pointed out that in many instances carbonate components are transported rather than produced *in situ* and, therefore, they are subjected to the same hydrodynamic principles as siliciclastics. This situation has been illustrated by Wu (1982), who documented colonization suites in carbonate tempestites. In the same vein, Pickerill *et al.* (1984) described a carbonate ichnofauna in which diagenetic processes, albeit important, did not mask the original environmental distribution of trace fossils.

Present knowledge of the ichnology of different carbonate environments is uneven, with most studies focused on shallow-marine tropical carbonates, reefs, and pelagic carbonates (i.e. chalk). A smaller proportion of studies have dealt with the ichnology of carbonate turbidites.

11.1.1 SHALLOW-MARINE TROPICAL CARBONATES

Most ichnologic studies on shallow-marine tropical carbonates have been based on Pleistocene and recent examples in the carbonate factories of Florida, the Bahamas Archipelago, the Seychelles Islands, and the Persian Gulf (e.g. Shinn, 1968; Farrow, 1971; Braithwaite and Talbot, 1972; Pemberton and Jones, 1988; Curran, 1992, 1994, 2007). In particular, San Salvador Island in the Bahamas has been the focus of intense

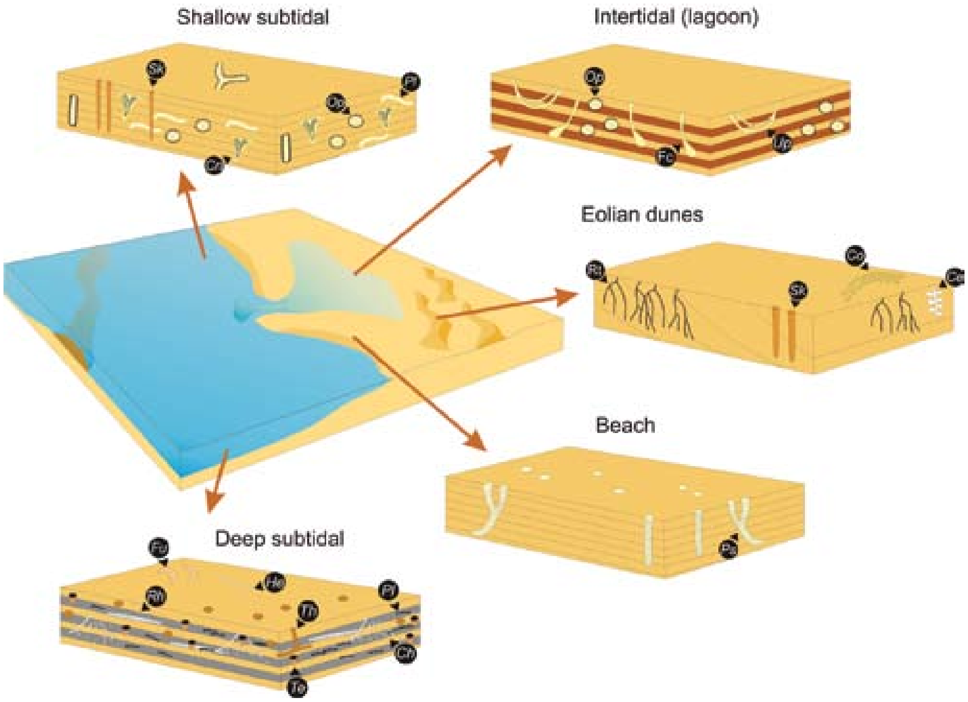


Figure 11.3 Schematic reconstruction of trace-fossil distribution in shallow-marine tropical carbonate environments. Coastal eolian-dune deposits contain *Cellicalichnus* (*Ce*), *Coenobichnus* (*Co*), *Skolithos* (*Sk*), and root traces (Rt). Sandy-beach deposits are dominated by *Psilonichnus* (*Ps*). Intertidal-lagoonal deposits may exhibit *Ophiomorpha* (*Op*), fiddler crab burrows (Fc) and *Upogebia* burrows (*Up*). Shallow-subtidal calcarenites may contain *Ophiomorpha* (*Op*), *Skolithos* (*Sk*), *Conichnus* (*Cn*), and *Planolites* (*Pl*). Deep-subtidal deposits host *Fuersichnus* (*Fu*), *Helicodromites* (*He*), *Planolites* (*Pl*), *Rhizocorallium* (*Rh*), *Thalassinoides* (*Th*), *Teichichnus* (*Te*), and *Chondrites* (*Ch*).

scrutiny (e.g. Curran, 1984, 1992, 1994, 2007; Curran and White, 1991, 2001). These studies allow comparisons between Pleistocene and Holocene deposits and their modern analogues, and documented distribution of biogenic structures from coastal dunes to sandy beaches, and intertidal and shallow-subtidal environments (Fig. 11.3). As noted by Curran (2007), tropical carbonate environments are extremely rich in biodiversity. However, their ichnological record is of relatively low diversity, probably as a result of taphonomic overprints, such as domination of burrows (*Ophiomorpha*) of deep-tier callianassids.

Coastal-dune deposits in tropical settings consist of large-scale, planar cross-stratified calcarenite with multiple truncation surfaces (Carew and Mylroie, 2001). In the Bahamas, the dunal ichnocoenosis is the most diverse of all trace-fossil suites (Curran and White, 2001; Curran, 2007). Root traces (Fig. 11.4a) are the most abundant, and may lead to complete obliteration of the primary fabric in the case of vegetated dunes showing paleosol development. Animal traces are represented by many different arthropod structures, including cluster burrows attributed to sphecid wasps, stellate burrows (*Cellicalichnus*) of halictid bees (Fig. 11.4b), and vertical insect or spider burrows (*Skolithos*) (Fig. 11.4c), as the most common structures. Land hermit crab trackways (*Coenobichnus*) are present also (Walker *et al*., 2003), together with burrows constructed by the land crab *Gecarcinus lateralis* (Seike and Curran, 2010). Terrestrial ichnofaunas from tropical carbonates illustrate the *Celliforma* ichnofacies discussed by Genise *et al*. (2000, 2010a) and Melchor *et al*. (2002).

Beach deposits typically consist of calcarenite with abundant shell fragments, with surfaces gently dipping landwards behind the berm. These deposits contain vertical J-, Y-, and U-shaped burrows assigned to *Psilonichnus* and constructed by ghost crabs, such as *Ocypode quadrata* (Frey *et al*., 1984a; Curran, 1984, 1994, 2007). In contrast to siliciclastic settings, the ghost crab *Ocypode quadrata* typically does not inhabit dunes in the tropics, being restricted to the unvegetated beach backshore zone (Curran and White, 1991; Curran, 2007) (Fig. 11.5a–b). Similar burrows have been documented not only in the backshore calcarenite of the Bahamas Archipelago but also in Bermuda (Curran, 1994) and the Persian Gulf (Knaust, 1997). It has been suggested that some of these crustacean burrows may have been later modified by a hymenopteran which constructed brooding chambers (Martin, 2006). Ichnofaunas from beach-backshore tropical carbonates represent the *Psilonichnus* ichnofacies (Curran, 1994, 2007). Towards the foreshore, high energy is detrimental to infaunal activity, and also reduces the preservation potential of biogenic structures.

Intertidal lagoons under slightly hypersaline conditions and fringed landwards by mangroves are common in the Bahamas (Curran, 1994; Curran and Martin, 2003). Deposits mostly consist of carbonate sands and minor amounts of mud, forming extensive tidal flats that display a topography of mounds and craters produced by the callianassid shrimp *Glypturus acanthochirus* (Curran, 1994, 2007; Curran and Martin, 2003) (see Section 6.6). *Glypturus acanthochirus* burrows are deep, large, and complex, with a downward spiraling morphology. Microbial growth allows mound stabilization and colonization by the shrimp *Upogebia vasquezi* and the fiddler crab *Uca major*, which produce U-shaped, commonly paired, burrows (Fig. 11.6a) and simple obliquely vertical burrows (Fig. 11.6b) with a basal bulbous turnaround, respectively. *Uca* trackways are common also (Fig. 11.6b). Large amounts of pellets (fecal, feeding, and excavation) are typically produced (Curran, 1994,

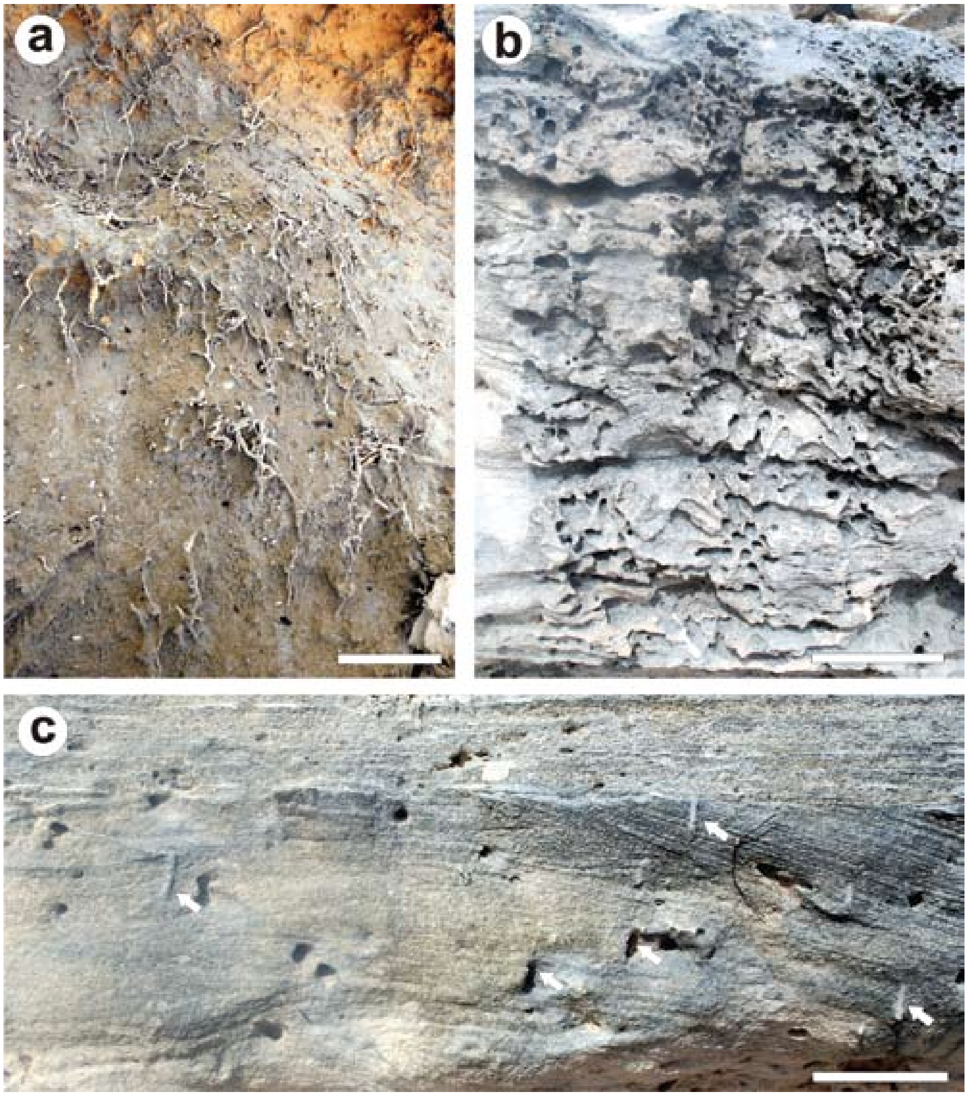


Figure 11.4 Characteristic trace fossils of coastal-dune deposits in tropical settings. (a) High density of rhizomorphs (or rhizoliths). Pleistocene, Cockburn Town Member, Grotto Beach Formation of San Salvador Island, Bahamas. Scale bar is 20 cm. (b) Stellate burrows (*Cellicalichnus*) probably produced by halictid bees Holocene, Hanna Bay Member, Rice Bay Formation of San Salvador Island, Bahamas. Scale bar is 10 cm. (c) Vertical insect or arachnid burrows attributed to *Skolithos* (arrows). Holocene, Hanna Bay Member, Rice Bay Formation of San Salvador Island, Bahamas. Scale bar is 10 cm. See Curran and White (2001).

Figure 11.5 Cast of modern Y-shaped burrows constructed by the ghost crab *Ocypode quadrata* in beach backshore deposits. These burrows would be assigned to *Psilonichnus upsilon* in the fossil record. Specimens housed at the Gerace Research Station of San Salvador Island, Bahamas. Scale bars are 10 cm. See Curran and White (1991) and Curran (2007).

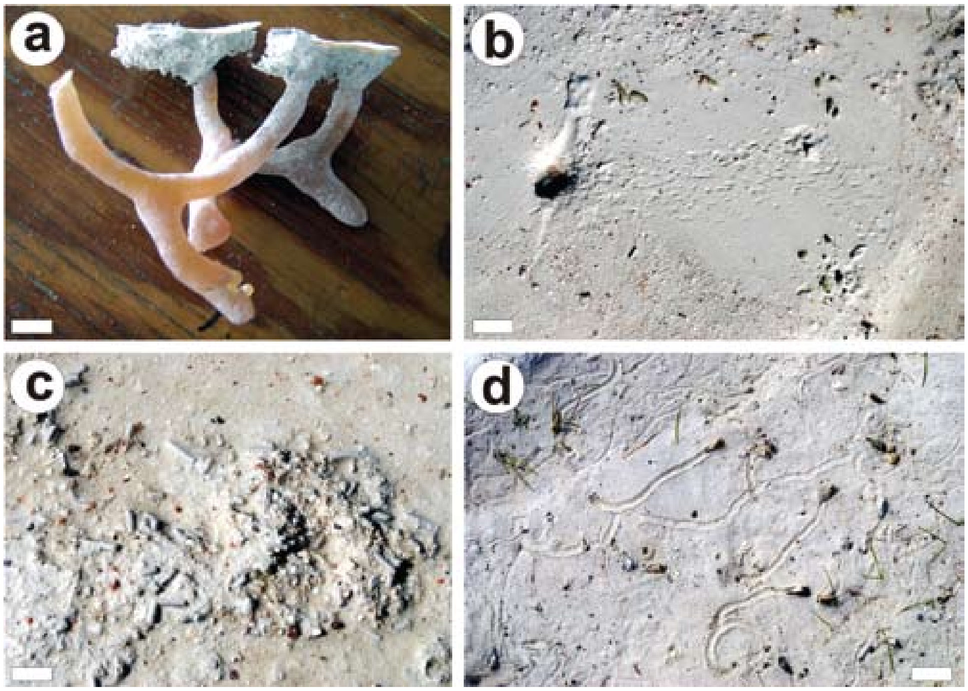


Figure 11.6 Biogenic structures in a modern carbonate lagoon flanked by mangroves. Pigeon Creek, San Salvador Island, Bahamas. (a) U-shaped, paired burrows of the shrimp *Upogebia vasquezi*. Scale bar is 1 cm. (b) Opening of simple vertical burrows and associated trackway of the fiddler crab *Uca major* Scale bar is 2 cm. (c) Concentration of *Uca major* feeding pellets. Scale bar is 1 cm. (d) Grazing trails of batillarid gastropods that in the fossil record would be assigned to the ichnogenus *Archaeonassa*. Scale bar is 2 cm. See Curran and Martin (2003).

2007; Curran and Martin, 2003) (Fig. 11.6c). During low tide, batillarid gastropods produce grazing trails in mangrove areas (Fig. 11.6d). Similar lagoonal ichnofaunas have been documented in the Seychelles (Farrow, 1971) and Belize (Dworschak and Ott, 1993). Large spiraling callianassid burrows occur in the Seychelles. In Belize, the mounded topography occurs in intertidal channels and subtidal zones of the lagoon, and is also the result of *Glypturus acanthochirus*. Mangrove channels include U- and Y-shaped vertical burrows of the shrimps *Alpheus floridanus* and *A. heterochaelis*. Burrows of the shrimp *Neocallichirus grandimana* occupy shallow tiers in intertidal zones. Other structures in Belize lagoonal deposits are J- and U-shaped burrows of *Corallianassa longiventris* and simple burrows of *Axiopsis serratifrons*.

In the fossil record, a common ichnotaxon in calcarenites of subtidal, higher energy settings is *Conichnus conicus* (Pemberton and Jones, 1988; Curran, 1994; Curran and White, 1997). This ichnotaxon is commonly present in planar cross-bedded calcarenites formed in back-reef and shallow-subtidal shoaling bar and tidal-channel settings. *Conichnus conicus* has often been attributed to the upward escape-burrowing activity of sea anemones, although other possibilities exist and should be considered (Curran and White, 1997; Buck and Goldring, 2003). Fossil burrows of *Upogebia vasquezi* also occur in Pleistocene lagoonal-margin deposits of the Bahamas (Curran and Martin, 2003). Extensive *Thalassinoides* systems can also be common, as described by Monaco and Giannetti (2002) from the Jurassic of the Southern Alps, Italy. Although Pleistocene lagoonal ichnofaunas are of low diversity, those in lagoonal calcarenites of Grand Cayman Island are more diverse, including *Bergaueria*, *Ophiomorpha*, and *Skolithos*, among other ichnogenera, illustrating the *Skolithos* ichnofacies (Pemberton and Jones, 1988; Jones and Pemberton, 1989). Jurassic lagoonal lithographic limestones of the Cerin fossil site (France) show a more complex pattern of trace-fossil distribution, in which unburrowed intervals alternate with beds containing polychaete (*Tubularina lithographica*) and crustacean burrows (*Rhizocorallium irregulare* and *Thalassinoides suevicus*) (Gaillard *et al.*, 1994). Also, a relatively diverse ichnofauna containing *Polarichnus*, *Palaeophycus*, *Skolithos*, *Bergaueria*, and *Helicodromites*, among other forms, was documented in Silurian intertidal deposits (Narbonne, 1984).

Open-marine shallow-subtidal carbonates in tropical environments host an incredibly diverse array of planktonic, nektonic, and benthic organisms. However, the preservation potential of the traces of many of these organisms is low. In fact, the ichnological record of Bahamian Pleistocene subtidal calcarenites is one of rather low diversity, with a clear bias towards deep-infaunal vertical burrows, such as *Ophiomorpha* (Fig. 11.7a–b) and, more rarely, *Skolithos*, representing the *Skolithos* ichnofacies (Curran, 1992, 1994, 2007). Similar ichnofaunas occur in high-energy shoals where *Ophiomorpha* and *Diplocraterion* dominate (Fürsich, 1998). In areas of relatively low energy during fair-weather times, but sporadically affected by storms, two contrasting suites occur as in the case of storm-influenced siliciclastic settings (see Section 7.1). *Ophiomorpha* is common in tempestites, while *Thalassinoides*, *Zoophycos*, and *Planolites* predominate in background deposits (Fürsich, 1998).

Under lower-energy conditions, such as those in distal carbonate ramps and platforms, more diverse suites dominated by horizontal trace fossils may be preserved, including *Thalassinoides*,

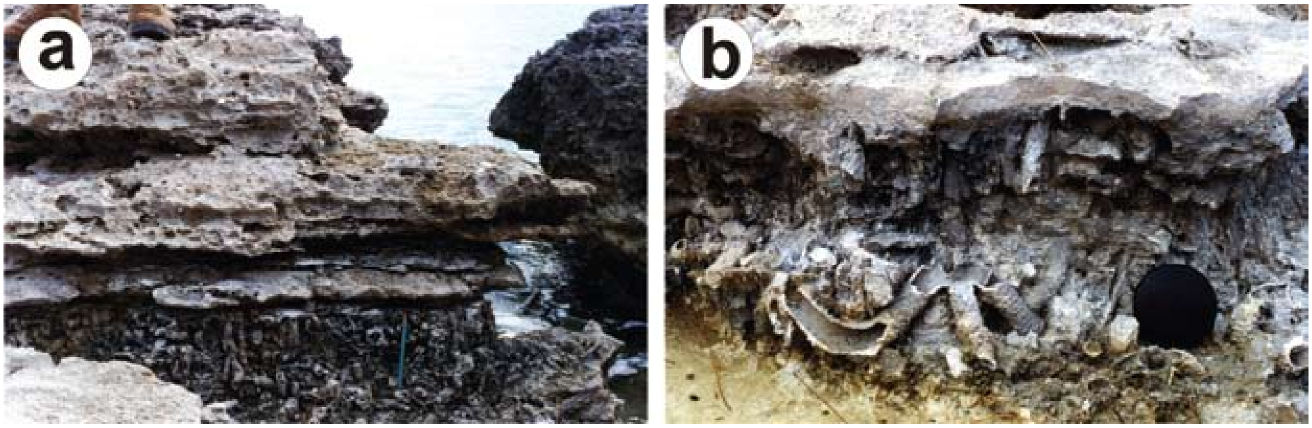


Figure 11.7 *Ophiomorpha nodosa* in carbonate sandy patches formed between reef areas. Pleistocene, Cockburn Town Member, Grotto Beach Formation of San Salvador Island, Bahamas. (a) General view. Pencil (lower center) is 16 cm. (b) Close-up showing dense mazes of *Ophiomorpha nodosa*. Lens cap is 5.5 cm. See Curran (1994, 2007).

Figure 11.8 Bioerosion by sea urchin in beachrock, French Bay, San Salvador Island, Bahamas. Scale bar is 2 cm.

Rhizocorallium, *Fuersichnus*, *Protovirgularia*, *Helicodromites*, *Palaeophycus*, *Teichichnus*, *Cruziana*, and *Chondrites*, among other ichnogenera (e.g. Narbonne, 1984; Maples and Archer, 1986; Fraaye and Werver, 1990; Fürsich, 1998). *Thalassinoides* is a common elite trace fossil in subtidal carbonates (e.g. Mángano and Buatois, 1994). These low-energy settings are represented by the *Cruziana* ichnofacies. *Chondrites* and, to a lesser extent, *Planolites* and *Thalassinoides*, are common in marly-limestone rhythmites formed under low-energy, dysaerobic conditions (e.g. Olóriz and Rodríguez-Tovar, 1999a).

Bioerosion is also important in shallow-marine carbonate settings. In particular, beachrock, which typically occurs discontinuously in the intertidal zone (Ginsburg, 1953), provides a substrate for many bioeroding organisms. These include sea urchins (Fig. 11.8), clionid sponges, polychaetes, bivalves, and sipunculans, among other organisms (e.g. Moran and Reaka, 1988; Stearley and Ekdale, 1989). Beachrock bioeroders may be highly variable depending on the complexity of the intertidal area (Stearley and Ekdale, 1989). On gently dipping regular surfaces, endolithic populations tend to be of higher density and lower diversity than those in more stepped and complex beachrock, comprising a network of pools and channels. In addition, cavities produced by bioeroders provide a shelter for a sessile and motile cryptic fauna that protect themselves from predation and physical stress (Moran and Reaka, 1988).

11.1.2 REEFS

Reefs are one of the most appropriate ecosystems for the establishment of bioeroding organisms (Warme, 1977; Bromley, 1978; Perry and Hepburn, 2008). Bioeroders play two main roles in reefs: (1) they effectively weaken the substrate, making it more susceptible to weathering and erosion, and (2) they may produce large amounts of sediment as a by-product (Perry and Hepburn, 2008). Sponges (e.g. *Cliona*) are typically the most important infaunal bioeroders, substantially contributing to substrate degradation. Sponges produce dense networks of inter-connected chambers up to several centimeters deep, included in the ichnogenus *Entobia* (Bromley and D'Alessandro, 1990). Bivalves, although producers of single discrete boreholes (ichnogenus *Gastrochaenolites*), are also effective agents of bioerosion in reefs (Perry and Hepburn, 2008). Boring polychaetes, producers of the ichnogenus *Trypanites* among other ichnotaxa, are small and, in comparison with sponges and bivalves, do not extract significant amounts of $CaCO_3$ (Perry and Hepburn, 2008). However, they may modify the substrate, facilitating bioerosion by other agents (Perry and Hepburn, 2008) and, in some cases, they have been documented to contribute significantly to bioerosion (Hein and Risk, 1975; Klein *et al.*, 1991). Other common bioeroders, albeit volumetrically of less impact, are chitons, cirripedians, and gastropods. Also, because coral reefs are living substrates, they are ideal for bioclaustration structures (see Section 1.4.14). Examples of these include cirripedian, bivalve, gastropod, and polychaete borings (Ekdale *et al.*, 1984).

Earlier studies in Bermuda did not detect bathymetric zonations of bioerosion structures in modern reefs (Bromley, 1978). However, subsequent work in the Mediterranean Sea demonstrated that shallow-water coral reefs display a higher diversity of borings than their deep-water equivalents, although no changes in abundance were detected (Bromley and D'Alessandro, 1990). Some differences in boring distribution occur at ichnospecific level. For example, *Entobia paradoxica* is abundant only in deep reefs, while *E. volti* and *E. gigantea* are restricted to coastal environments.

Although most bioerosion studies on reefs have been undertaken in modern environments, there are a few detailed analyses dealing with fossil material. James *et al.* (1977) documented the ichnogenus *Trypanites* in Lower Cambrian archaeocyatid reefs. Bertling (1997) identified 24 ichnospecies in a Jurassic reef. This highly diverse ichnofauna includes sponge (*Entobia*), polychaete (*Caulostrepsis*, *Maeandropolydora*), bivalve (*Gastrochaenolites*), phoronid (*Talpina*), and cirripedian (*Rogerella*) borings, among other ichnogenera. Sedimentation rate is a major limiting factor. Low sedimentation rates promote intense bioerosion on dead coral, mostly by siphunculids, polychaetes, and lithophagians. With high rates of sedimentation bioerosion is less intense and bivalves become the dominant forms, mostly in living coral (Bertling, 1997). Perry (2000) documented boring distribution in a Pleistocene fringing reef complex in Jamaica. This fossil reef contains *Entobia*, *Gastrochaenolites*, *Maeandropolydora*, and *Trypanites*. Diverse assemblages of borers, dominated by sponges and polychaetes, with bivalves being locally important, occur in back-reef/lagoon facies. Shallow fore-reef facies are dominated by borings produced by sponges, with polychaete borings being locally important and bivalve borings rare or absent.

11.1.3 SHELF AND DEEP-SEA CHALK

The term "chalk" refers to pelagic sediment mostly consisting of calcareous nanoplankton (Scholle *et al.*, 1983). Arguably, most ichnological studies in carbonates have focused on chalk (e.g. Bromley, 1967; Frey, 1970, 1972; Frey and Bromley, 1985; Bromley and Ekdale, 1984a, 1986; Ekdale and Bromley, 1984a, 1991). In addition, chalk deposits represent the birthplace of a number of ichnological concepts, such as tiering, ichnofabrics, and ichnoguilds (see Chapter 5). In chalk deposits observations are usually performed in cross-section due to the absence of available bedding planes. In addition, a number of techniques are used in order to visualize biogenic structures in cores (Bromley and Ekdale, 1984a). The combination of very slow rates of sedimentation and fully marine conditions leads to complete biogenic reworking of chalk deposits (Ekdale and Bromley, 1991).

Two main types of chalk deposits can be distinguished, shelf and deep-sea chalk. Shelf chalk forms between water depths of 50 and 300 m, while deep-sea chalk occurs at much greater depths, up to thousands of meters (Scholle *et al.*, 1983). Both are similar in terms of texture and composition because they share the same pelagic components regardless of water depth. However, minority components show some differences. Shelf chalk commonly contains fine detrital particles (e.g. quartz, feldspar), while those formed below the carbonate compensation depth (CCD) contain siliceous organisms, such as diatoms and radiolarians. In any case, the most significant controls on the infauna are linked to post-depositional processes (e.g. early cementation and erosion by currents; Ekdale and Bromley, 1984). In general, deep-sea chalk is compositionally and texturally more homogeneous.

Shelf-chalk ichnofaunas have been documented in Upper Cretaceous outcrops of Europe (England, Denmark) and United States (Alabama, Kansas) (Bromley, 1967; Kennedy, 1967, 1970, 1975; Frey, 1970, 1972; Frey and Bromley, 1985; Bromley and Ekdale, 1984a; Ekdale and Bromley, 1984, 1991) (Box 5.2). Crustacean burrow systems, such as *Thalassinoides* (Fig. 11.9), are dominant in shelf chalk (Ekdale and Bromley, 1984). Preferential preservation of these systems results from differential cementation or silicification of burrow fills, commonly accompanied by changes in colors, leading to the formation of elite trace fossils (Bromley and Ekdale, 1984a; Bromley, 1990, 1996) (see Section 5.2.2). Extensive development of omission surfaces and hardgrounds is conducive to the establishment of pre-omission, omission, and post-omission suites, which may be delineated based on the morphology and architecture

Figure 11.9 Trace fossils from chalk. Deep-tier *Thalassinoides* isp. and *Chondrites* isp. Upper Cretaceous, Austin Chalk, east of Austin, central Texas, United States. Scale bar is 1 cm.

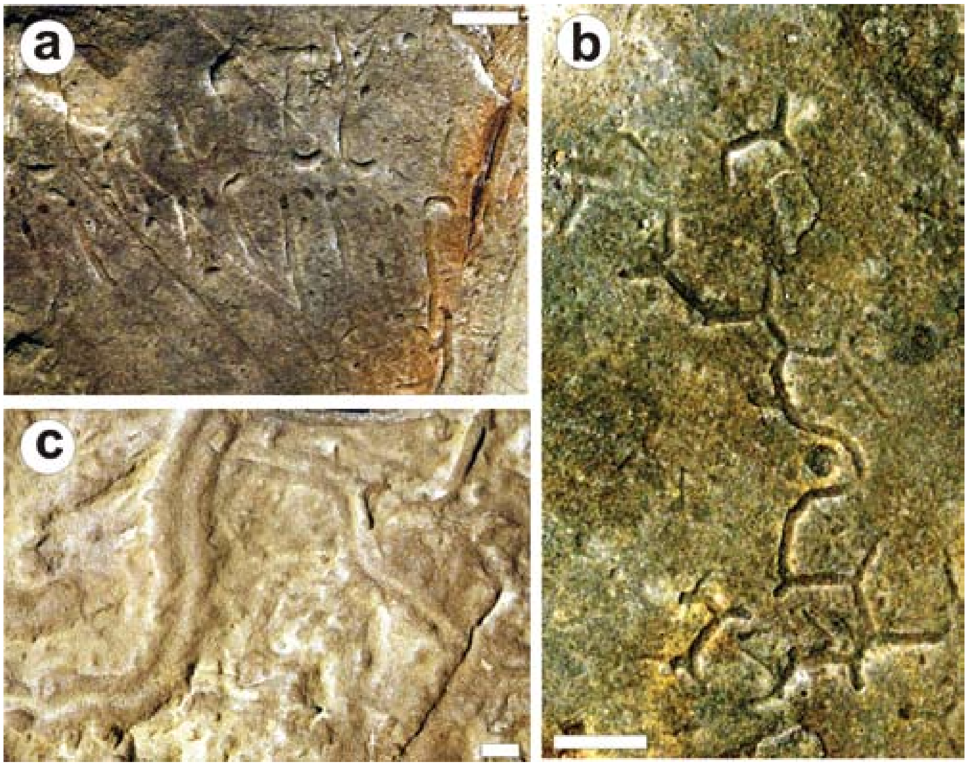


Figure 11.10 Trace fossils preserved at the base of carbonate turbidites. Eocene, Punta Carnero Formation, Margarita Island, Venezuela. (a) *Desmograpton* isp. (b) *Megagrapton submontanum*. (c) *Scolicia strozzi*. Scale bars are 1 cm.

of the associated *Thalassinoides* systems. Pre-omission burrows are commonly ideomorphic (e.g. *T. suevicus*). With progressive cementation and formation of calcareous nodules (omission and post-omission suites), burrows of irregular architecture having abundant constrictions (e.g. *T. paradoxicus*) tend to dominate (Bromley, 1967; Kennedy and Garrison, 1974). Other crustacean structures, such as *Ophiomorpha* and *Gyrolithes*, may occur as subordinate components (Bromley and Ekdale, 1984a). Feeding trace fossils (e.g. *Chondrites*, *Zoophycos*, *Planolites*, *Teichichnus*) are relatively common, but are less conspicuous because they are not usually affected by differential cementation (Bromley and Ekdale, 1984a). Another typical structure is the large burrow *Bathichnus paramoudrae*, which has been linked to rapid sedimentation (Nygaard, 1983). Bioerosion is commonly both in hardground surfaces and invertebrate shells (e.g. Bromley, 1970, 1979).

Deep-sea chalks are known almost exclusively by the study of deep-sea cores from the southwest Pacific, Mediterranean, Caribbean, and Philippine seas, as part of the Deep-Sea Drilling Project (e.g. Ekdale, 1977, 1978, 1980). The age of these deposits ranges from late Mesozoic to Holocene (Scholle *et al.*, 1983). Feeding trace fossils, such as *Planolites*, *Zoophycos*, and *Chondrites*, are dominant (Ekdale and Bromley, 1984a). Other differences with respect to their shallow counterparts are the absence of crustacean burrows and substrate-controlled suites, as well as the lower ichnodiversity. However, the latter feature may simply reflect the small width of cores (Ekdale and Bromley, 1984a).

11.1.4 CARBONATE TURBIDITES

The ichnology of carbonate turbidites is poorly understood and only a few studies have been undertaken. Eocene carbonate turbidites from Margarita Island (Venezuela) contain a moderately diverse ichnofauna dominated by graphoglyptids, such as *Paleodictyon*, *Helminthorhaphe*, *Desmograpton* (Fig. 11.10a), *Megagrapton* (Fig. 11.10b), *Protopaleodictyon*, and *Urohelminthoida* (Muñoz, 1986; Muñoz *et al.*, 1997). Other elements include *Scolicia* (Fig. 11.10c) and *Thalassinoides*. In contrast to siliciclastic turbidites of similar age, ichnodiversity and abundance seem to be lower. Jurassic carbonate turbidites of Morocco also contain graphoglyptids (*Paleodictyon*), but feeding structures, such as *Teichichnus*, *Zoophycos*, and *Chondrites*, are dominant (Ekdale and Warme, 1975). In addition, studies in Cretaceous–Paleocene carbonate turbidites in Italy suggest that diagenetic processes may favor preservation of full-relief structures, in comparison with the typical semirelief preservation which is dominant in siliciclastic turbidites (Powichrowski, 1989).

11.2 ROCKY SHORELINES

Rocky shorelines are extensive in modern environments (one third of the world's present coastlines), but have not been recognized in the fossil record to the same degree (Johnson, 1988, 2006). Bioerosion is extremely common in rocky shorelines, particularly in those formed by limestone (Fig. 11.11a–c) and represented by the *Trypanites* ichnofacies, the archetypal association in these settings. Although other substrates

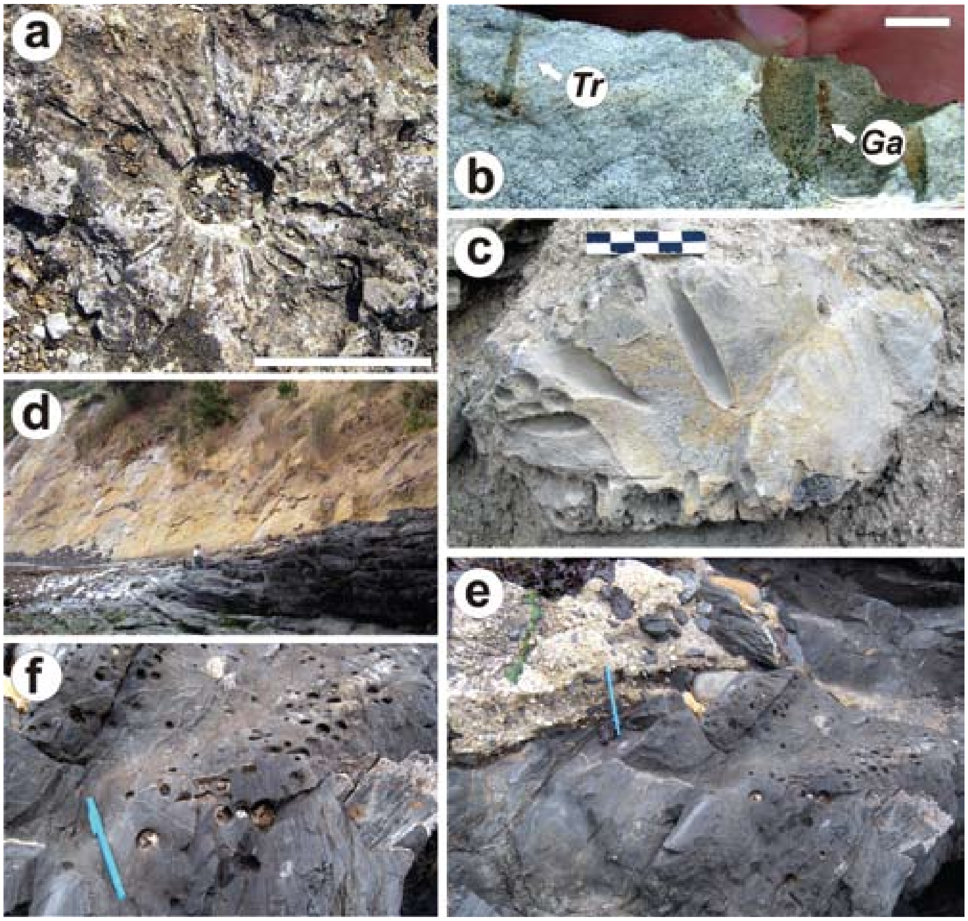


Figure 11.11 Trace fossils in rocky shorelines (a) *Entobia cracoviensis*. A large chambered sponge boring formed in a Late Cretaceous abrasion platform cut into Upper Jurassic limestone. Upper Cretaceous, Bonarka Quarry, Cracow, Poland. See Bromley *et al.* (2009a). Scale bar is 5 cm. (b) *Trypanites* isp. (*Tr*) and *Gastrochaenolites* isp. (*Ga*) in a rocky shoreline formed during a Middle Miocene transgression. Borings are emplaced in an Upper Jurassic limestone. Skotniki Quarry, Holy Cross Mountains, Poland. Scale bar is 1 cm. (c) Cliff conglomerate clast containing deep borings of *Gastrochaenolites* isp. Middle Miocene, Skotniki Quarry, Holy Cross Mountains, Poland. See Radwański (1969). (d) General view of Cretaceous shoreface sandstone (Quiriquina Formation) overlying the Upper Paleozoic metamorphic basement. Cocholgue, Chile. See Buatois and Encinas (2011). (e) Detailed view of the contact showing several specimens of *Gastrochaenolites* isp. penetrating the metamorphic basement. Pen is 16 cm. See Buatois and Encinas (2011). (f) Close-up of *Gastrochaenolites* isp. Pen is 16 cm. See Buatois and Encinas (2011).

Box 11.1 Ichnology of a Pliocene rocky shoreline in Rhodes, Greece

Pliocene rocky coasts of the Island of Rhodes have been closely scrutinized to elucidate patterns of distribution of bioerosion structures. A wide variety of habitats were identified along a transgressed rocky shoreline, including cliff-foot platforms, steep surfaces along cliff-lines, caves, and overhangs. Thirty one ichnospecies were recognized, belonging to the ichnotaxa *Caulostrepsis*, *Entobia*, *Gastrochaenolites*, *Gnathichnus*, *Oichnus*, *Radulichnus*, *Rogerella*, and *Trypanites*, among others. These borings can be ascribed to living tracemakers with different degrees of confidence. The bivalves *Lithophaga lithophaga*, *Jouannetia semicaudata*, *Gastrochaena dubia*, and *Petricola lapicida* are producers of different ichnospecies of *Gastrochaenolites*. The endolithic sponge *Aka* sp. and several species of clionid sponges are producers of different *Entobia* ichnospecies. Six ichnoguilds were recognized. Ichnoguild I is the most superficial and consists of the rasping traces *Radulichnus* and *Gnathichnus*, produced mechanically by algae-browsing mollusks and echinoderms. Ichnoguild II occurs immediately below ichnoguild I, and includes *Centrichnus* and *Renichnus*, produced by sessile mollusks etching the surface of the substrate chemically. Ichnoguild III is represented by shallow-tier suspension-feeder sponge borings illustrated by several *Entobia* ichnospecies. Ichnoguild IV consists of worm borings included in *Trypanites*, *Caulostrepsis*, and *Maeandropolydora*, which record various feeding strategies. Ichnoguild V records the activity of borer bivalves, and is represented by *Gastrochaenolites* and *Phrixichnus*. Finally, Ichnoguild VI is illustrated by the predator boring *Oichnus*. Two main associations are identified. The *Entobia* association occurs in the cliff surface, and records the activity of the deeper tiers. The *Gnathichnus* association is present on the surface of rapidly buried shell material, allowing for the preservation of very shallow-tier rasping borings.

Reference: Bromley and Asgaard (1993b).

may be bioeroded, diversity and abundance of structures is typically lower (Fig. 11.11d–f). Bathymetric gradients from supratidal to subtidal settings are commonly displayed by modern bioeroders (Lewis, 1964; Stearley and Ekdale, 1989), and similar trends have been found in the fossil record (e.g. Bromley and Asgaard (1993b) (Box 11.1).

The inclination of the rock surface plays a role in controlling colonization by borers (Johnson, 2006). Time-averaged

Box 11.2 Volcanic eruption, bioturbation, and ash-layer preservation in the South China Sea

Excellent ichnological work was done following the eruption of Mount Pinatubo (Philippines) in 1991. The volcanic ash produced during this eruption was transported westward to the South China Sea, strongly affecting the deep-sea fauna. The resultant ash layer is up to 10 cm thick, and covers an area of more than 400 000 km^2. Because volcanic ash is barren of organic matter, benthic food availability was restricted to newly produced organic flocs. In addition, deposition of ash layers, at least 3 cm thick, diminished the oxygen diffusion into the sediment below, leading to anoxia in the interstitial waters. Also, as ash consists of angular to subrounded grains exhibiting a granular behavior different from that of mud, unlined burrows tend to collapse. As a result, organisms exhibited a number of adaptations. While surface grazers disappeared, deep burrowers reopened their connection to the sea floor and were able to survive. Bioturbators interacted with the ash layer in three main ways. Some were able to dig through the ash layer, producing significant mixing. In other cases, animals reworked the ash layer from below, as illustrated by the echinoid tracemaker of *Scolicia*, which can completely mix layers up to 6 cm thick. Finally, other organisms mixed the layer from above. The preservation of the ash layer is highly variable across the South China Sea. In general, ash deposits thinner than 1 mm have not been observed as a continuous layer, while an approximately 2 mm layer is patchily bioturbated. In addition, a number of factors control preservation, and allow four main provinces to be distinguished: (1) In areas of high primary production along the Philippines margin, mixing of the layer is intense because the benthic fauna is adapted to variable grain sizes and rapid deposition. (2) In areas affected by turbidity currents and hyperpycnal flows typical of canyons in front of river margins, rapid deposition allows preservation of the ash layer. (3) In areas with low amounts of benthic food, the ash is preserved due to limited mixing. (4) In the central part of the South China Sea, the ash is thinner than 3 cm and the benthic food content is high, resulting in less preservation potential for the ash layer. This work opens new perspectives to understand how benthic organisms respond to catastrophic events in basins affected by explosive volcanism.

Reference: Wetzel (2009).

communities seem to be more common in low-angle to horizontal surfaces. High topographic relief areas tend to contain more rapidly emplaced suites that form during a short span coeval with rising sea level. As a result, boring overlap is less common on vertical to high-angle rock surfaces than in horizontal ones. Some rocky shorelines are exposed to wave action, while others occur in more protected areas (Johnson, 2006; Johnstone *et al*., 2006). Open rocky shorelines exposed to wave action may be extensively bioeroded, containing dense concentrations of organisms that bore or nestle to shelter from waves (Johnson, 2006). Sediments associated with storm-swept rocky shoreline ichnofaunas tend to be sparsely bioturbated and contain typical ichnotaxa of high-energy settings, such as *Macaronichnus*, *Ophiomorpha*, and *Skolithos*, illustrating a *Skolithos* ichnofacies (Johnstone *et al*., 2006). However, continuous deepening during transgression leads to replacement by elements of the *Cruziana* ichnofacies (e.g. *Asterosoma*, *Chondrites*), signaling a change to lower-energy conditions. Overall bioturbation is sparse in sediments associated with storm-swept rocky shorelines. Rocky shorelines formed in protected environments may enclose sediments which are slightly more bioturbated than their storm-swept equivalents, but ichnodiversity remains very low and suites are dominated by opportunistic ichnotaxa (*Ophiomorpha*, *Palaeophycus*). With transgression, sheltered shorelines become more exposed to open-ocean storms and fair-weather waves, and ichnodiversity remains significantly low. The degree of bioturbation decreases as a result of higher-energy conditions.

11.3 VOLCANIC TERRANES

Present knowledge on the ichnology of volcanic terranes is patchy at best. The absence of studies most likely results from the common scarcity of trace fossils in environments strongly affected by volcanism, particularly in proximal zones of volcanic arcs (Crimes, 1970b), and the lower number of paleoenvironmental analyses dealing with volcaniclastic successions in comparison with siliciclastic and carbonate rocks. However, modern studies in marine basins affected by volcanism are providing valuable data for better understanding of benthic fauna response to volcanic eruptions (Wetzel, 2009) (Box 11.2).

A number of ichnological studies were focused on Ordovician volcanic-arc related rocks of Argentina (Mángano *et al*., 1996c; Mángano and Buatois, 1996, 1997). Although trace fossils are relatively uncommon, dense assemblages occur locally, suggesting short-term colonization windows during pauses in volcaniclastic sedimentation (Fig. 11.12a). Slope apron successions include *Planolites montanus*, *Palaeophycus tubularis*, and *Helminthopsis abeli* in overbank deposits adjacent to a submarine channel. Shallow-marine successions include *Cruziana furcifera*, *Helminthopsis* isp., *Palaeophycus tubularis*, *Phycodes* isp., and *Planolites beverleyensis* in tempestites. Low-ichnodiversity levels probably result from overall environmental instability in volcanic-arc related settings. A large supply of volcaniclastic material in high-gradient areas promotes frequent sediment gravity flows that inhibit the establishment of a diverse resident fauna. These deposits may locally contain burrows that

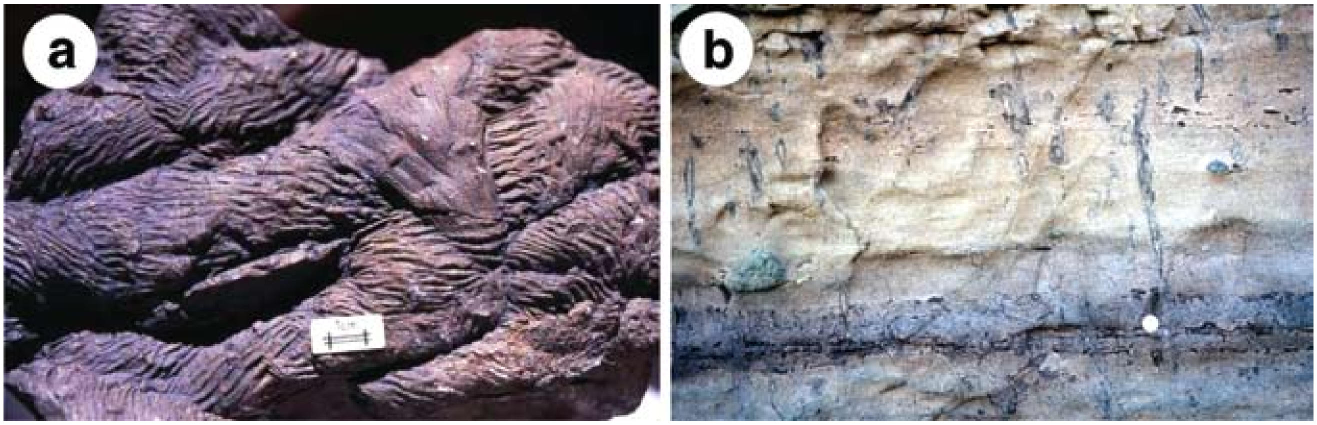


Figure 11.12 Trace fossils in volcaniclastic-flow deposits. (a) *Cruziana furcifera* cross-cut by *Phycodes* isp. preserved at the base of a shallow-marine volcaniclastic sandstone. Lower Ordovician, Loma del Kilómetro Member, Suri Formation, Punta Pétrea, Chaschuil, northwest Argentina. See Mángano *et al*. (1996c). (b) Deep *Rosselia socialis* penetrating from a colonization surface at the top of a shallow-marine volcaniclastic sandstone. Upper Permian, Kiama Sandstone Member, Broughton Formation, Pheasant Point, southern Sydney Basin, eastern Australia. Lens cover is 5.5 cm. See Shi and Weldon (2002).

penetrate from the top of the event layer reflecting opportunistic colonization (Fig. 11.12b).

Silurian carbonate turbidites emplaced in a slope apron adjacent to a volcanic arc contain trace-fossil assemblages that are similar in both overall features and taxonomic composition (Soja, 1991). This ichnofauna contains a few poorly specialized ichnotaxa (*Palaeophycus*, *Planolites*, *Chondrites*). Recurrent local catastrophes were regarded as the most important limiting factor affecting the benthic fauna. Similarly, Cretaceous deep-marine deposits of Turkey, rich in volcaniclastic grains make of sharp-edged glass shards, contain an unusually low diversity ichnofauna (Uchman *et al*., 2004a). It has been argued that those materials were unsuitable for the development of a bacterial film that is essential for the infaunal food chain, and that hydrochemical conditions and the release of poisonous substances due to active volcanism were detrimental to benthic life (Uchman *et al*., 2004a). On the other hand, Cretaceous volcaniclastic shallow-marine deposits in Antarctica emplaced in a most distal position with respect to the volcanic arc contain more diverse suites that resemble those from similar environments in siliciclastic settings (Scasso *et al*., 1991).

Part III A matter of time

12 Trace fossils in sequence stratigraphy

> For my part, following out Lyell's metaphor, I look at the natural geological record, as a history of a world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines.
>
> Charles Darwin
> *On the Origin of Species* (1859)

> Trace fossils are proving to be one of the most important groups of fossils in delineating stratigraphically important boundaries related to sequence stratigraphy.
>
> George Pemberton and James MacEachern
> "The sequence stratigraphic significance of trace fossils: examples from the Cretaceous Foreland Basin of Alberta, Canada" (1995)

The appearance of sequence stratigraphy in the late eighties resulted in a revolution in the study of sedimentary rocks. The shift from seismic stratigraphy (Vail *et al*., 1977) to sequence stratigraphy brought the incorporation of outcrops and cores as sources of data in stratigraphic analysis (Posamentier *et al*., 1988; Posamentier and Vail, 1988; Van Wagoner *et al*., 1990). Coincident with this shift, ichnological studies began to emphasize the importance of trace fossils in sequence stratigraphy (e.g. Savrda, 1991b; MacEachern *et al*., 1992; Pemberton *et al*., 1992b). In little more than a decade, the field experienced a rapid increase in the number of studies devoted to exploring the applicability of ichnology in refining sequence-stratigraphic analysis (e.g. MacEachern *et al*., 1992, 1999a, 2007c; Savrda *et al*., 1993; Taylor and Gawthorpe, 1993; Pemberton and MacEachern, 1995; Ghibaudo *et al*., 1996; Martin and Pollard, 1996; Buatois *et al*., 1998d, 2002b; Pemberton *et al*., 2001, 2004; Carmona *et al*., 2006). At present, ichnological aspects are currently covered in sequence-stratigraphic textbooks (e.g. Catuneanu, 2006). The aim of this chapter is to provide a detailed review of the applications of ichnology in sequence stratigraphy. Although a large part of this chapter deals with the recognition of discontinuity surfaces in marine siliciclastic successions, we will also cover other topics which are commonly overlooked in the literature. These include characterization of parasequences, parasequence sets, and systems tracts, but also the potential of trace fossils to address sequence-stratigraphic issues in carbonates and continental deposits.

12.1 RECOGNITION OF DISCONTINUITY SURFACES

Recognition of discontinuity surfaces is key to sequence stratigraphy (e.g. Posamentier and Allen, 1993; Catuneanu, 2006), and trace fossils have proven to be particularly useful in this respect (MacEachern *et al*., 1992; Pemberton *et al*., 2001, 2004). Identification of these stratal surfaces highlights allogenic processes, which are external to the depositional system, as opposite to autogenic processes, which are internal to the depositional system and lead to the accumulation of environmentally related facies successions. By identifying trace-fossil suites in hard, firm, and xylic substrates of siliciclastic successions, allostratigraphic surfaces can be identified. The recognition of substrate-controlled ichnofacies, such as *Glossifungites, Trypanites*, and *Teredolites*, is critical in identifying stratigraphic discontinuities.

Of the above three ichnofacies, the *Glossifungites* ichnofacies has been the most intensively used in sequence stratigraphy (Fig. 12.1). The *Glossifungites* ichnofacies develops in firm (but unlithified) substrates. In siliciclastic sediments, dehydration is the result of burial and substrates become available for colonization by organisms if exhumed by subsequent erosion (MacEachern *et al*., 1992) (Fig. 12.2a–b). For carbonates, occurrence of the *Glossifungites* ichnofacies is not necessarily indicative of erosive exhumation because early diagenetic processes may take place at the water–sediment interface (e.g. Bromley, 1975; Mángano and Buatois, 1991).

The elements of substrate-controlled ichnofacies typically cut across a pre-existing softground suite (Fig. 12.2c). Therefore, they reflect new conditions which commonly do not coincide with those controlling early deposition. Thus, the substrate-controlled association develops during a hiatus between the erosive event (which exhumed the substrate) and the deposition of the overlying unit. During such periods of time, the dehydrated and/or cemented bed is colonized by organisms (MacEachern *et al*., 1992). The *Glossifungites* ichnofacies is generally easy to identify in cores, and is preserved in lithological interfaces (typically mudstone overlain by sandstone or conglomerate). In these cases, sharply defined, unlined wall burrows occur in fine-grained sediments and are passively filled by coarser material from the overlying bed. However, the *Glossifungites* ichnofacies may also occur in sandstone (e.g. Pemberton *et al*., 2004).

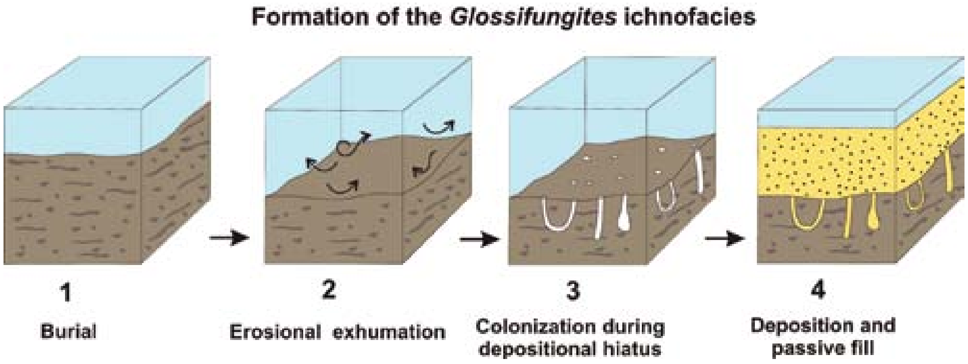


Figure 12.1 Origin of the *Glossifungites* ichnofacies. Modified from MacEachern *et al*. (1992).

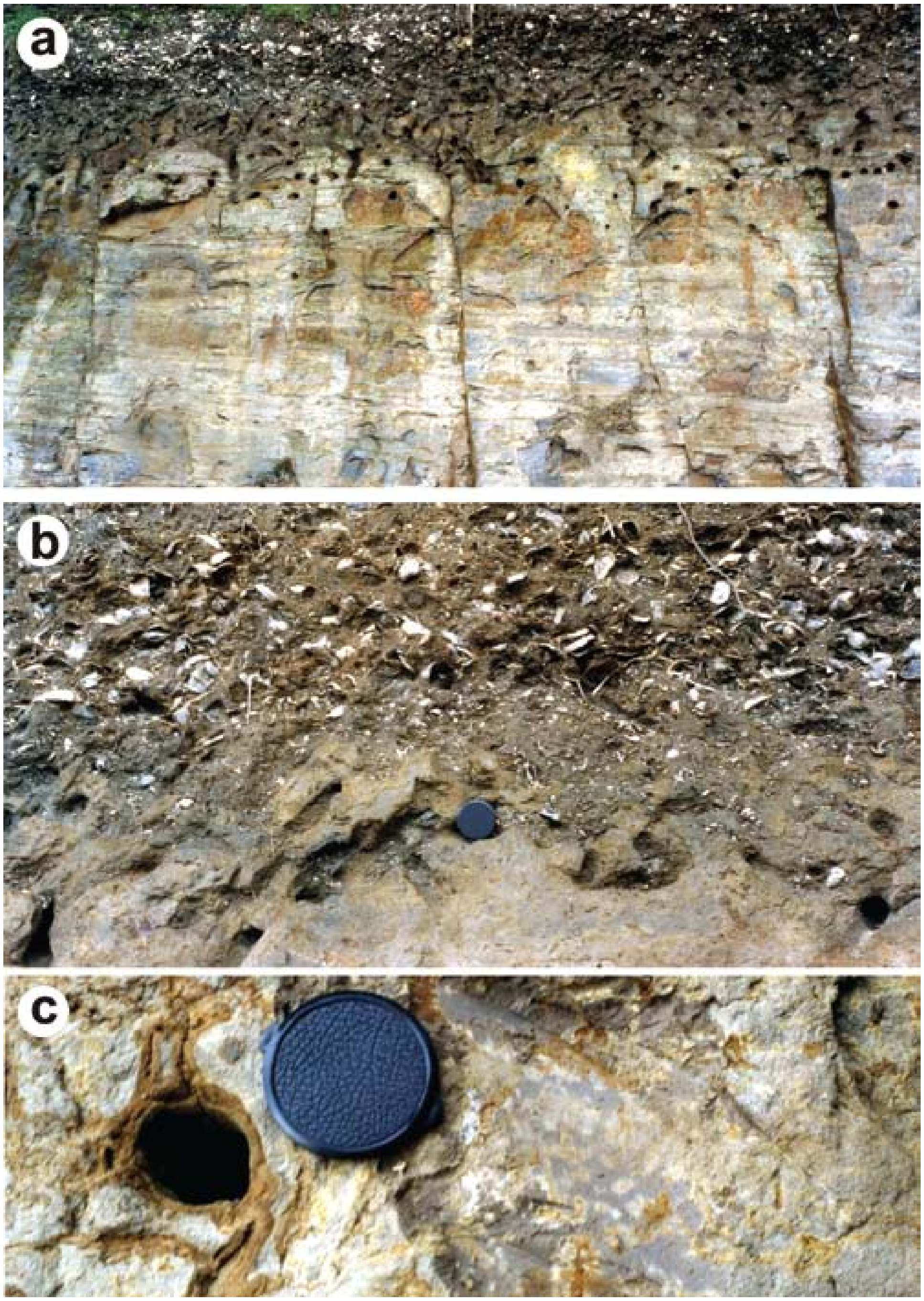


Figure 12.2 Formation of the *Glossifungites* ichnofacies in erosional discontinuities, Holocene, Willapa Bay, Washington, United States. (a) General view of transgressive-lag deposits overlying intertidal-channel deposits with inclined heterolithic stratification (note surfaces gently dipping towards the right). *Thalassinoides* penetrates into the heterolithic deposits from the erosive surface. Pen (lower right) is 16 cm. (b) Close-up showing firmground *Thalassinoides* passively filled with shell fragments from the overlying transgressive lag. Lens cap is 5.5 cm. (c) Firmground burrows overprinted to a poorly defined softground background trace-fossil suite. Lens cap is 5.5 cm. See Gingras *et al*. (2001) for additional information.

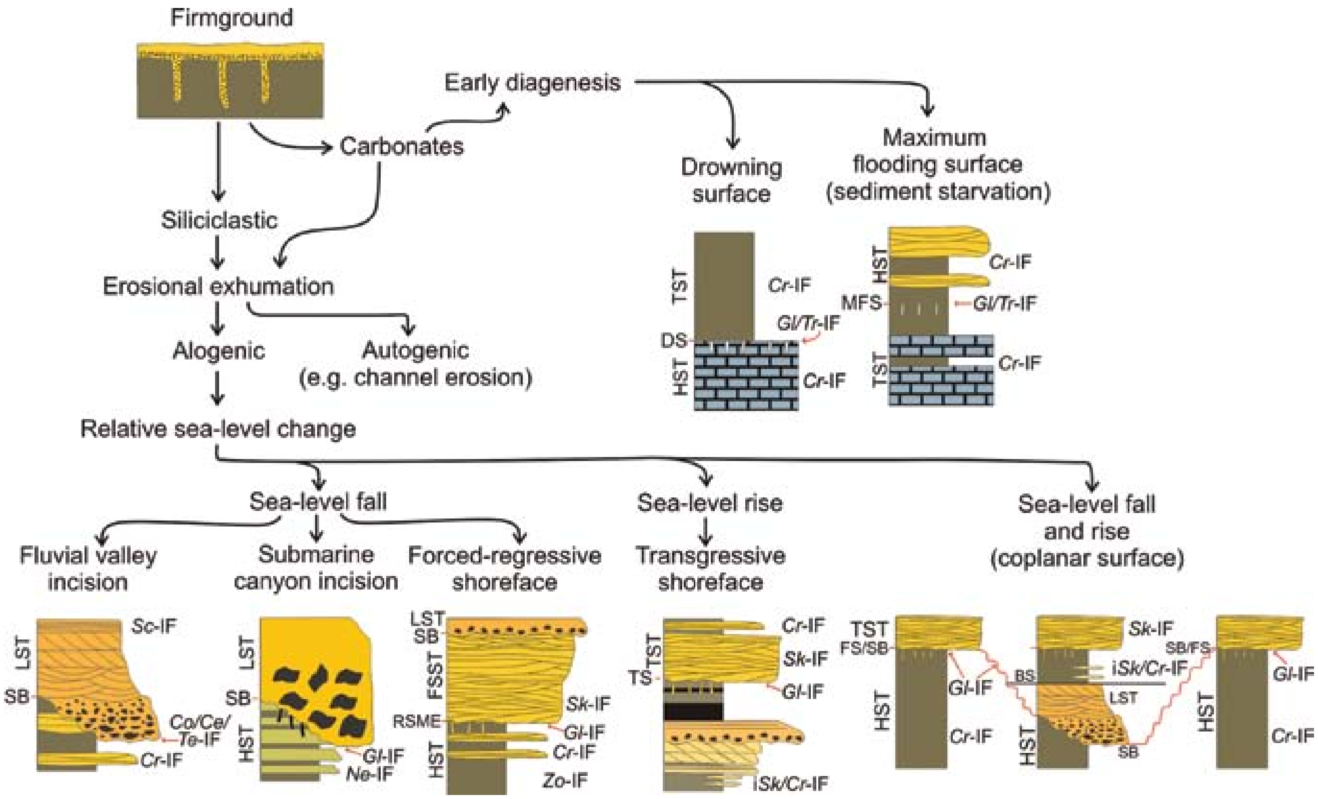


Figure 12.3 Sequence-stratigraphic significance of the *Glossifungites* ichnofacies and associated softground ichnofacies. LST = lowstand systems tract, TST = transgressive systems tract, HST = highstand systems tract, SB = sequence boundary, FS/SB = flooding surface/sequence boundary, TS = transgressive surface, DS = drowning surface, BS = bayline surface, MFS = maximum flooding surface, *Sk*-IF = *Skolithos* ichnofacies, *Cr*-IF = *Cruziana* ichnofacies, i*Cr*/*Sk*-IF = mixed impoverished *Cruziana*/*Skolithos* ichnofacies, *Zo*-IF = *Zoophycos* ichnofacies, *Ne*-IF = *Nereites* ichnofacies, *Gl*-IF = *Glossifungites* ichnofacies, *Gl*/*Tr*-IF = *Glossifungites* or *Trypanites* ichnofacies, *Sc*-IF = *Scoyenia* ichnofacies, *Co*/*Ce*/*Te*-IF = *Coprinisphaera, Celliforma*, or *Termitichnus* ichnofacies.

Whereas identifying substrate-controlled ichnofacies results in the recognition of an erosional discontinuity, an accurate interpretation of such surfaces requires the detailed analysis of the soft substrate trace-fossil assemblages occurring in the underlying and overlying units (Fig. 12.3) (MacEachern *et al.*, 1992; Pemberton *et al.*, 2004). Recognition of vertical changes in softground ichnofaunas allows interpretation of the type or types of sea-level fluctuations involved. Stratigraphic discontinuities can be divided into two major groups, erosional and non-erosional discontinuities. Most ichnological studies on sequence stratigraphy focus on the former group.

12.2 EROSIONAL DISCONTINUITIES

There are several available schemes for subdividing sedimentary packages into systems tracts and placing the sequence boundary (see Catuneanu, 2006). Here, we adopt a model that considers four systems tracts (lowstand, transgressive, highstand, and falling stage) and places the sequence boundary at the base of the lowstand systems tract (Plint and Nummedal, 2000). Erosional discontinuities are subdivided into regressive surfaces of marine erosion, lowstand surfaces of erosion, transgressive surfaces of erosion, and co-planar surfaces of lowstand erosion and transgressive erosion, also known as flooding surfaces/sequence boundaries or FS/SB (Pemberton *et al.*, 1992b; 2004; MacEachern *et al.*, 1992).

12.2.1 REGRESSIVE SURFACES OF MARINE EROSION

The regressive surface of marine erosion is formed due to wave scouring during relative sea-level fall associated with forced regression (Plint and Nummedal, 2000). Forced regressions represent the rapid seaward migration of shoreline and nearshore deposits in response to a relative sea-level fall (Plint, 1988; Posamentier *et al.*, 1992). Forced-regression strata are included in the falling stage systems tract (Plint and Nummedal, 2000). While normal regressions are generally characterized by a gradual progradation of the shoreline during stillstands or highstands (Fig. 12.4a), forced regressions are abrupt and triggered by a drop in sea-level (Fig. 12.4b). In contrast to shorefaces formed during normal regressions, those incised during the falling stage are fairly thin due to diminished accommodation space during sea-level fall (MacEachern *et al.*, 1999a). Shoreface progradation during forced regression occurs irrespective of sediment supply (Catuneanu, 2006).

During forced regressions, wave scouring leads to the exhumation of compacted and dewatered sediments, making a firm

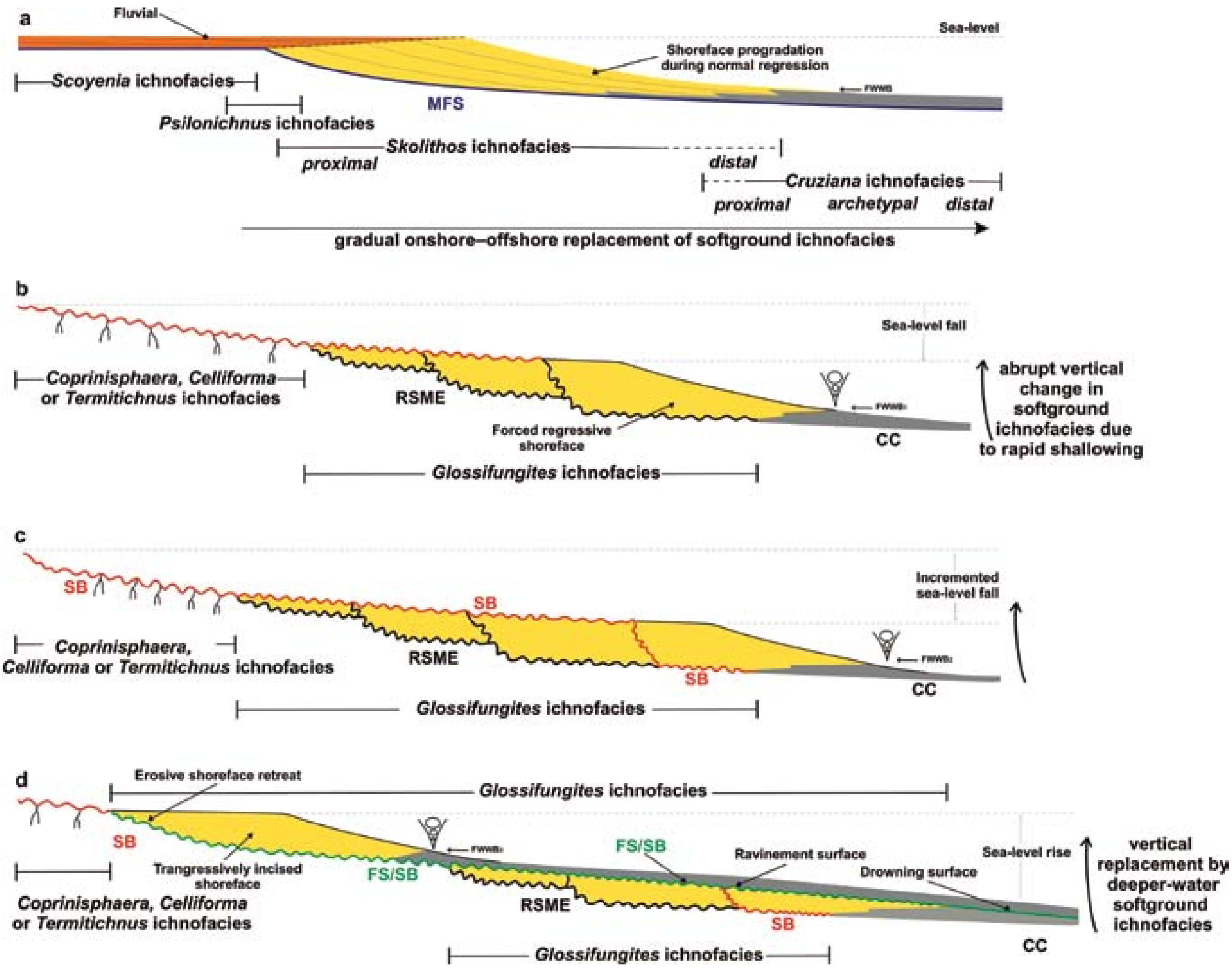


Figure 12.4 Distinction between normal-regressive, and sharp-based (forced-regressive, lowstand, and transgressively incised) shorefaces. (a) Normal-regressive shoreface (highstand systems tract). Vertical softground ichnofacies replacement is gradual due to progressive shallowing. (b) Forced-regressive shoreface (falling stage systems tract). Vertical softground ichnofacies replacement is abrupt due to rapid shallowing. The base of the forced-regressive shoreface is delineated by the *Glossifungites* ichnofacies. (c) Lowstand shoreface (lowstand systems tract). Vertical softground ichnofacies replacement is abrupt due to rapid shallowing. The base of the lowstand shoreface is delineated by the *Glossifungites* ichnofacies. Cannibalization of the underlying forced-regressive shoreface is significant. (d) Transgressively incised shoreface (transgressive systems tract). Vertical softground ichnofacies reflects deepening due to transgression. The base of the transgressively incised shoreface is delineated by the *Glossifungites* ichnofacies. Firmground colonization is typically more extensive than in forced-regressive and lowstand shorefaces because of prolonged colonization windows during depositional hiatus. MFS = maximum flooding surface. SB = sequence boundary. RSME = regressive surface of marine erosion. FWWB = fairweather wave base. CC = correlative conformity. FS/SB = flooding surface/sequence boundary. Modified from MacEachern *et al*. (2007c).

substrate available for the *Glossifungites* producers. Accordingly, the *Glossifungites* ichnofacies locally delineates the basal erosional surface of forced-regression packages (MacEachern *et al*., 1992; Monaco, 1995; Pemberton and MacEachern, 1995; Buatois *et al*., 2002b). Colonization windows may be rather narrow, due to a short hiatus followed by rapid deposition. In contrast to shorefaces formed during normal regressions, those incised during forced regressions are fairly thin due to diminished accommodation space during sea-level fall (MacEachern *et al*., 1999a).

Prograding shoreface successions form during normal regressions separated by periods of relative sea-level rise, and exhibit a gradual change in softground trace-fossil associations reflecting progressive shallowing (Pemberton *et al*., 1992b; Pemberton and MacEachern, 1995). Conversely, falling-stage shorefaces are characterized by the abrupt occurrence of proximal ichnofaunas that sharply contrast with those of the underlying, more distal sediments (Pemberton and MacEachern, 1995). Typically, pervasively bioturbated offshore-transition to offshore deposits, which contain a distal to archetypal *Cruziana* ichnofacies, are sharply replaced by erosive-based, coarser-grained shoreface deposits containing the *Skolithos* or the proximal *Cruziana* ichnofacies.

Mid-shelf and shelf-edge deltas can also form as a result of forced regression, and are included in the falling stage systems tract (Porębski and Steel, 2006). Empirical data on the ichnology of these systems are not available yet. However, it would be reasonable to expect that due to forced progradation of the delta elements of the distal *Cruziana* to *Zoophycos* ichnofacies are replaced by more proximal and depauperate ichnofaunas, as a response of combined shallowing and fluvial discharge.

12.2.2 LOWSTAND SURFACES OF EROSION

The lowstand surface of erosion is produced as a result of relative sea-level fall. During sea-level fall, fluvially transported sediment by-passes the alluvial and coastal plain, eroding into the underlying older deposits. Sediment by-pass is associated either with incision of fluvial valleys, or formation of unincised fluvial channels (Posamentier, 2001). In any case, these processes result in the establishment of a subaerial unconformity that is regarded as a sequence boundary. Although erosion results in firmground development, no substrate-controlled ichnofacies occur at the base of incised fluvial valleys or unincised fluvial systems because of freshwater or terrestrial conditions (MacEachern *et al.*, 1992). However, because typically subaerial unconformities correspond to the largest stratigraphic hiatuses, paleosol development may be extensive and rooted horizons together with the *Coprinisphaera*, *Celliforma*, or *Termitichnus* ichnofacies may occur in interfluve areas (Buatois and Mángano, 2004a; Catuneanu, 2006).

In addition, subaerial unconformities can be detected by looking not at the surfaces themselves, but at the changes of ichnofaunas throughout the interval analyzed. The typical example is the vertical replacement of elements of the *Skolithos* or *Cruziana* ichnofacies in highstand systems tract deposits by the *Scoyenia* ichnofacies in continental lowstand systems tract deposits. It should be noted, however, that in the absence of a sharp change in sedimentary facies and associated erosion, this change in ichnofaunas may simply result from normal progradation of the highstand systems tract and no sequence boundary is implied.

The subaerial unconformity may extend basinwards into an erosional surface produced subaqueously during maximum lowstand. This surface is excavated prior to burial due to lowstand progradation, resulting in the incision of sharp-based lowstand shorefaces (Fig. 12.4c). In terms of their ichnological signatures, substrate-controlled ichnofacies, particularly the firmground *Glossifungites* ichnofacies, may be present at the base of lowstand surfaces (MacEachern *et al.*, 1992, 2007c; Pemberton *et al.*, 2004). However, because of rapid deposition after formation of the erosive surface the colonization window may close relatively fast, preventing extensive excavation of the substrate.

Lowstand shorefaces are difficult to distinguish from forced-regressive shorefaces. Both record rapid progradation and overlie erosional surfaces cut by wave erosion (MacEachern *et al.*, 2007c). Another similarity with lowstand shorefaces is the abrupt occurrence of proximal ichnofaunas over more distal ichnofaunas (Pemberton and MacEachern, 1995; Buatois *et al.*, 2002b). However, falling-stage shorefaces are thinner than their lowstand counterparts because of reduced accommodation space during falling sea level (Mellere and Steel, 1995; Catuneanu, 2006; MacEachern *et al.*, 2007c). As recently discussed by MacEachern *et al.* (2007c), one of the main differences between falling-stage and lowstand shorefaces resides in the lower preservation potential of the former. Because continuing sea-level fall leads to the subaerial exposure of falling-stage shorefaces, cannibalization is quite intense. In addition, the correlative conformity of the regressive surface of erosion is unlikely to be preserved due to subsequent incision of the lowstand shoreface emplaced in a further seaward position. In basinal positions, lowstand shorefaces tend to be gradationally based and the sequence boundary passes into its correlative conformity. Because the lowstand shoreface lies in the most seaward position prior to the subsequent sea-level rise, the preservation potential of the sequence boundary, and the correlative conformity is high (MacEachern *et al.*, 2007c). Shelf-edge deltas also form during lowstand (Porębski and Steel, 2006), but the ichnology of these systems is still poorly understood.

Sea-level fall also plays a major role in slope and basin settings either by shifting depocenters towards the shelf edge or by producing incisions of submarine canyons (Posamentier and Allen, 1999; Posamentier and Kolla, 2003). In the case of incised submarine canyons, extensive firmground surfaces are formed during incision due to erosional exhumation of previously deposited sediment (MacEachern *et al.*, 1992). Surfaces associated to incised submarine canyons are typically delineated by the *Glossifungites* ichnofacies (e.g. Hayward, 1976; Anderson *et al.*, 2006) (Figs. 12.5a–b, and 12.6). Additional information is provided by the related softground ichnofaunas. Highstand systems tract deposits underlying the incision surface commonly contain elements of the *Zoophycos* ichnofacies that characterizes outer shelf to slope environments. Although a dominance of low-diversity suites of suspension feeders were originally considered as typical of canyon-fill deposits (Crimes, 1977), subsequent studies documented more variability of biogenic structures (Pickerill, 1981). This is consistent with the relatively wide variability of submarine canyon-fill sediments. In general, those ichnofaunas present immediately above the unconformity may contain elements of the *Zoophycos* or *Skolithos* ichnofacies (Fig. 12.5c) depending of the energy levels involved in canyon filling. Alternatively, canyon deposits may be virtually unbioturbated as a result of rapid sedimentation (Pemberton *et al.*, 2004).

12.2.3 TRANSGRESSIVE SURFACES OF EROSION

Transgressive surfaces of erosion, also known as ravinement surfaces, are formed due to scouring by tides and waves during the landward shift of the shoreline (Cattaneo and Steel, 2003; Catuneanu, 2006). Commonly they mark the boundary between the lowstand systems tract and the transgressive systems tracts (Posamentier and Allen, 1999). However, they may also delineate parasequence boundaries formed under high-energy conditions (Pemberton *et al.*, 1992b), representing within-trend facies contacts (Catuneanu, 2006). Typically, the ravinement surface is delineated by the firmground *Glossifungites* ichnofacies (MacEachern *et al.*, 1992) (Figs. 12.4d, 12.7a–c, and 12.8a–c). In fact, the landward shift of the shoreline generates extensive erosion leading to widespread exhumation of the underlying marine, and marginal-marine deposits under brackish to fully marine conditions. Furthermore, because during transgressions

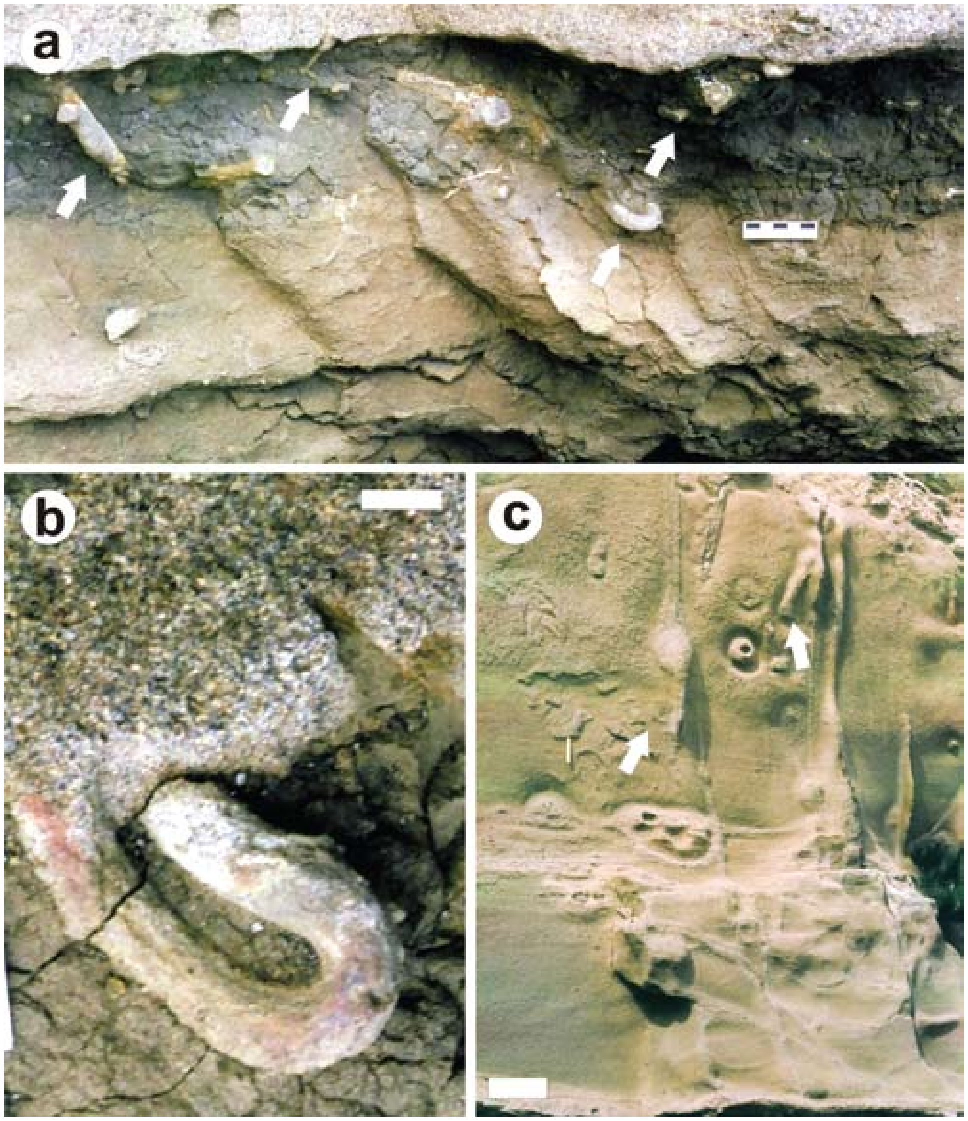


Figure 12.5 Ichnofaunas of lowstand surfaces of erosion in incised submarine canyons, Lower Miocene, Nihotopu and Tirikohua formations, Bartrum Bay, New Zealand. (a) General view of the erosive contact between slope deposits of the Nihotopu Formation below and canyon-fill deposits of the Tirikohua Formation above. Elements of the firmground *Glossifungites* ichnofacies (arrows) penetrate into the slope deposits, and are passively infill by submarine-canyon very coarse- to coarse-grained sand. Scale bar is 5 cm. (b) Close-up of a firmground *Rhizocorallium* specimen with scratch marks. Scale bar is 1 cm. (c) Vertical specimens of *Ophiomorpha* (arrows) forming the high-energy softground suite of canyon-fill deposits. Scale bar is 5 cm. See Hayward (1976).

sediment is trapped in the most proximal positions, sedimentation rate is very low in nearshore to shelf areas, providing relatively continuous colonization windows. As a consequence, conditions for colonization by the *Glossifungites* producers are ideal during transgressions. Although the *Glossifungites* ichnofacies is the most common substrate-controlled ichnofacies in transgressive surfaces of erosion, the *Trypanites* and *Teredolites* ichnofacies may occur if hardgrounds and woodgrounds are formed, respectively. In particular, the ichnogenus *Teredolites* may occur in large densities in transgressive lags (Savrda, 1991a; Savrda *et al*., 1993). Continuous scouring during ravinement tends to concentrate logs bored with *Teredolites* that accumulate after erosion of forested coastal plains during flooding (Box 12.1).

During transgressive retreat followed by a stillstand, sharp-based, incised shorefaces can be formed (Downing and Walker, 1988; Pemberton and MacEachern, 1995; MacEachern *et al*., 1998). Under these conditions a wave-ravinement surface, produced by wave scouring during transgression, is formed. Discerning between transgressively incised shorefaces, and forced-regression and lowstand shorefaces is difficult because tracemakers are subject to identical environmental parameters in both settings (Pemberton and MacEachern, 1995). MacEachern *et al*. (1999a) noted that transgressively incised, and forced-regressive shorefaces may be distinguished on the basis of detailed analysis of the erosional extent of the basal discontinuity (Fig. 12.4d). The basal discontinuity of transgressively incised shorefaces remains erosional even seaward of fair-weather wave base during subsequent progradation because the surface was cut prior to stillstand progradation while sea level was considerably lower. In contrast, the basal discontinuity of forced-regressive shorefaces becomes non-erosional where overlying facies are deposited below fair-weather wave base.

Transgressive surfaces of erosion are also associated with abandonment of deltaic systems (Fig. 12.7b). In proximal positions, alluvial and delta-plain deposits containing freshwater to brackish-water ichnofaunas are sharply replaced by more

Figure 12.6 Firmground *Thalassinoides* of the *Glossifungites* ichnofacies delineating the base of an incised submarine canyon, Lower Cretaceous, Brewster Sands, Vulcan Formation, Gorgonichnthys field, Northwest Shelf Australia. Core width is 10 cm.

diverse ichnofaunas as a result of deepening. Ravinement surfaces cut into floodplain, interdistributary-bay, and abandoned-channel fine-grained clastic deposits are commonly delineated by the *Glossifungites* ichnofacies, while coals are most likely penetrated by elements of the *Teredolites* ichnofacies (e.g. Dam, 1990; Buatois *et al*., 2002a). In subaerial to paralic settings, the *Glossifungites* may truncate paleosols (e.g. Driese and Foreman, 1991) (Fig. 12.7c). Towards distal positions, transgressive surfaces of erosion demarcated by the *Glossifungites* ichnofacies may display extremely high densities and relatively high diversity of firmground burrows (e.g. Buatois, 1995; Buatois *et al*., 2002a).

During shoreline transgression, tidal currents may scour the underlying sediments resulting in the formation of a tidal-ravinement surface. This surface is typical of estuarine settings and specifically occurs between the finer-grained deposits of the estuary basin and the sandy deposits of the estuary-mouth complex (Allen and Posamentier, 1993) (Fig. 12.10). Another transgressive surface in estuarine settings, specifically in those that are wave-dominated, is the wave ravinement surface (Zaitlin *et al*., 1994). This surface separates the overlying transgressive shoreface from the underlying estuary-mouth-deposits (Fig. 12.10). The tidal- and wave-ravinement surfaces do not represent boundaries between different systems tracts but occur within the transgressive systems tract. The firmground *Glossifungites* ichnofacies is extremely common in both tidal- and wave-ravinement surfaces (MacEachern and Pemberton, 1994).

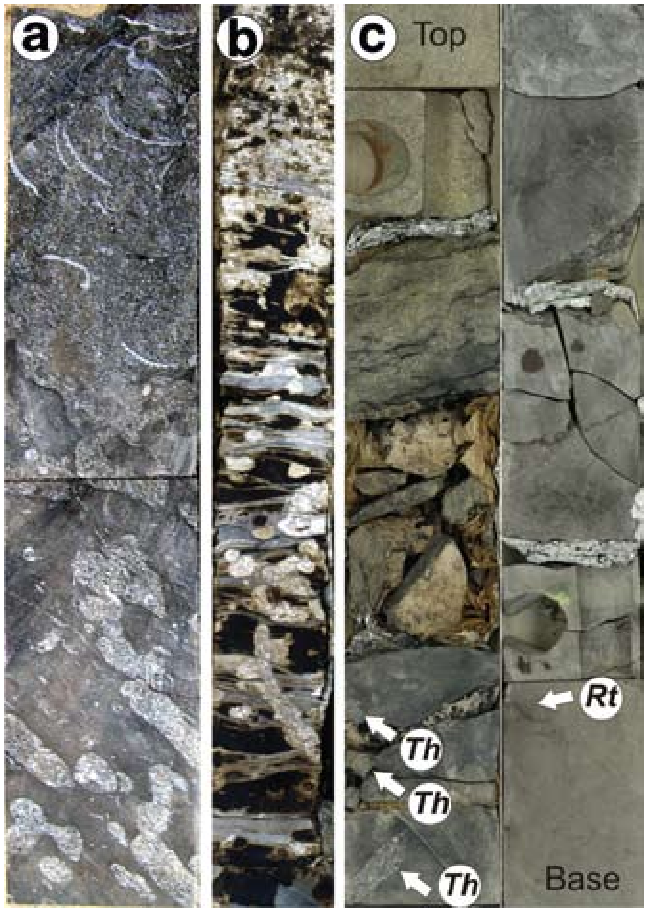


Figure 12.7 *Glossifungites* ichnofacies in transgressive surfaces of erosion. (a) High density of firmground *Thalassinoides* and *Rhizocorallium* in a ravinement surface. Burrows are filled with coarse- and very coarse-grained sand and shell fragments from the overlying transgressive deposit. Oligocene, Los Jabillos Formation, Orocual Field, Eastern Venezuela Basin. Core width is 6.5 cm. (b) High density of *Thalassinoides* in a ravinement surface associated with delta abandonment. Burrow systems penetrate into underlying interdistributary-bay deposits, and are filled with coarse- and very coarse-grained sand and shell fragments from the overlying transgressive deposits. Lower to Middle Miocene, Oficina Formation, Oritupano Field, Eastern Venezuela Basin. Core width is 9 cm. (c) Firmground *Thalassinoides* (*Th*) penetrating from transgressive deposits above into a paleosol below. Note root trace fossils (Rt) in paleosol. Lower Miocene, Naricual Formation, El Furrial Field, Eastern Venezuela Basin. Core width is 9 cm.

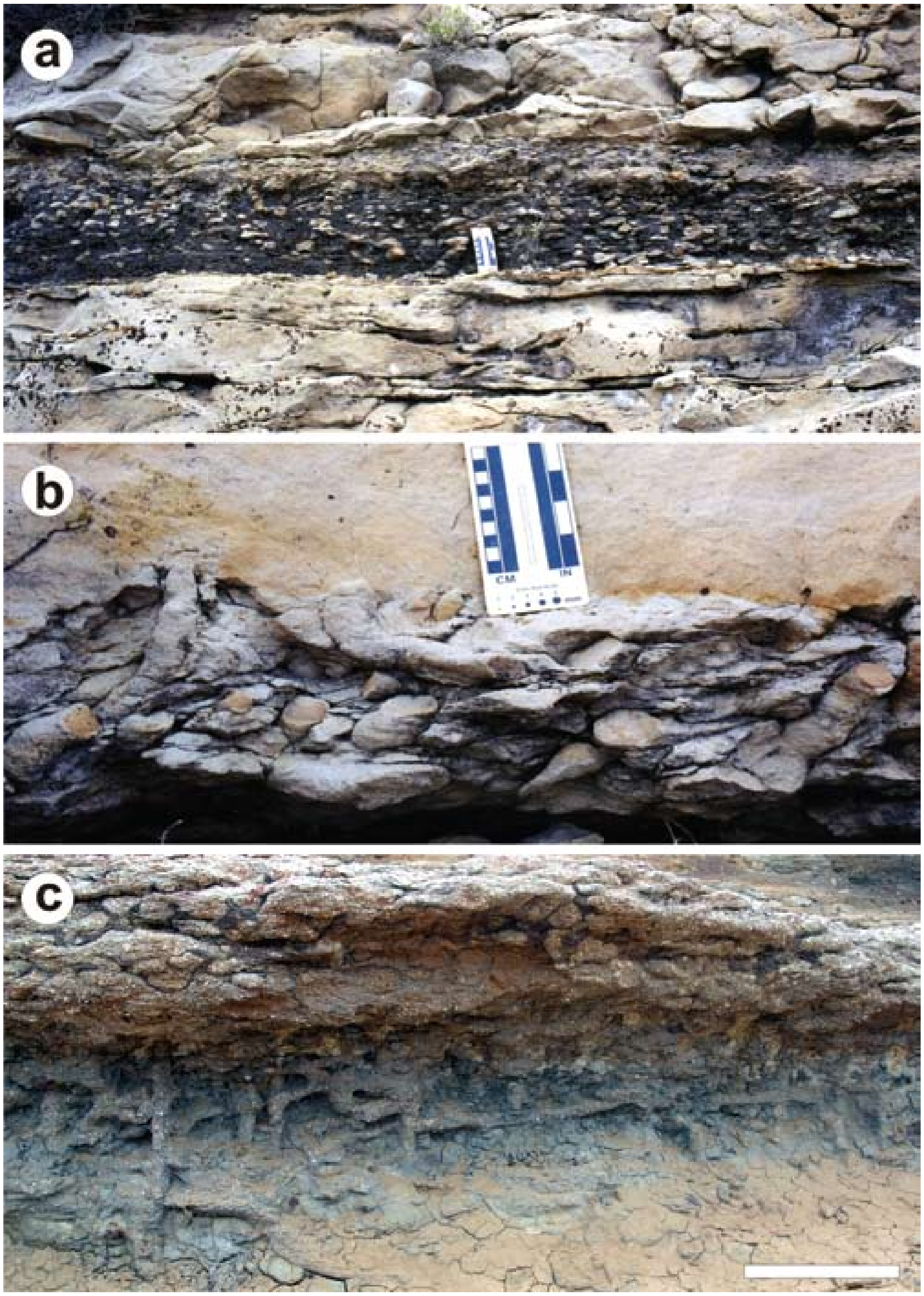


Figure 12.8 Ravinement surfaces delineated by firmground *Thalassinoides* suites of the *Glossifungites* ichnofacies. (a) The surface separates estuarine basin deposits below from sandy-channel deposits above. Upper Cretaceous, Desert Member, Blackhawk Formation, Book Cliffs, Utah, United States. (b) Close-up of firmground burrows shown in (a). (c) Transgressive deposits with thick shell lag overlying delta-plain deposits. Middle to Upper Miocene, Urumaco Formation, Urumaco River, northwestern Venezuela. Scale bar is 30 cm.

12.2.4 CO-PLANAR SURFACES OF LOWSTAND EROSION AND TRANSGRESSIVE EROSION

Co-planar surfaces of lowstand erosion and transgressive erosion occur when the fluvially cut, subaerial unconformity is modified during subsequent transgression, and no fluvial deposits are preserved above the surface (Pemberton *et al.*, 1992b). Co-planar surfaces represent sequence boundaries that are overlain not by lowstand systems tract deposits, but by transgressive systems tract deposits. The most common occurrence of co-planar surfaces is associated with incised estuarine valleys (Figs. 12.9, 12.10, and 12.11a–d). In incised valleys, fluvial deposits tend to accumulate along the valley axis during a late phase of sea-level fall, and are part of the lowstand systems tract. During the subsequent transgression, the downstream portion of incised valleys is converted into estuaries (Zaitlin *et al.*, 1994). Estuarine deposits showing varying degrees of tidal influence tend to accumulate along the valley axis, but also onlap the interfluves where they mantled a co-planar surface of lowstand and transgressive erosion.

Co-planar surfaces are commonly delineated by a whole array of substrate-controlled ichnofacies, with the *Glossifungites* ichnofacies being the most common of all (MacEachern and Pemberton, 1994). MacEachern *et al.* (1992) suggested that the

Box 12.1 *Teredolites* and sea-level changes

Studies in the Lower Paleocene Clayton Formation of Alabama have demonstrated the utility of the wood bivalve boring *Teredolites* in delineating transgressive systems tracts (TST) (Fig. 12.9). The Clayton Formation contains a thin (approximately 1.5 m) TST interval bounded at the top by a condensed section. *Teredolites* is present in high densities in logs forming a transgressive lag at the base of the TST interval. This accumulation results from an influx pulse of wood fragments from flooded forested coastal plains into marginal-marine and shallow-marine areas, and concentration of logs due to continuous scouring during ravinement. A second concentration of drifted bored logs occurs in the condensed section, marking the maximum flooding surface formed under conditions of sediment starvation. In addition, four preservational styles in *Teredolites* log-grounds have been recognized: well-preserved log-grounds, relict log-grounds, ghost log-grounds, and reworked *Teredolites*. All four preservational styles are present in the transgressive lag, albeit with different abundances and commonly showing patchy distribution. Only ghost log-grounds are present in the condensed section. Biochemical degradation is highest in the ghost log-grounds as a result of reduced sedimentation rates. Similar patterns in *Teredolites* distribution to those detected originally in the Clayton Formation have subsequently been recognized in other regions of the United States Gulf coastal plain and elsewhere.

References: Savrda (1991a); Savrda *et al.* (1993).

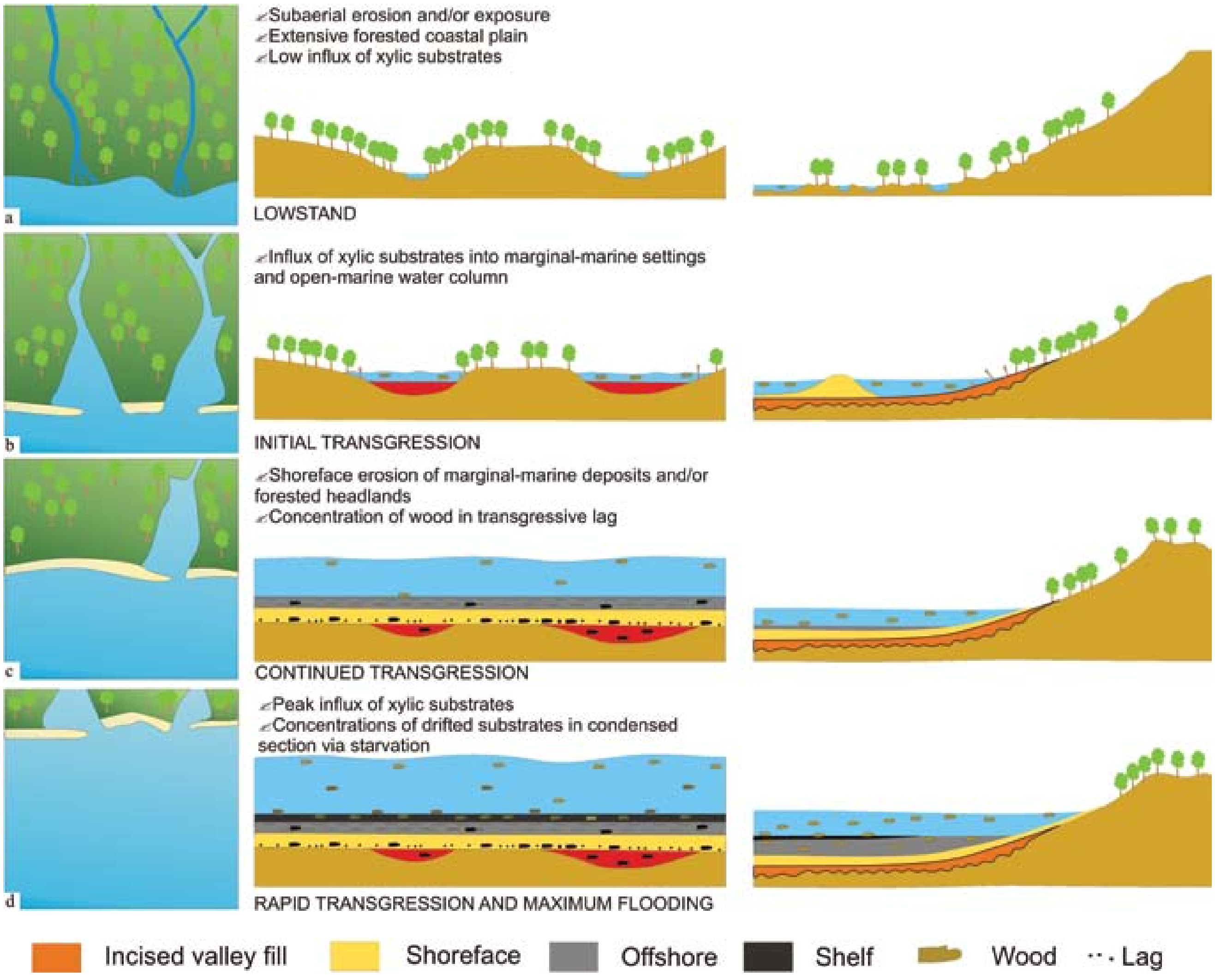


Figure 12.9 Relationships between *Teredolites* and sea-level changes. (a) During lowstand, influx of xylic substrates is low. (b) During the initial transgression, influx of xylic substrates increases due to continuous scouring during transgressive ravinement across forested coastal plains, and logs become abundant in the water column. (c) Dense concentrations of wood fragments with *Teredolites* accumulate forming transgressive lags. (d) Condensed sections form during maximum flooding. These are characterized by ghost log-grounds that have suffered intense biodegradation (modified from Savrda *et al.*, 1993).

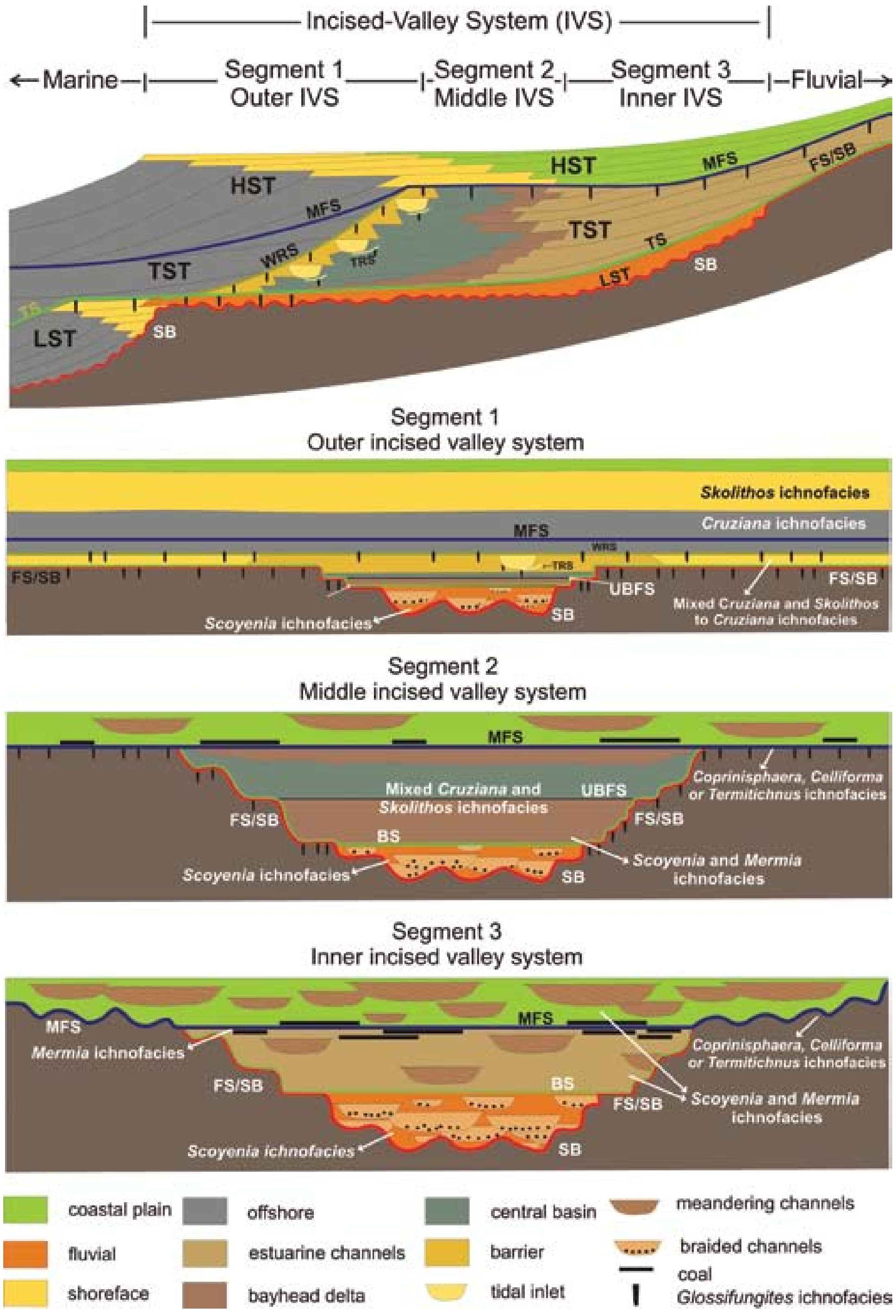


Figure 12.10 Ichnology of incised-valley systems. Modified from MacEachern and Pemberton (1994) and Buatois *et al.* (1998d). Valley segments based on Zaitlin *et al.* (1994). Segment 1 extends from the most seaward extent of valley incision, near the lowstand mouth of the incised valley, to the point where the shoreline stabilizes at the beginning of highstand progradation. Segment 2 lies between the inner end of segment 1 (i.e. the initial highstand shoreline) and the estuarine limit (i.e. the landward limit of recorded tidal influence) at the time of maximum flooding. Segment 3 is located in the innermost region of the valley, lying landward of the transgressive marine–estuarine limit, but it is still influenced by changes in base level associated with relative sea-level change. The *Glossifungites* ichnofacies occurs at multiple levels, delineating flooding surfaces/sequence boundaries, tidal-ravinement surfaces, and wave-ravinement surfaces. Note that this ichnofacies is not present if the sequence boundary is coincident with the base of lowstand fluvial deposit. LST = lowstand systems tract. TST = transgressive systems tract, HST = highstand systems tract, SB = sequence boundary, FS/SB = flooding surface/sequence boundary, TS = transgressive surface, BS = bayline surface, UBFS = upper-bay flooding surface, TRS = tidal-ravinement surface, WRS = wave-ravinement surface, MFS = maximum flooding surface.

distribution of the *Glossifungites* ichnofacies along the base of the valley may be useful to delineate the maximum landward limit of marine influence in the incised valley during initial deposition. This distribution results from the fact that the *Glossifungites* producers cannot colonize under freshwater conditions. Accordingly, the ichnofacies is not developed at the base of the lowstand systems tract (Savrda, 1991b). Carmona *et al.* (2006, 2007) noted that careful evaluation of the ichnological content, truncation of trace fossils, and the relationship between firmground biogenic structures commonly indicates a complex history for co-planar surfaces, suggesting successive events of ravinement erosion and benthic colonization during the transgression.

Bored substrates are also common along co-planar surfaces, particularly where rocky shorelines and cliffs are transgressed. The *Trypanites* ichnofacies occurs in such settings (Gibert and Martinell, 1992, 1993, 1996; Martinell and Domènech, 1995). Uchman *et al.* (2002) noted that as transgression progresses different suites of bioeroders are emplaced in the discontinuity

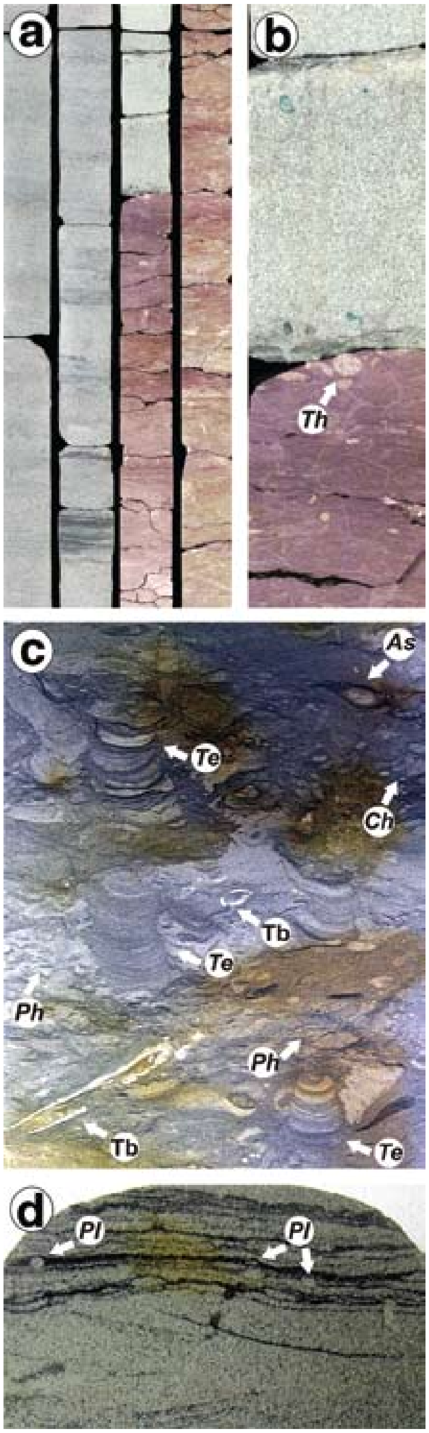


Figure 12.11 *Glossifungites* ichnofacies in a valley-incision surface, Upper Cretaceous, Magallanes Formation, Austral Basin, Patagonia, Argentina. (a) Sparsely bioturbated incised valley-fill deposits with a depauperate *Cruziana* ichnofacies sharply replace lower-offshore deposits with an archetypal to distal *Cruziana* ichnofacies. Core is read from base at lower right to top at upper left. (b) Close-up showing firmground *Thalassinoides* (*Th*) of the *Glossifungites* ichnofacies at the incision surface. (c) Close-up of intensely bioturbated lower-offshore deposits. Evenly distributed *Phycosiphon* (*Ph*) cross-cut by *Asterosoma* (*As*), *Chondrites* (*Ch*) and deep *Teichichnus* (*Te*). Note thick wall in "Terebellina (Tb)". (d) Close-up of sparsely bioturbated incised valley-fill deposits. Small *Planolites* (*Pl*) occurs in mud drapes. Core widths are 10 cm.

as a result of a decrease in light and energy that parallels an increase in water depth. In their example, the polychaete boring *Caulostrepsis* was emplaced with water depths of less than 2 m and subsequently overprinted by the bivalve boring *Gastrochaenolites* when the water depth reaches approximately 10 m. Finally, the sponge boring *Entobia* cross-cuts the other ichnofossils in water depths of a few tens of meters. Therefore, assemblages in these co-planar surfaces represent the work of several overprinted communities.

12.3 NON-EROSIONAL DISCONTINUITIES

Other surfaces of importance in sequence stratigraphy are not erosive in nature and, therefore, lack substrate-controlled ichnofacies if they are formed in siliciclastic sediments. Non-erosional discontinuities developed in carbonates are much more complex and will be addressed below. Three main situations can be recognized: low-energy drowning surfaces, low-energy flooding surfaces and maximum flooding surfaces.

Low-energy drowning surfaces separate deeper-water deposits resting on shallower-water strata (Posamentier and Allen, 1999). These surfaces are characterized by a vertical change in softground trace-fossils assemblages reflecting that deepening trend (e.g. Taylor and Gawthorpe, 1993). Examples include foreshore or upper-shoreface sandstone with a *Skolithos* ichnofacies that is sharply replaced by offshore or offshore-transition mudstone having a proximal to archetypal *Cruziana* ichnofacies. This same surface is represented seaward by offshore mudstone with a *Cruziana* ichnofacies replaced by shelf deposits containing a distal *Cruziana* ichnofacies or a *Zoophycos* ichnofacies.

Low-energy flooding surfaces separate subaerially exposed sediments from overlying subaqueous deposits as a result of a rise in base level (Posamentier and Allen, 1999). Flooding surfaces represent a special category of drowning surfaces and, in actuality, they are the landward extension of the drowning surface. These surfaces can be recognized by a vertical change in softground trace-fossil assemblages that reflect inundation of the substrate (e.g. Taylor and Gawthorpe, 1993). A typical situation is the vertical passage from alluvial or coastal-plain deposits containing the *Scoyenia* ichnofacies or paleosol trace-fossil assemblages to nearshore deposits hosting marine or brackish-water ichnofacies.

Maximum flooding surfaces refer to the surface of deposition at the time the shoreline is at its maximum landward position and, therefore, separates the transgressive from the highstand systems tract (Posamentier and Allen, 1999). Because during maximum transgression coastal depocenters are located at their maximum landward position, slow sedimentation occurs in the offshore and shelf. As a result, maximum flooding is characterized by a condensed section representing thin deposits that accumulate during long periods of time (Loutit *et al.*, 1988). The ichnological signatures of maximum flooding surfaces have not been explored in detail. However, it is well known that these surfaces are commonly associated with oxygen-poor conditions.

Therefore, condensed sections commonly are unbioturbated or display suites that are typical of dysaerobic sediments (Savrda, 1992; Pemberton *et al*., 1992b). Where transgressions are associated with flooding of forested coastal plains, maximum flooding surfaces may be characterized by concentrations of logs with *Teredolites* that accumulate under sediment starvation (Savrda, 1991a; Savrda *et al*., 1993, 2005) (Box 12.1).

12.4 CHARACTERIZATION OF PARASEQUENCES

In addition, recognizing changes in ichnofaunal content across a succession may help to identify parasequences. A parasequence is a shallowing-upward succession bounded by marine flooding or drowning surfaces (Van Wagoner *et al*., 1990). The concept is particularly useful for the study of shallow-marine successions and, less commonly, lake systems, but its application to the study of alluvial and deep-marine strata is not recommended (Posamentier and Allen, 1999). The use of ichnology to delineate parasequences is based on the fact that trace-fossil associations are excellent indicators of environmental conditions that generally change according to a bathymetric gradient. In parasequences of clastic shallow-marine settings, two situations must be considered depending on the predominant depositional process: wave-dominated coasts and tide-dominated coasts. A third type of parasequence is generated in deltaic systems. Little is known about the architecture, grain-size vertical trends, and trace-fossil distribution in parasequences formed in mixed tide- and wave-dominated systems. However, preliminary information from modern environments (see Section 7.3) suggests that tidal beaches may show parasequences that are very similar to those of wave-dominated shallow-marine settings, while parasequences in wave-dominated tidal flats may display much more similarity to those of tide-dominated shorelines, particularly if inner mud-flat zones are developed.

12.4.1 WAVE-DOMINATED PARASEQUENCES

A wave-dominated parasequence coarsens and thickens upward, recording shoreline progradation (Van Wagoner *et al*., 1990). In terms of associated environmental factors, each parasequence reflects a progressive upward increase in hydrodynamic energy, degree of oxygenation, sand content, amount of organic particles in suspension, and mobility of the substrate that control the vertical distribution of trace fossils (Pemberton *et al*., 1992c; Mángano *et al*., 2002a, 2005a). Parasequences in wave-dominated strandplain environments pass gradually, from base to top, from a distal *Cruziana* ichnofacies in the lower offshore, an archetypal *Cruziana* ichnofacies in the upper offshore to offshore transition, a proximal *Cruziana* ichnofacies that is partially combined with a *Skolithos* ichnofacies in the lower shoreface, a *Skolithos* ichnofacies from the middle shoreface to the foreshore, and a *Psilonichnus* ichnofacies across the backshore (MacEachern and Pemberton, 1992; MacEachern *et al*., 1999a; Mángano *et al*., 2002a, 2005a). It should be noted, however, that this ideal parasequence is the exception rather than the rule because not all subenvironments are represented in each parasequence. This environmental zonation is based on the characteristics of the resident ichnofauna, and the displacement of the *Skolithos* ichnofacies towards more distal parts in response to storm events (Pemberton and MacEachern, 1997) renders it complicated.

12.4.2 TIDE-DOMINATED PARASEQUENCES

Less attention has been focused on tide-dominated parasequences, and several problems have arisen as a result of arbitrarily extrapolating the wave-dominated model to environments where tide is the driving process. A tide-dominated parasequence fines and thins upward, recording tidal-flat progradation (Van Wagoner *et al*., 1990). The energy peak is in the deeper-subtidal zone rather than in intertidal areas. Therefore, each parasequence reflects an upward decrease in hydrodynamic energy, degree of oxygenation, sand content, amount of organic particles in suspension, and substrate mobility. Vertical ichnofacies replacement in a tide-dominated parasequence is just the opposite to that of a wave-dominated parasequence (Mángano *et al*., 2002a, 2005a; Mángano and Buatois, 2004a). A typical tide-dominated parasequence begins with non-bioturbated sandstone accumulating in subtidal-sandbar and dune complexes which upwards may contain colonization surfaces with low-diversity assemblages of the *Skolithos* ichnofacies. Lower-intertidal sand-flat deposits containing a mixture of elements from the *Skolithos* and *Cruziana* ichnofacies occur above. The *Cruziana* ichnofacies gets increasingly important to the point of becoming predominant in mixed intertidal flat, despite the fact that ichnodiversity is not necessarily high. The upper part of the parasequence generally involves mudstone deposits containing root trace fossils and elements of the *Psilonichnus* ichnofacies. Ichnofacies zonation depends largely on tidal regime (Mángano and Buatois, 2004a). In high-energy systems, lower-intertidal sectors tend to be dominated by elements of the *Skolithos* ichnofacies, which turn out to be similar to subtidal deposits from the ichnological viewpoint. In contrast, under lower-energy conditions, lower-intertidal zones are dominated by the *Cruziana* ichnofacies.

12.4.3 DELTAIC PARASEQUENCES

Deltaic parasequences are highly variable, depending on the dominant process operating (waves, tides, and fluvial). Parasequences can be particularly delineated in the prodelta to delta front. Recognition of parasequences in the delta plain remains a contentious issue (Posamentier and Allen, 1999). In addition, shallowing-upward successions apparently limited by flooding surfaces may be produced by deltaic-lobe switching rather than by true allogenic processes, such as sea-level change (e.g. Törnqvist *et al*., 1996). Little is known about trace-fossil distribution in parasequences formed in tide-dominated deltas and our discussion is, therefore, focused on parasequences from wave- and river-dominated deltas.

Parasequences from wave-dominated deltas are similar to those formed in wave-dominated, non-deltaic shorelines because wave energy tends to buffer fluvial effects (MacEachern *et al*., 2005). As in strandplain parasequences, a wave-dominated parasequence coarsens and thickens upward, recording delta progradation (Van Wagoner *et al*., 1990). Parasequences formed in these settings pass gradually, from base to top, from a distal *Cruziana* ichnofacies in the distal prodelta, an archetypal *Cruziana* ichnofacies in the proximal prodelta to distal delta front and a proximal *Cruziana* ichnofacies or *Skolithos* ichnofacies in the proximal delta front. However, subtle differences can be detected. The *Cruziana* ichnofacies may be slightly impoverished with respect to its more fully marine bathymetric equivalents of strandplain parasequences. In addition, high concentration of silt and clay in the water column reduces the amount of suspension feeders, producing an anomalous *Skolithos* ichnofacies.

Parasequences formed in river-dominated deltas also coarsen and thicken upward. In contrast to those from wave-dominated settings, river-induced stresses are more profound (MacEachern *et al*., 2005). Parasequences from river-dominated deltas pass gradually, from base to top, from a distal *Cruziana* ichnofacies in the distal prodelta, a depauperate *Cruziana* ichnofacies in the proximal prodelta to distal delta front and sparse indistinct bioturbation, if any, in the proximal delta front. River discharge often results in dilution of marine salinity, resulting in impoverishment of the *Cruziana* ichnofacies. In addition, water turbidity is very high, resulting in the suppression of the *Skolithos* ichnofacies.

12.5 DELINEATION OF PARASEQUENCE SETS AND SYSTEMS TRACTS

Integrating ichnological evidence, and sedimentological and stratigraphic data, sedimentary successions at the parasequence-set scale can be characterized in order to detect transgressive and regressive trends, assisting in systems-tract recognition. In this respect, two situations will be addressed: progradational and retrogradational patterns. The former is illustrated by either prograding deltas or strandplains and the latter by transgressive estuarine valley fill.

12.5.1 PROGRADATIONAL PATTERNS

Because deltas are, by definition, progradational, deltaic parasequences tend to stack forming progradational parasequence sets. Ichnofaunas are generally indicative of vertical replacement of forms which are typical of alternating normal or nearly normal salinity and brackish-water environments across the prodelta and delta front by forms adapted to brackish-water across the delta plain. As discussed above, whether deltas are river-, tide-, or wave-dominated results in great variations in ichnofossil content. The top of the parasequence set may even exhibit biogenic structures resulting from freshwater fauna living in water bodies across deltaic plains or in distributary streams.

12.5.2 RETROGRADATIONAL PATTERNS

In contrast to deltaic and strandplain successions, however, identification of parasequences in incised valleys is not straightforward (Posamentier and Allen, 1999). In any case, successions recording an estuarine valley fill typically show a clear retrogradational trend that illustrates transgressive stratigraphy (Fig. 12.10). The estuarine valley incision surface is carved during a sea-level fall but the valley fill corresponds mostly to the subsequent transgressive phase (Zaitlin *et al*., 1994). Lowstand-fluvial deposits may even be preserved along the valley axis above the basal incision surface. These deposits commonly exhibit limited bioturbation, resulting from the activity of freshwater biotas or, more commonly, are devoid of biogenic structures.

According to Dalrymple *et al*. (1992), the onset of estuarine deposition is indicated by the lowest occurrence of sandstone with clay drapes of tidal origin, which therefore can be used to detect the boundary between the lowstand systems tract and the transgressive systems tract. The surface separating these two systems tracts within incised valleys is referred to as the bayline surface (Thomas and Anderson, 1994) (Fig. 12.10). Substrate-controlled ichnofacies delineate the valley incision surface where basal fluvial-lowstand deposits do not separate the sequence boundary from the initial flooding surface (Savrda, 1991b). Estuarine valley fill deposits overlying the bayline surface along the valley axis or the incision surface towards the valley margins contain an impoverished ichnofauna characterized by a mixture of the *Skolithos* and *Cruziana* ichnofacies (Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994) (Fig. 12.10). This depauperate ichnofauna records the activity of an opportunistic community developed under stressful conditions in a brackish-water estuarine setting.

Another surface present within incised valleys is the upper-bay flooding surface, which separates sandy upper-estuary deposits from overlying finer-grained facies of the estuary basin (Thomas and Anderson, 1994). The passage from upper-estuary into lower-energy estuary-basin deposits is usually paralleled by a slight increase in ichnodiversity. Upward into the sequence, estuary-basin deposits are separated from the estuary-mouth complex by the tidal-ravinement surface. Due to tidal scouring, this surface commonly hosts a *Glossifungites* ichnofacies (MacEachern and Pemberton, 1994) (Fig. 12.10). Because the estuary mouth commonly experiences near-marine salinity conditions, trace-fossil assemblages may be fairly diverse in this outer region of the incised valley (e.g. Buatois and Mángano, 2003c). Overlying the estuary-mouth complex and underlying the transgressive shoreface, the wave-ravinement surface occurs. Above this surface, ichnofaunas are typically fully marine.

A slight variation to this pattern may occur in the innermost zone of macrotidal estuarine systems that are characterized by arthropod-dominated, diverse assemblages (Buatois *et al*., 1997b). These ichnofaunas belong to mixed *Scoyenia* and *Mermia* ichnofacies, and tend to occur in the basal transgressive deposits immediately above the co-planar surface (Fig. 12.10). In this specific setting and at this particular stage of estuarine valley evolution, freshwater conditions coexist with tidal influence (Buatois *et al.*, 1998d). As transgression proceeds, backstepping brackish-water deposits accumulate. The ichnological signature of such a change in depositional conditions is reflected in the upward replacement of the mixed *Scoyenia* and *Mermia* ichnofacies by the mixed *Skolithos* and impoverished *Cruziana* ichnofacies.

Overall, and in contrast with deltaic successions that typically display a vertical decrease in ichnodiversity due to an increased influence of fluvial processes, estuarine valley-fill successions show vertical passage of brackish-water ichnofaunas exhibiting increasing marine influence into more diverse associations which are indicative of normal salinity (MacEachern and Pemberton, 1994; Buatois *et al.*, 1998d, 2002b). In compound valley systems, which record more that one cycle of relative sea-level change, the ichnological record is more complex and more diverse climax and depauperate opportunistic trace-fossil assemblages tend to alternate as a result of reincision.

12.6 CARBONATE SEQUENCE STRATIGRAPHY

Comparatively little is known with respect to the sequence-stratigraphic significance of trace fossil in carbonates. Carbonate sequence stratigraphy shows significant departures with respect to its siliciclastic equivalent (Bosence and Wilson, 2003; Schlager, 2005; Catuneanu, 2006). Most of these differences stem from the fact that carbonates are produced within the basin itself in the so-called "carbonate factory". Carbonate production is directly proportional to the area of flooded platform top. Accordingly, sediment availability in carbonate systems shows an opposite trend to that of siliciclastic systems. While in siliciclastic systems there is an increased in sediment supply during lowstands and sediment starvation characterizes transgressions, in carbonate systems carbonate factories achieve their maximum production during transgressions, but sea-level fall generates their shutdown. However, if the rise of sea level is very fast and the water depth exceeds the photic limit, carbonate production is terminated and a drowning unconformity is formed. During highstand, the volume of carbonate sediment exceeding accommodation space is shed to the deep water (highstand shedding; see Bosence and Wilson, 2003).

A major departure with respect to siliciclastic substrate-controlled ichnofacies results from the fact that firmgrounds and hardgrounds can be formed in carbonates without erosional exhumation, simply as a result of early diagenetic changes in the substrate (Bromley, 1975). Consequently, the *Glossifungites* and *Trypanites* ichnofacies can develop during periods of reduced depositional rates or breaks in sedimentation. While substrate-controlled ichnofacies in siliciclastic settings are not typically associated with low-energy transgressive surfaces, the opposite is true in carbonate systems. Drowning unconformities may contain firmground and hardground suites. Surfaces containing deep and widespread borings of the *Trypanites* ichnofacies may occur due to the shutdown of the carbonate factory during rapid drowning. In addition, condensation may occur along maximum flooding surfaces in carbonate ramps, leading to the development of substrate-controlled ichnofacies.

If sufficient time is involved, composite ichnofabrics showing progressive changes in substrate consistency are formed (Bromley, 1975; Frey and Bromley, 1985; Ekdale and Bromley, 1991; Lewis and Ekdale, 1992). Omission surfaces and hardgrounds are commonly associated. Omission surfaces are characterized by pre-omission, omission, and post-omission trace-fossil suites (Bromley, 1975, 1996). Pre- and post-omission suites contain softground assemblages, while the omission suite is characterized by the firmground *Glossifungites* ichnofacies. Because no cementation is involved in the formation of omission surfaces, no hardground suites developed. Pre- and post-omission suites in hardgrounds also host softground suites. However, and in contrast to omission surfaces in firmgrounds, the omission suite in hardgrounds is subdivided into pre- and post-lithification suites (Bromley, 1975, 1996). The former hosts the *Glossifungites* ichnofacies, while the latter contains the *Trypanites* ichnofacies. The *Trypanites* suite typically cross-cuts the *Glossifungites* suite, resulting in palimpsest surfaces (e.g. Mángano and Buatois, 1991; Bertling, 1999). In some cases, these surfaces contain bored shells that also reveal breaks in sedimentation (e.g. Martinius and Molenaar, 1991).

In addition to these cases, substrate-controlled ichnofacies may also occur in erosional surfaces, and are commonly associated with rocky shorelines consisting of truncated limestone. Transgressive surfaces of erosion formed by wave ravinement of carbonate substrates contain the *Glossifungites* ichnofacies, commonly exhibiting high-density suites of firmground burrows (e.g. Rodríguez-Tovar *et al.*, 2007). Well-known examples are also associated with co-planar surfaces. During lowstands, carbonates dissolve and karstic surfaces develop under subaerial conditions. Calcareous paleosols may form, and display an ichnofauna dominated by nests of halictid bees, representing the *Celliforma* ichnofacies (Melchor *et al.*, 2002). During the subsequent transgression, karstic surfaces are colonized, and the *Trypanites* ichnofacies is the typical ichnofacies present (e.g. Pemberton *et al.*, 1980; Hanken *et al.*, 1996; Wilson *et al.*, 1998). Some of these surfaces may evidence a complex history of colonization, particularly in reef systems (Fig. 12.12a–d). Shallow borings emplaced in the reef can be removed due to erosion during sea-level fall and only the deepest borings (*Gastrochaenolites*) are preserved. A second generation of borings occurs on the same surface after the subsequent transgression (Wilson *et al.*, 1998).

Studies dealing with the ichnological characterization of carbonate parasequences are uncommon, but examples are known from tropical carbonates (Pemberton and Jones, 1988; Jones and Pemberton, 1989; Curran, 1992, 1994, 2007). Parasequences documented in modern and Quaternary Bahamian-type carbonates consists, from base to top, of: (1) shallow-subtidal coral reef, coral rubblestone, and calcarenite with borings of the *Trypanites* ichnofacies (e.g. *Gastrochaenolites*), and burrows

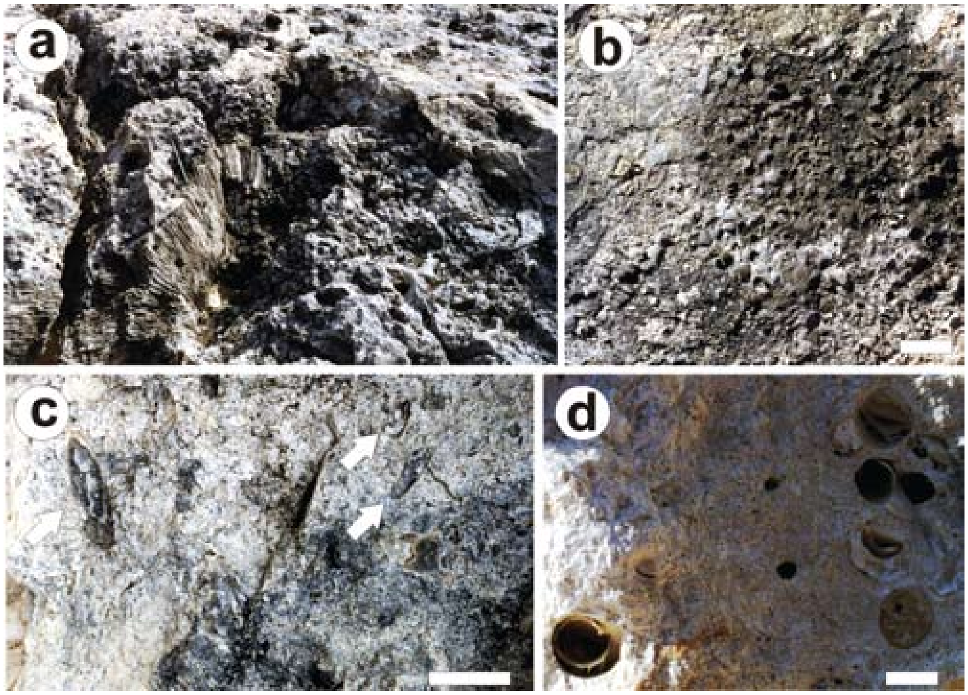


Figure 12.12 Substrate-controlled ichnofacies delineating a co-planar surface in carbonates. Pleistocene, Cockburn Town Member, Grotto Beach Formation, San Salvador Island, Bahamas. (a) Erosional surface sculpted in a coral reef. Note the presence of the encrusting coral *Diploria strigosa*. Pencil (center left) is 16 cm. (b) Close-up of the erosional surface showing high density of the bivalve boring *Gastrochaenolites torpedo*. Some of these borings are truncated, and only their bases are preserved. These borings represent colonization prior to erosion due to sea-level fall. Scale bar is 5 cm. (c) *Gastrochaenolites torpedo* (arrows) emplaced in the encrusting coral *Acropora palmata*. Scale bar is 3 cm. (d) *Gastrochaenolites torpedo* formed prior to the sea-level fall and filled with material derived from a terra rossa paleosol developed during the lowstand. Scale bar is 1 cm. See Wilson *et al*. (1998).

of the *Skolithos* ichnofacies (e.g. *Skolithos*, *Ophiomorpha*), (2) lagoonal intertidal oolitic limestone with the mixed *Skolithos–Cruziana* ichnofacies, (3) beach-backshore calcarenite containing the *Psilonichnus* ichnofacies, and (4) coastal eolian-dune calcarenite, and paleosols with insect and arachnid trace fossils (see Section 11.1.1).

12.7 CONTINENTAL SEQUENCE STRATIGRAPHY

In comparison with their marine counterparts, continental ichnology has been less explored with respect to its utility in sequence stratigraphy, and trace fossils are undoubtedly still underutilized in this field. Application of ichnology in continental sequence stratigraphy cannot be simply based on the extrapolation of marine sequence stratigraphy and a modified conceptual framework should be adopted (Buatois and Mángano, 2004a, 2007, 2009a). While substrate-controlled ichnofacies reflect erosive exhumation of the sediment in marine environments, this is rather unusual in continental settings. In continental successions, substrate-controlled ichnofacies are commonly related to firmgrounds that rapidly developed under subaerial exposure by autogenic processes, without implying a significant hiatus (e.g. Fürsich and Mayr, 1981; Zonneveld *et al*., 2006).

12.7.1 LAKE BASINS

Further problems result from the application of sequence-stratigraphic concepts in continental environments, particularly in the case of lacustrine systems. As noted by Bohacs *et al.* (2000), lacustrine systems differ from oceans in several ways, including the smaller volumes of sediment and water included in lakes, the direct link between lake level and sediment supply, and the fact that shoreline migration may be due not only to progradation but also to withdrawal of water. Bohacs *et al.* (2000) recognized three different types of lake basins, overfilled, balanced-fill, and underfilled, providing a conceptual and practical framework to evaluate the potential of trace fossils in lacustrine sequence stratigraphy (Buatois and Mángano, 2004a, 2007, 2009a) (Fig. 12.13). This framework has been also used to place changes in species diversity in modern and ancient lakes (Gierlowski-Kordesch and Park, 2004).

OVERFILLED LAKES

Overfilled-lake basins are formed when rate of sediment/water input exceeds potential accommodation (Bohacs *et al.*, 2000). According to these authors, overfilled lakes are commonly hydrologically open, contain fluvio-lacustrine siliciclastic deposits and display parasequences driven mainly by shoreline progradation and delta-channel avulsion. Overfilled-lake basins contain well-developed softground trace fossils that are useful to delineate parasequences and parasequence sets (e.g. Buatois and Mángano, 1995c; Melchor *et al.*, 2003; Melchor, 2004). Fluvial discharge into overfilled lakes commonly contributes to the formation of underflow currents that oxygenate lake bottoms. These density currents allow epifaunal and infaunal communities to become established (Buatois and Mángano, 1998).

In addition to being well oxygenated, overfilled lakes are typically freshwater and no stress due to hypersalinity occurs, leading to the development of a relatively diverse benthos. Shallowing-upward successions due to delta and shoreline

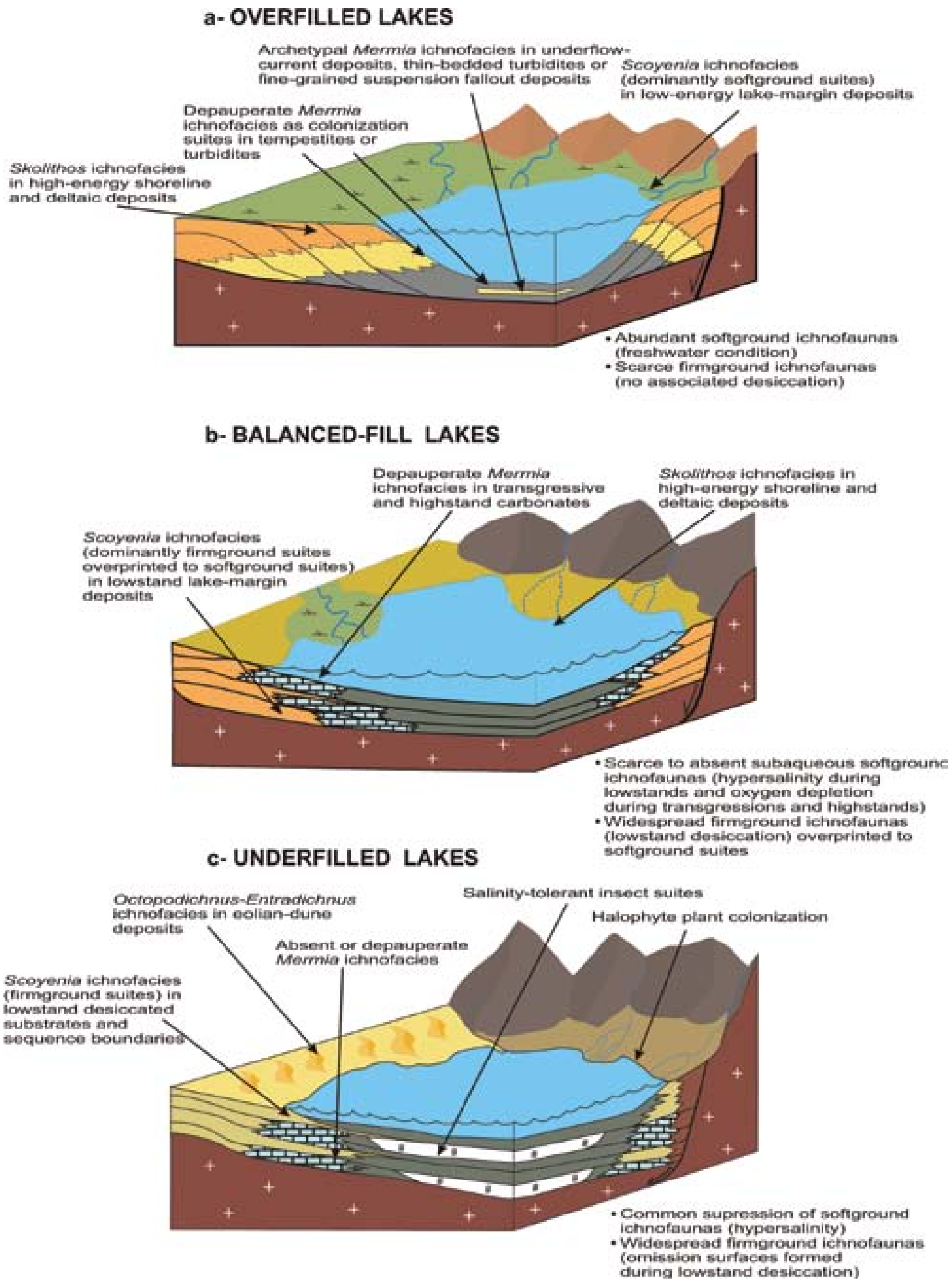


Figure 12.13 Trace-fossil assemblages, environmental controls, and lacustrine sequence stratigraphy. (a) Overfilled lakes. (b) Balanced-fill lakes. (c) Underfilled lakes. Modified from Buatois and Mángano (2004a, 2009a) with stratal patterns illustrated after Bohacs *et al.* (2000).

progradation are the rule (Fig. 12.14). Distal facies commonly consist of underflow-current and background-fallout deposits hosting the *Mermia* ichnofacies. Intermediate facies may contain wave-dominated delta-front and nearshore deposits, including storm-emplaced hummocky cross-stratified sandstone and fair-weather wave- and combined-flow ripple cross-laminated sandstone. Grazing trails of the *Mermia* ichnofacies may form colonization suites at the top of storm beds in such settings. However, assemblages are commonly impoverished with respect to those of the more distal facies (Buatois and Mángano, 1998). Under conditions of moderate to high energy due to continuous wave action, the *Skolithos* ichnofacies tends to occur. More energetic, proximal facies, encompassing trough and tabular cross-bedded distributary-channel sandstone, are commonly unbioturbated. Locally, these deposits may contain escape trace fossils, and vertical domiciles of suspension feeders, representing the *Skolithos* ichnofacies (e.g. Melchor *et al.*, 2003).

In the case of deep overfilled lakes, extensive basin-floor turbidite systems are formed. Middle to distal regions of turbidite-lobe successions are characterized by the *Mermia* ichnofacies which may comprise both pre- and post-depositional suites in thin-bedded turbidite sandstone (e.g. Buatois *et al.*, 1996b; Buatois and Mángano, 1998). Thick-bedded turbidites are typically unbioturbated. Paleoenvironmental zonations in aggradational and progradational turbidite lobes can be established by integrating ichnological and sedimentological evidence (e.g.

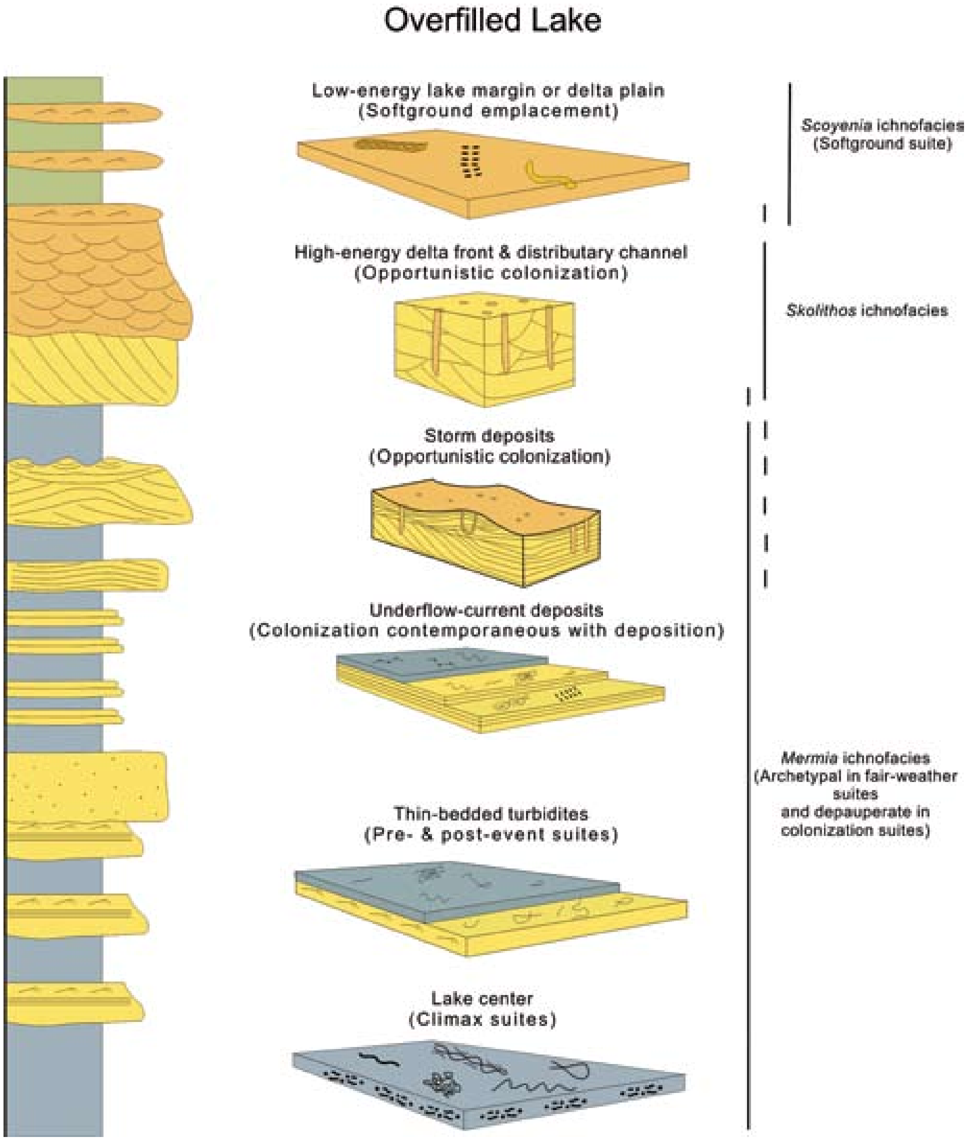


Figure 12.14 Trace-fossil distribution in overfilled lake basins. Note the overwhelming dominance of softground suites and the progressive replacement of ichnofacies due to shallowing (after Buatois and Mángano, 2009a).

Buatois and Mángano, 1995c; Buatois *et al.*, 1996b). Organic matter in overfilled lakes is essentially derived from land plants, representing the prime source of nutrients and, therefore, favoring the development of a deposit-feeding benthic fauna in permanently subaqueous, low-energy zones. Because such large lakes usually do not experience desiccation, firmground suites are rare, and only the softground suite of the *Scoyenia* ichnofacies is present.

BALANCED-FILL LAKES

Balanced-fill lake basins are characterized by rates of sediment/water supply in balance with potential accommodation (Bohacs *et al.*, 2000). Carbonate and siliciclastic facies accumulate in lakes that periodically shift from hydrologically open to closed and vice versa. In contrast to overfilled lakes, successions record not only progradational parasequences, but also aggradation of chemical sediments due to desiccation. Abundant firmground trace-fossil suites occur in balanced-fill lakes, but softground assemblages are usually depauperate (Fig. 12.15). During lowstands, shallow balanced-fill lakes are characterized by relatively thin aggradational parasequences due to desiccation (Bohacs *et al.*, 2000). Due to pervasive desiccation, lowstand deposits tend to host abundant and widespread ichnofaunas of the *Scoyenia* ichnofacies. In particular, the firmground suite of this ichnofacies, containing striated trace fossils, such as *Scoyenia* and *Spongeliomorpha*, is common (e.g. Bromley and Asgaard, 1979; Gierlowski-Kordesch, 1991; Metz, 1995; Clemensen *et al.*, 1998). Biogenic structures are usually preserved during subsequent flooding by rapid influx of sand.

During lowstands relatively thick aggradational parasequence sets form in lake-floor turbidite systems if the balanced-fill lakes are of sufficient depth (Bohacs *et al.*, 2000). Under

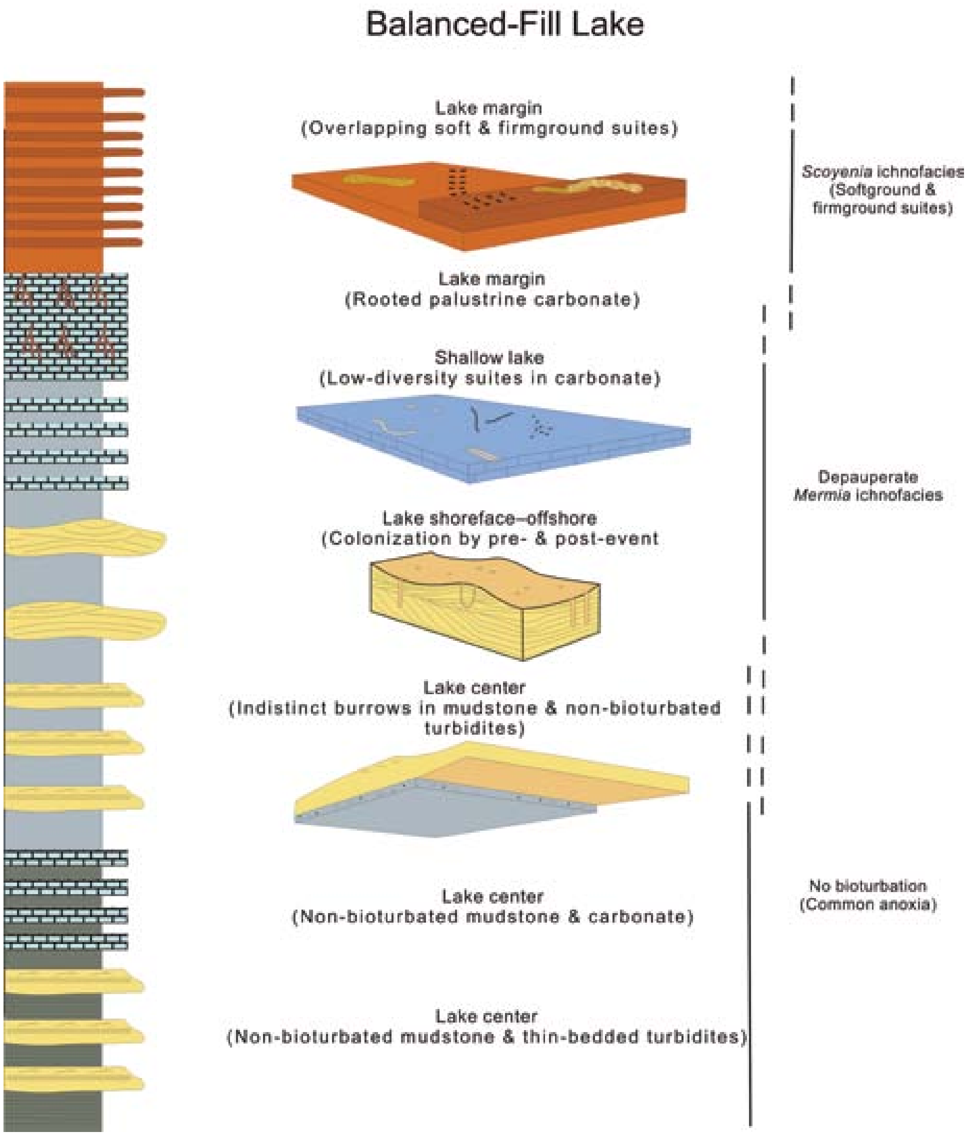


Figure 12.15 Trace-fossil distribution in balanced-fill lake basins. Note the paucity of subaqueous suites and the common superimposition of softground and firmground suites in lake-margin deposits (after Buatois and Mángano, 2009a).

these conditions, no firmground suites occur in the lowstand package. Lake hydrology is closed during lowstands and salinity usually increases (Bohacs *et al.*, 2000), imposing a stress factor on the lake biota and, therefore, softground ichnofaunas are of low diversity if not absent at all. Ichnofaunas in thin-bedded turbidites of balanced-fill lakes are less abundant and diverse than those in turbidites of overfilled lakes (Buatois *et al.*, 1996b; Buatois and Mángano, 2007; Uchman *et al.*, 2007).

Parasequences formed during transgressions are relatively thick and display retrogradational stacking patterns, while highstand parasequences are variable in thickness and are either aggradational or progradational (Bohacs *et al.*, 2000). Freshwater conditions are common during transgression, but dysaerobic conditions may prevail, imparting a stress factor on lacustrine communities. Although trace fossils may occur locally in transgressive and highstand carbonates, ichnodiversity is low and trace fossils are produced by epifaunal rather than infaunal organisms, suggesting brief periods of oxygenated bottom waters, but permanently anoxic interstitial waters (e.g. Buatois *et al.*, 2000). The depauperate *Mermia* ichnofacies is characteristic of these deposits. Further complications result from the low preservation potential of trace fossils in carbonates due to diagenetic alteration. Scarcity or even absence of biogenic structures due to oxygen depletion may also be the rule in transgressive and highstand siliciclastic deposits of balanced-fill lakes (e.g. Olsen, 1989; Mángano *et al.*, 1994, 2000; Metz, 1995). During highstand progradation of deltaic systems, elements of the *Skolithos* ichnofacies may occur in delta mouth-bar deposits (Bromley and Asgaard, 1979; Mángano *et al.*, 1994, 2000).

UNDERFILLED LAKES

Underfilled-lake basins occur when rates of accommodation exceed rate of supply of sediment/water (Bohacs et al., 2000). In

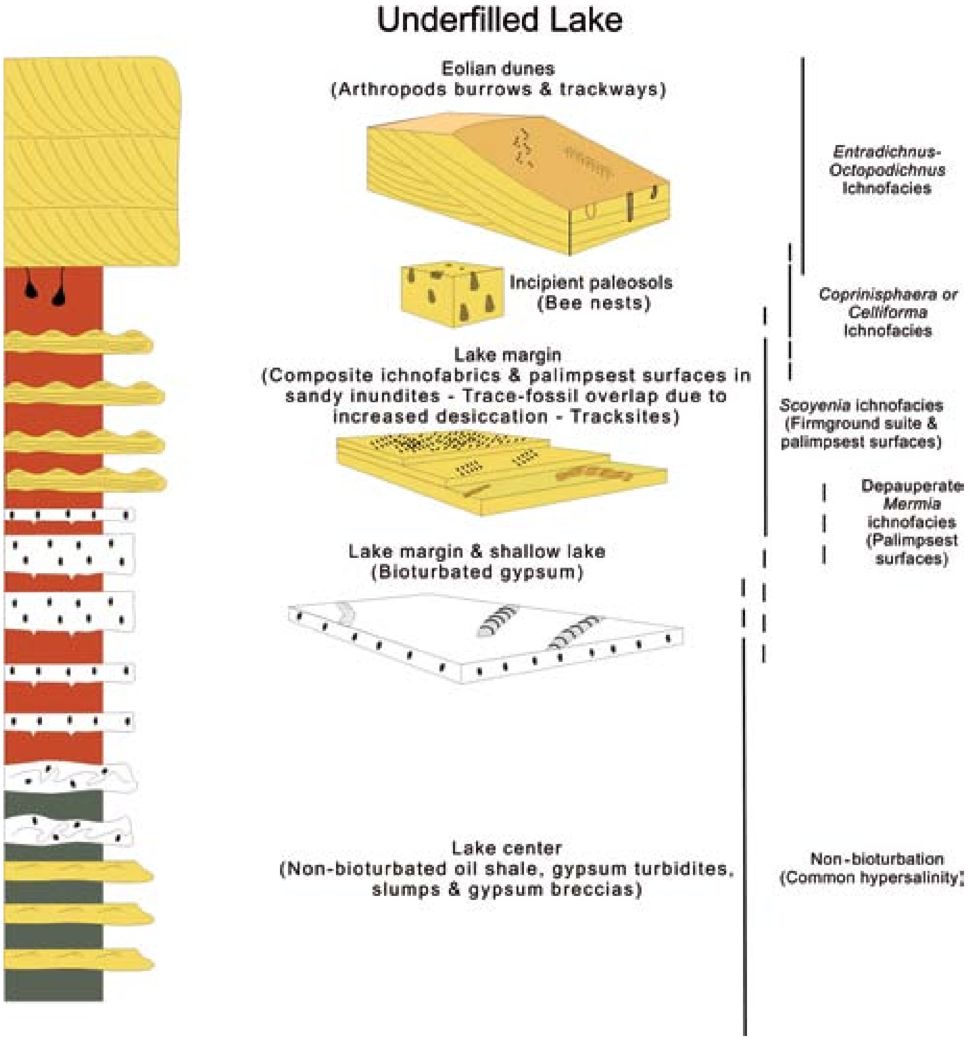


Figure 12.16 Trace-fossil distribution in underfilled lake basins. Note the typical absence of bioturbation in most of the subaqueous deposits as a result of hypersalinity. Instead of progressive replacement of ichnofacies throughout the stratigraphic column, a complex overlap of suites characterizes the lake-margin interval reflecting omission surfaces formed in response to desiccation (after Buatois and Mángano, 2009a).

hydrologically closed lakes, deposition of evaporites dominates and parasequences record vertical aggradation. The *Scoyenia* ichnofacies is widespread in underfilled lake basins, but the *Mermia* ichnofacies is commonly absent (Fig. 12.16). Lowstand deposition is characterized by evaporite accumulation in remnant pools developed in the zones of maximum subsidence (Bohacs *et al*., 2000). Evaporite pools are very stressful environments and almost invariably lack biogenic structures. In the remaining zones, sediments that accumulated during the previous highstand experience extreme desiccation during lowstand (Bohacs *et al*., 2000).

The *Scoyenia* ichnofacies is associated with lowstand desiccated substrates in underfilled lakes (e.g. Metz, 1996, 2000; Scott *et al*., 2007b). The density of arthropod trackways, as well as various trace fossils produced by insects, may be high, forming tracked omission surfaces (e.g. Zhang *et al*., 1998; Minter *et al*., 2007b; Scott *et al*., 2007b; Bohacs *et al*., 2007). Extensive surfaces with high densities of tetrapod trackways or tracksites occur also (e.g. Farlow and Galton, 2003; Szajna and Hartline, 2003). Some of these omission surfaces may represent sequence boundaries expressed by co-planar surfaces of lowstand and subsequent flooding (Scott *et al*., 2009) (Box 12.2). Lake-level fluctuations, particularly in gently dipping lacustrine coastal plains, are conducive to complex cross-cutting relationships due to trace-fossil suite overprinting, particularly where the surfaces involve more than one transgressive-regressive cycle (Scott *et al*., 2009). During pluvial periods, underfilled lakes experience rapid expansion and flash floods reach the basin, leading to deposition of event sandstones. Trace-fossil preservation is mostly linked to rapid influx of sand via sheet floods entering into the lake (Zhang *et al*., 1998).

Hypersalinity usually prevents the establishment of a subaqueous *Mermia* ichnofacies during transgression and highstand. However, elements of the *Mermia* ichnofacies may occur, albeit in reduced numbers, in very shallow-water thin deposits immediately above flooding surfaces at the base of parasequences. This assemblage is abruptly replaced upward by the *Scoyenia* ichnofacies reflecting lake regression (Metz 1996, 2000). Additionally, dwelling traces possibly produced by aquatic chironomid larvae may be present (Rodríguez-Aranda and Calvo, 1998; Uchman and Álvaro, 2000).

Box 12.2 Ichnological complexity of co-planar surfaces in underfilled lakes

A set of interfingering Upper Pleistocene and Holocene exhumed surfaces in the underfilled saline Lake Bogoria of Kenya reveals a complex story of changes in lake level and environmental controls on biogenic structures through time. Ongoing exhumation of the surface near the present shoreline has reactivated the sediments as a substrate for animal and plant colonization. The modern environmental setting at Lake Bogoria is very similar to that of the preserved exhumed surfaces, favoring comparisons on both sides of the fossilization barrier. These exhumed surfaces are amalgamated in places forming a co-planar surface that includes up to five suites of animal and plant traces, which are commonly overprinted forming palimpsest surfaces. Suite 1 includes the traces of chironomid larvae formed in subaqueous lacustrine environments. Suite 2 consists of flamingo traces formed at the shoreline. This suite is comparable to the *Grallator* ichnofacies. Suite 3 comprises trails (incipient *Gordia* isp. and *Helminthoidichnites* isp.) and burrows systems (incipient *Labyrintichnus* and *Vagorichnus* isp.). These were emplaced in relatively fresh, saturated to extremely shallow subaqueous substrates. This suite compares well with the *Mermia* ichnofacies. Suite 4 consists of simple vertical (*Skolithos* ispp.), simple horizontal (*Planolites* isp.) and branched (incipient *Vagorichnus* isp. and *Spongeliomorpha* isp.) burrows, trackways (e.g. incipient *Diplichnites*, *Diplopodichnus*, and *Siskemia*), rhizoliths, and various vertebrate footprints including mainly birds and mammals. This suite is present at the lake margin and is associated with substrates of various degrees of consolidation, commonly near fresh and brackish water sources, including hot-springs and rivers. The striated burrows (i.e. *Spongeliomorpha* isp.) occur in drying, firmer, and slightly indurated substrates. This suite illustrates the *Scoyenia* ichnofacies, including both pre- and post-desiccation elements. Suite 5 contains termite (?*Termitichnus* isp.) and ant nests, simple burrows (*Planolites* isp., *Palaeophycus* isp.), meniscate trace fossils (?*Beaconites* isp., *Taenidium* isp.), and rhizoliths. This suite records colonization in subaerially exposed substrates associated with low water tables, and favors comparison with paleosol assemblages described elsewhere. Suite overprinting of the exhumed surface reflects lake-level fluctuations. For example, in some areas the terrestrial suite 5 overprints the lake-margin suite 4 and the subaqueously emplaced suite 2 as a result of shoreline regression. Because the surface is active today, overprinting of the subaerial, shoreline, and subaqueous portions of the surfaces by animal and plant traces, representing the five suites recognized, is occurring in response to the various sets of environmental factors that control the lateral distribution of biogenic structures. The example from Lake Bogoria clearly illustrates the complexity of the ichnology of lacustrine co-planar surfaces and sheds new light onto the nature of continental ichnofacies.

References: Scott *et al*. (2009).

Transgressive systems tracts recorded by thin transgressive parasequences usually reflect drastic ichnofaunal changes, from terrestrial assemblages (*Coprinisphaera* or *Celliforma* ichnofacies) to transitional terrestrial–subaqueous assemblages (*Scoyenia* ichnofacies) and salinity-tolerant subaqueous monospecific assemblages of *Beaconites filiformis* attributed to chironomids (Uchman and Álvaro, 2000). Rapid changes in depositional conditions reflecting desiccation during vertical aggradation led to the formation of composite ichnofabrics reflecting successive bioturbation events.

12.7.2 ALLUVIAL PLAINS

In alluvial settings, the sparse distribution of trace fossils primarily reflects changes in depositional systems which, in turn, may be linked to systems tracts (Buatois and Mángano, 2004, 2007). Widespread erosion, and high energy and sedimentation rates lead to channel amalgamation, and extensive reworking of fluvial deposits, preventing formation and/or preservation of biogenic structures in fluvial channels. As previously discussed, interfluve areas are commonly characterized by rooted paleosols, and terrestrial insect ichnofossils may occur, particularly in late Mesozoic and Cenozoic strata (Genise *et al*., 2000, 2004b; Genise, 2004). In particular, any of the various paleosol ichnofacies may delineate sequence boundaries.

Due to higher accommodation during the late lowstand, increasingly isolated fluvial channels encased in overbank deposits tend to occur, promoting preservation of biogenic structures. Eventually transgressive lacustrine and marsh deposits accumulate when rate of accommodation exceeds sediment supply (Legarreta *et al*., 1993; Posamentier and Allen, 1999). These changes may be paralleled by the progressive replacement of vertical dwelling burrows, and escape trace fossils of the *Skolithos* ichnofacies in active channels by low-diversity assemblages of meniscate trace fossils in abandoned channels. Both the softground and firmground suites of the *Scoyenia* ichnofacies, and even the subaqueous *Mermia* ichnofacies in overbank deposits and ponds may occur as a result of increased accommodation (Buatois and Mángano, 2004a, 2007). If, during transgression the alluvial plain becomes affected by marine processes (e.g. tides), depauperate examples of the brackish-water *Skolithos* and *Cruziana* ichnofacies may occur. This situation is not uncommon because tidal influence and brackish-water conditions may extend for tens of kilometers inland (Shanley *et al*., 1992). This trend in ichnofacies replacement is reversed under increased sediment supply, and decreased fluvial accommodation leading to deltaic progradation, and increased establishment of channel bodies during the subsequent highstand.

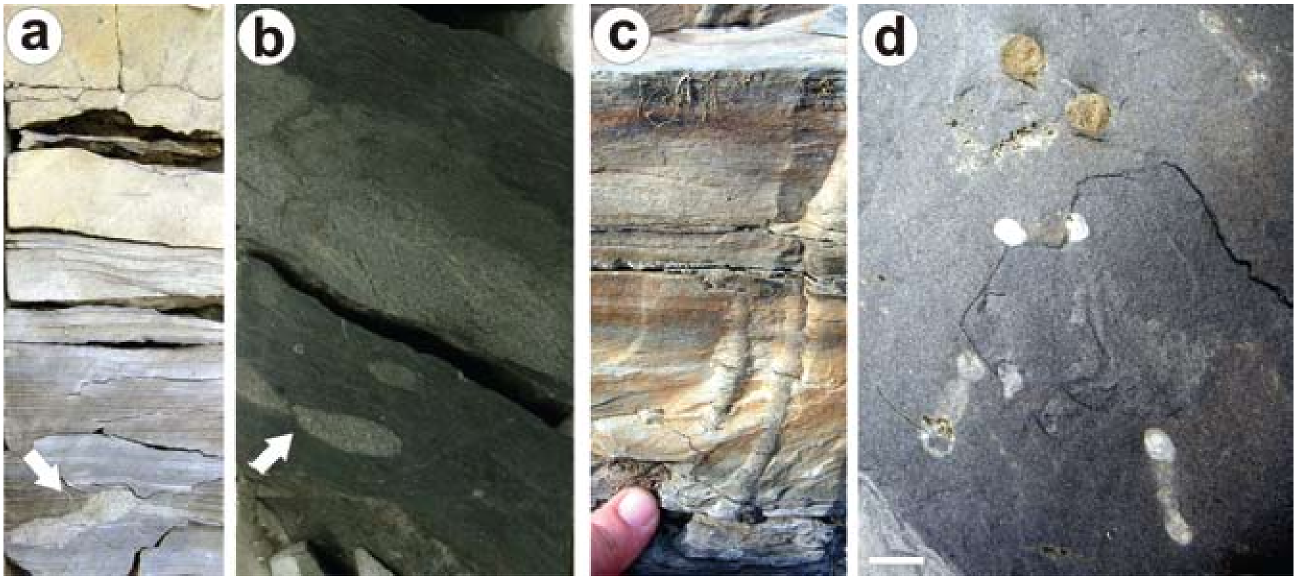


Figure 12.17 Autogenic examples of the *Glossifungites* ichnofacies. (a) Erosionally based distributary-channel deposits upon fine-grained interdistributary-bay deposits. The *Glossifungites* ichnofacies, represented by *Rhizocorallium* (arrow), occurs at the base of the channel delineating an autogenic firmground. Lower Miocene, Tácata Field, Eastern Venezuela Basin. See Buatois *et al.* (2008). Core width is 9 cm. (b) Thin-bedded turbidites. The erosive base is delineated by an autogenic *Glossifungites* ichnofacies, illustrated by *Rhizocorallium* (arrow), representing an autogenic firmground. Lower Miocene, La Blanquilla Basin, Offshore Venezuela. Core width is 6.5 cm. (c) Cross-section view of a firmground *Diplocraterion* penetrating from the base of a turbidite sandstone. Lower Oligocene, Sub-Cergowa Beds, Szczawa–Centrum, Outer Carpathians, Poland. See Uchman and Cieszkowski (2008b). (d) Bedding-plane view of several specimens of firmground *Diplocraterion* filled with coarser-grained sediment. Lower Oligocene, Sub-Cergowa Beds, Szczawa-Centrum, Outer Carpathians, Poland. See Uchman and Cieszkowski (2008c). Scale bar is 1 cm.

12.8 EVALUATION OF THE MODELS

Even its critics recognized that sequence stratigraphy represents a revolution in sedimentary geology (Miall, 1995). Undoubtedly, the success of ichnology as a tool in sequence stratigraphy records an expansion of the discipline, which has greatly enhanced its value to solve problems in sedimentary geology and basin analysis, particularly in the petroleum industry. However, a series of misconceptions surrounds the application of ichnology in this field. The widely accepted belief that the *Glossifungites* ichnofacies indicates sequence boundaries is somewhat surprising despite the fact that its true significance has been reiterated in several papers (e.g. MacEachern *et al.*, 1999a). As discussed above, in siliciclastic successions the *Glossifungites* ichnofacies delineates not only sequence boundaries, but also other surfaces, such as transgressive surfaces of erosion.

In addition, while erosional exhumation due to relative sea-level changes is commonly invoked to explain occurrences of substrate-controlled ichnofacies in siliciclastic rocks, some surfaces may be autogenic (e.g. McIlroy, 2007b; Buatois *et al.*, 2008; Yang *et al.*, 2009). As noted by MacEachern *et al.* (2007b), regional correlation of the surface is essential to recognize its allogenic nature. Allogenic surfaces tend to be regionally mappable and separate genetically unrelated facies successions.

Examples of autogenic surfaces in marginal- and shallow-marine settings are known to be produced due to erosion along the base of estuarine, distributary (Fig. 12.17a) and tidal channels, as well as cut-bank margins of tidal channels and creeks (e.g. Gingras *et al.*, 2000; MacEachern *et al.*, 2007c; Buatois *et al.*, 2008). Autogenic tidal scouring is a common process in a wide variety of subenvironments within tide-dominated deltas, further complicating recognition of firmgrounds produced by relative sea-level changes (Willis, 2005). Widely distributed examples of the *Glossifungites* ichnofacies have been noted to be associated with autogenic erosion in tidal channels of tide-dominated deltas (McIlroy, 2007). The *Glossifungites* ichnofacies also occurs as result of intense erosion in the zone of maximum wave energy of wave-dominated tidal flats (Yang *et al.*, 2009). More rarely, firmground surfaces can form even without erosion, during pauses in lateral accretion of tidal point bars (Bechtel *et al.*, 1994).

In the deep-marine realm, different types of currents, including bottom, oceanic and turbidity currents (Fig. 12.17b–d), may significantly scour the sea bottom, exposing previously buried firmground sediment to colonization (Ozalas *et al.*, 1994; Savrda *et al.*, 2001; Wetzel *et al.*, 2008). Particularly relevant is the increased recognition that deep *Diplocraterion* of the *Glossifungites* ichnofacies occur commonly at the base of turbidite channels penetrating into muddy sediment and indicating significant erosion and bypass of coarser-grained sediment (Gibert *et al.*, 2001a, b; Hubbard and Shultz, 2008; Gerard and Bromley, 2008; Uchman and Cieszkowski, 2008c). Gerard and Bromley (2008) noted the more subtle presence of these firmground burrows not only at the base of channels but also within graded mudstone. Occurrence of firmground burrows penetrating from by-pass surfaces suggests the potential presence of thick sands in more axial and/or downcurrent positions of the channel.

13 Trace fossils in biostratigraphy

> Invertebrate trace fossils can be used for the stratigraphic correlation of otherwise nonfossiliferous clastic sequences, provided that they share particular "fingerprints" and thus reflect behavioral diversification within taxonomically coherent groups of (commonly unknown) tracemakers.
>
> Dolf Seilacher
> *Trace Fossil Analysis* (2007)

In contrast to body fossils, trace fossils are often characterized by long temporal ranges and narrow facies ranges (see Section 1.2.8). As a consequence, trace fossils are highly useful in paleoenvironmental analysis and less so in biostratigraphic studies. Although most ichnogenera display long temporal ranges, it is also true that some biogenic structures can preserve specific fingerprints of their producers. If the producers record significant evolution, then the trace fossils may also yield biostratigraphic implications (Seilacher, 2007b). There are some ichnofossils that reflect particular kinds of animals in which body morphology and behavior underwent closely related evolutionary transformations through time (Seilacher, 2000). The more complex (in terms of fine morphological detail) a structure is, the more direct its biological relationship, distinctive its behavioral program, and hence, larger its biostratigraphic significance. Historically invertebrate trace fossils have been applied in biostratigraphy in two main areas: the positioning of the Proterozoic–Cambrian boundary (e.g. Seilacher, 1956; Banks, 1970; Alpert, 1977; Crimes *et al.*, 1977; Narbonne *et al.*, 1987; Crimes, 1992, 1994; Jensen, 2003) and the establishment of relative ages in lower Paleozoic clastic successions based on *Cruziana* and related trilobite trace fossils (e.g. Seilacher, 1970, 1992a, 1994; Crimes, 1975). In recent years, attempts have been made to incorporate other ichnotaxa, such as *Arthrophycus* and related trace fossils (e.g. Seilacher, 2000; Mángano *et al.*, 2005b). In the field of vertebrate ichnology, tetrapod trackways have a long tradition in biostratigraphy, particularly in upper Paleozoic–Mesozoic strata (e.g. Haubold and Katsung, 1978; Lucas, 2007). In this chapter we will address the utility of both invertebrate and vertebrate trace fossils in biostratigraphy.

13.1 THE PROTEROZOIC–CAMBRIAN BOUNDARY

Arguably, the most intensely researched area in ichnostratigraphy is the Proterozoic–Cambrian boundary (Fig. 13.1). In fact, the Proterozoic–Cambrian boundary Global Standard Stratotype-section and Point (GSSP) has been established at the base of the *Treptichnus pedum* zone at Fortune Head, Newfoundland (Narbonne *et al.*, 1987; Brasier *et al.*, 1994; Landing, 1994). Subsequently, the *Treptichnus pedum* zone was extended approximately 4 m below the boundary at the GSSP (Gehling *et al.*, 2001). Trace-fossil data are, therefore, essential to establish the position of the most important boundary in the stratigraphic record.

Alpert (1977) established one of the first syntheses by defining three main groups of trace fossils. Group 1 contains ichnotaxa restricted to the Proterozoic (e.g. *Harlaniella*, *Intrites*). Since the trace-fossil origin of these structures has now been abandoned (see Section 14.1.2), group 1 is no longer valid. Group 2 includes all those ichnotaxa that occur for the first time in the Proterozoic, but range into the Phanerozoic (e.g. *Helminthopsis, Helminthoidichnites*). Finally, group 3 contains ichnotaxa that first occur in Lower Cambrian rocks (e.g. *Diplocraterion*, *Arenicolites*). Within this group, there are some ichnotaxa with a stratigraphic range restricted to the Lower Cambrian, such as *Syringomorpha nilssoni* (Fig. 13.2a), *Psammichnites gigas* (Fig. 13.2b), and *Didymaulichnus miettensis* (Fig. 13.2c).

Further research by Crimes (1987, 1994), Narbonne *et al.* (1987), Walter *et al.* (1989), MacNaughton and Narbonne (1999), and Jensen (2003) led to the definition of a series of biostratigraphic zones encompassing the Proterozoic–Cambrian boundary. In particular, Jensen (2003) presented a tentative biostratigraphic scheme that includes six zones: three in the Neoproterozoic and three in the Lower Cambrian. The lowermost Neoproterozoic zone supposedly consists of simple horizontal trace fossils assigned to *Planolites*, but its validity is still questionable (Jensen *et al.*, 2006) and is not considered here.

Accordingly, a scheme of two Ediacaran zones and three Lower Cambrian zones is adopted (Fig. 13.3). The lower Ediacaran zone consists of poorly specialized grazing trails, such as *Helminthoidichnites*, *Helminthopsis*, and *Archaeonassa*. Dickinsonid and *Kimberella* trace fossils occur also in this zone (see Section 14.1.2). Dickinsonid resting traces have been attributed to the recently proposed ichnogenus *Musculopodus* (Getty and Hagadorn, 2008), but they differ from the type specimens of this ichnotaxon and, therefore, they best represent a new, still unnamed ichnogenus. *Kimberella* rasping trace fossils have

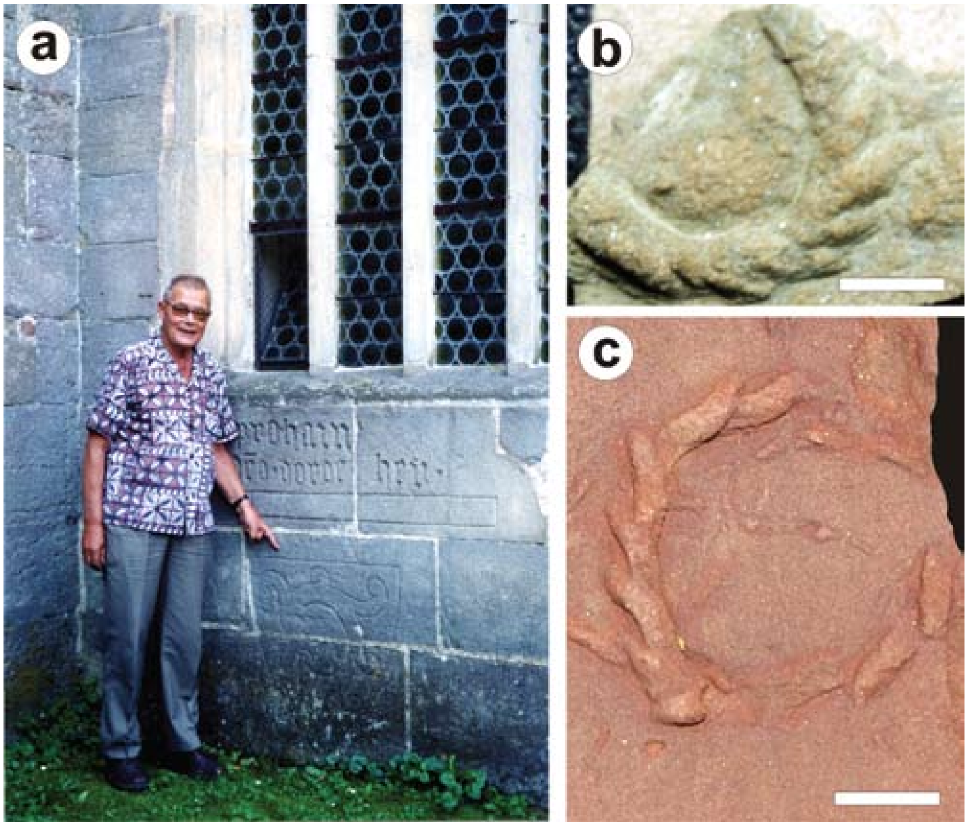


Figure 13.1 *Treptichnus pedum*, whose first appearance indicates the Proterozoic–Cambrian boundary. (a) Dolf Seilacher pointing towards the image of a *pedum* (i.e. crook) carved on a wall of a Tubingen church, where he lived while a university student after the Second World War. Photo taken in the summer of 2003. (b) *Treptichnus* (*Phycodes*) *pedum*. Lower Cambrian, Nobulus Shale, Salt Range, Pakistan. Seilacher introduced this ichnospecies in a classic paper on the ichnology of the Salt Range Cambrian in 1955. (c) *Treptichnus* (*Phycodes*) *pedum*. Lower Cambrian, Klipbak Formations, Brandkop Subgroup, Gannabos Farm, South Africa. Scale bars are 1 cm.

been included in *Radulichnus* (Seilacher *et al.*, 2005). This lower Ediacaran zone is represented in the Ediacara Member of South Australia (Gehling *et al.*, 2005) and the Ust Pinega Formation of the White Sea, Russia (Fedonkin, 1985). The age of this interval is approximately 560–550 Ma (Martin *et al.*, 2000; Jensen *et al.*, 2006). The upper Ediacaran zone includes the oldest branching burrow systems (*Treptichnus* and *Streptichnus*), as well as three-lobate trace fossils similar to *Curvolithus*. This zone is represented in the Urusis Formation of the Nama Group in Namibia (Jensen *et al.*, 2000). Radiometric dating in Namibia indicates that this zone is approximately bracketed between 550 and 542 Ma (Grotzinger *et al.*, 1995; Jensen *et al.*, 2006).

The lowermost Lower Cambrian zone is referred to as the *Treptichnus pedum* zone, and is of Fortunian age. Its base, the Proterozoic–Cambrian boundary, is marked by the first appearance of *T. pedum*. The zone also contains *Gyrolithes polonicus* and *Bergaueria*. This zone has been identified in many sections worldwide, including the Chapel Island Formation of Avalon Peninsula, Newfoundland (Narbonne *et al.*, 1987; Droser *et al.*, 2002), the upper interval of the Ingta Formation in the Mackenzie Mountains, Canada (MacNaughton and Narbonne, 1999), and the Nomtsas Formation of Namibia (Crimes and Germs, 1982; Geyer and Uchman, 1995), among many other areas. The *Rusophycus avalonensis* zone contains the oldest bilobate, trilobite-like resting traces (*R. avalonensis*) together with a bilobate epichnial trail that has been historically referred to as *Taphrelminthopsis circularis*, although it should be removed from this ichnogenus (Jensen *et al.*, 2006). This zone has been identified in the Chapel Island Formation of Avalon Peninsula (Narbonne *et al.*, 1987), and the Backbone Ranges Formation and lower interval of the Vampire Formation in the Mackenzie Mountains (MacNaughton and Narbonne, 1999). The *Cruziana tenella* (= *problematica*) zone contains the oldest bilobate, trilobite-like locomotion traces (*Cruziana problematica*) together with large back-filled traces (*Psammichnites gigas*). This zone occurs in the middle to upper interval of the Vampire Formation in the Mackenzie Mountains (MacNaughton and Narbonne, 1999).

To a large extent, this biostratigraphic scheme is based on shallow-marine ichnofaunas, which were considerably more diverse than their deep-marine counterparts by the Ediacaran–Cambrian (Buatois and Mángano, 2004). The ichnogenus *Oldhamia* has a widespread distribution, particularly in Lower Cambrian deep-marine deposits and its potential in biostratigraphy has been noted (e.g. Seilacher, 1974, 2007b; Lindholm and Casey, 1990; Seilacher *et al.*, 2005; MacNaughton, 2007). *Oldhamia curvata*, *O. radiata* (Fig. 13–2d), and *O. flabellata* are known from Lower Cambrian rocks, and *O. antiqua* has been recorded in Lower Cambrian to, more rarely, lower Middle Cambrian rocks (Seilacher *et al.*, 2005). Unfortunately, *Oldhamia* typically occurs in intensely tectonized rocks that are devoid of body fossils, and extensive empirical support to proposed evolutionary lineages (Lindholm and Casey, 1990; MacNaughton, 2007) is not available yet.

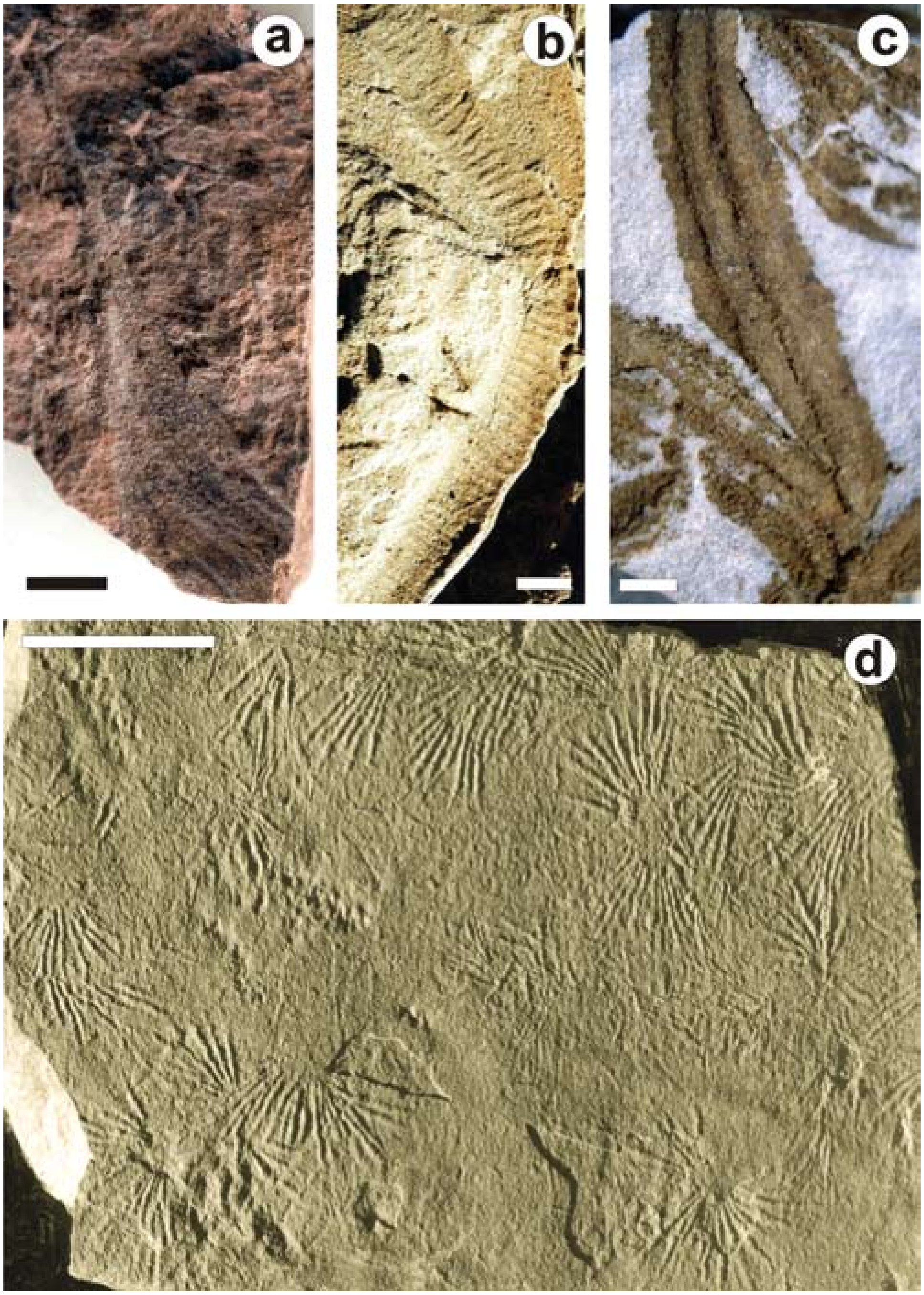


Figure 13.2 Typical Lower Cambrian trace fossils. (a) *Syringomorpha nilssoni*. Campanario Formation, Alfarcito Hills, northwest Argentina. See Mángano and Buatois (2004a). (b) *Psammichnites gigas* (= *Plagiogmus arcuatus*). Parachilna Formation, Ediacara Hills, Australia. See Gehling (2002). (c) *Didymaulichnus miettensis*. Meishucun Formation, Meishucun, Yunnan Province, China. See Crimes and Jiang (1986). (d) *Oldhamia antiqua*. Grand Pitch Formation, Maine, United States. See Seilacher *et al*. (2005). Scale bars are 1 cm.

13.2 *CRUZIANA* STRATIGRAPHY

The so-called *Cruziana* stratigraphy was first developed in the seventies and early eighties based on rocks containing trilobite trace fossils from Wales and Spain, particularly of Furongian (Late Cambrian)–Early Ordovician age (e.g. Crimes, 1969, 1970a, b, 1975; Seilacher, 1970; Moreno *et al*., 1976; Baldwin, 1977; Crimes and Marcos, 1976; Pickerill *et al*., 1984b). However, it was Seilacher (1970, 1990b, 1992a) who further developed the time range and geographic extension of the model. Additional studies have considerably extended this ichnostratigraphic scheme by documenting *Cruziana* and related ichnotaxa from the Lower Cambrian (Series 2) of Western Canada (Magwood and Pemberton, 1990; Seilacher, 1994), Sweden (Jensen, 1990, 1997), Lower to Middle Cambrian of Argentina (Mángano and Buatois, 2003b), and Egypt (Seilacher, 1990b), and Jordan (Seilacher, 1990b); Middle Cambrian (Series 3) of Spain (Legg, 1985), and Poland (Orłowski, 1992); Middle Cambrian to Lower Ordovician of Norway (Knaust, 2004b); Furongian–Lower Ordovician of Argentina (Mángano *et al*., 1996b; 2001b, 2002c,

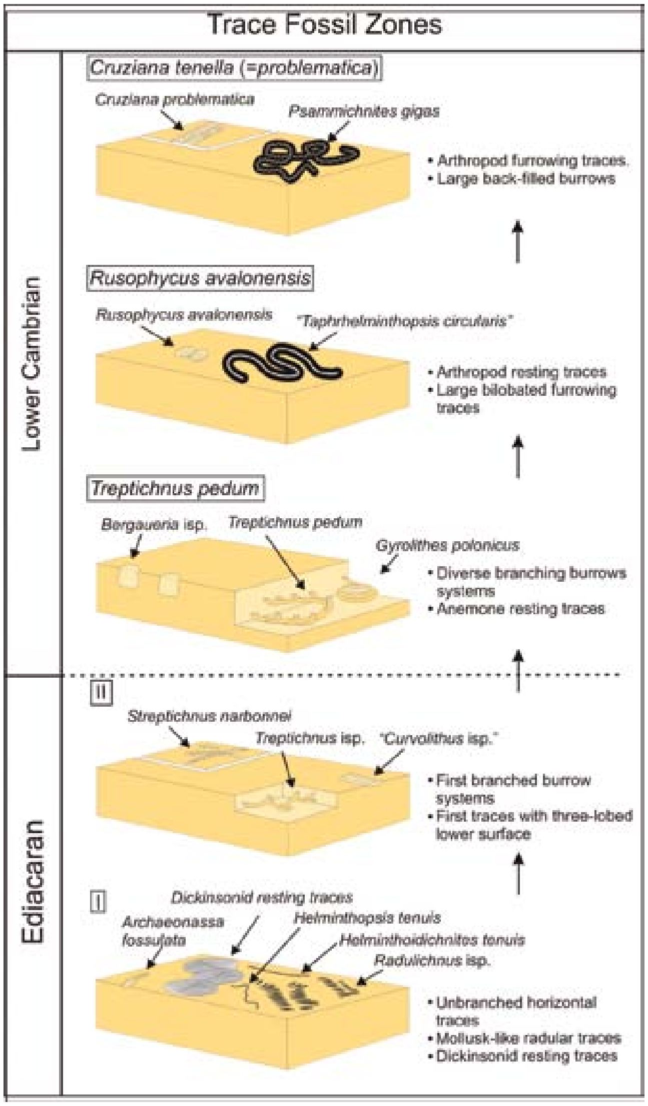


Figure 13.3 Trace-fossil zones spanning the Ediacaran–Cambrian boundary (modified from Jensen, 2003). As noted by Jensen *et al.* (2006), evidence for a lowermost Ediacaran zone characterized by *Planolites* is questionable and, therefore, it has been omitted here.

2005a; Mángano and Buatois, 2003a), Libya (Seilacher *et al.*, 2002), Poland (Radwański and Roniewicz, 1963, 1972; Orłowski *et al.*, 1971; Żylińska, 1999), and Eastern Canada (Seilacher and Crimes, 1969; Bergström, 1976; Pickerill and Fillion, 1983; Fillion and Pickerill, 1990); Lower Ordovician of Saudi Arabia (El Khayal and Romano, 1988), and Australia (Draper, 1980; Webby, 1983); Upper Ordovician of United States (Osgood, 1970), and Eastern Canada (Stanley and Pickerill, 1998); and Upper Ordovician–Lower Silurian (Llandovery) of Argentina (Seilacher *et al.*, 2004; Seilacher, 2005), Libya (Seilacher, 1996, 2005; Seilacher *et al.*, 2004), Benin (Seilacher and Alidou, 1988), and Chad (Seilacher *et al.*, 2004).

The *Cruziana* stratigraphy is based on ribbon-like bilobate structures (*Cruziana sensu stricto*) and coffee bean-shaped structures (*Rusophycus*) identified at ichnospecies level. Although trilobites were the most likely producers of these structures in lower Paleozoic marine settings, other arthropods may have been involved. Other arthropod trace fossils (e.g. *Dimorphichnus*) have been proposed as having biostratigraphy utility (Seilacher, 1990b). However, their use is still limited. *Cruziana* and *Rusophycos* ichnospecies are based on fine morphological features, particularly the so-called "claw formula" (i.e. the fingerprint left by claws or setae present in the distal part of the walking appendages). However, as leg morphology may be convergent in different groups of trilobites, other features reflecting burrowing behavior (e.g. presence of cephalic impressions, coxal marks, exopodal brushings, pleural or genal spine impressions) are also included in defining a particular ichnotaxon. If leg morphology displays high rates of evolutionary change, then it is possible to establish narrow stratigraphic ranges for the different ichnospecies of *Cruziana* and *Rusophycus*. The most likely correlation is between a particular ichnospecies of *Cruziana* and a number of trilobite species probably phylogenetically related (i.e. belonging to the same family). Fortey and Seilacher (1997) showed the co-occurrence of *C. semiplicata* and *Maladiodella*. However, *C. semiplicata* is common ichnospecies in the Furongian to Tremadocian of northwest Argentina. where *Maladiodella* has not been recorded. The same discrepancy has been noted in the Furongian of the Holy Cross Mountains in Poland (Żylińska, 1999). It is clear that *C. semiplicata* can be produced by other olenids.

Cruziana stratigraphy has been essentially developed for Gondwana, where more than 30 ichnospecies of *Cruziana* (and *Rusophycus*) with biostratigraphic significance have been identified (Seilacher, 1970, 1992a). The stratigraphic ranges of these ichnospecies comprise between one and three series, but the majority of these ichnotaxa are restricted to only one or two series (Fig. 13.4). The most extensive dataset comes from the Furongian to Middle Ordovician interval, although recent improvements have been produced for the Lower Silurian (Llandovery) (Seilacher, 1996) (Figs. 13.5a–j and 13.6a–h). In the stratigraphic scheme proposed by Seilacher (1970, 1992a), *Cruziana* ichnospecies are in turn clustered into groups. This author recognized 11 groups throughout the Paleozoic (e.g. *dispar* group, *semiplicata* group, *rugosa* group). Groups are defined based fundamentally on the claw formula as recorded by scratch-mark morphology and grouping. However, if claw marks are too small, the presence of well-developed exopodal marks and lobes can be used (e.g. *semiplicata* group). Some of these groups display wide geographic distribution validating their use in biostratigraphy. However, many are known only from their type localities. Some of these groups may have just one appearance in the stratigraphic record (e.g. *semiplicata* group), but others may characterize more than one stratigraphic interval. For example, the *omanica* group is mostly Furongian–Tremadocian, but reappears in the Caradocian (represented by *C. petraea*) and the Lower Silurian (Llandovery) (*C. acacensis*). According to Seilacher (1970, 1992a), the Lower Cambrian (Series 2) is represented by the *fasciculata* group, while the *dispar* group spans the Lower to Middle Cambrian (Series 2 to 3). However, *C. fasciculata* has been recently recorded in Upper Cambrian rocks (Mángano

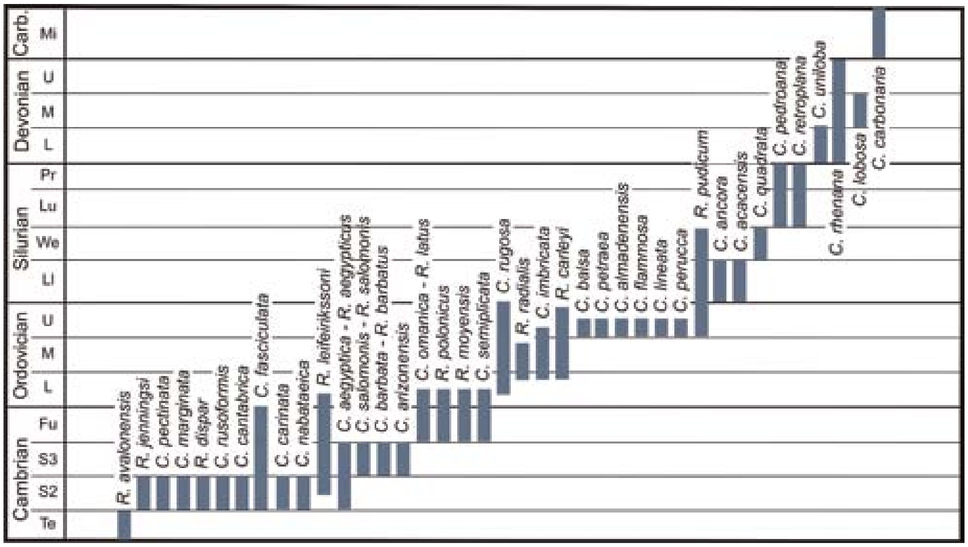


Figure 13.4 *Cruziana* and *Rusophycus* stratigraphy. Some of the stratigraphic ranges should be regarded as tentative due to limited occurrences. *Cruziana rugosa* comprises three ichnosubspecies, *C. rugosa rugosa*, *C. rugosa goldfussi*, and *C. rugosa furcifera*. Modified from Seilacher (1992a).

and Buatois, 2003a). The *semiplicata* group characterizes the Lower Cambrian to Tremadocian. The *rugosa* group is typically Arenigian–Llanvirnian, while the *imbricata* group seems to be restricted to the Arenigian. The Caradocian contains the *almadenensis* group, although one of its ichnospecies (*C. pedroana*) is Upper Silurian (Ludlow–Pridoli). The Ashgillian is characterized by the distinctive *carleyi* group, while the *pudica* group spans the Caradocian–Lower Carboniferous. The *quadrata* group is Lower Silurian–Devonian. The *costata* group seems to be restricted to the Carboniferous, but the true affinities of *C. costata* are doubtful. To illustrate *Cruziana* stratigraphy, we will address the *dispar*, *semiplicata*, and *rugosa* groups in more detail.

The *dispar* group consists of forms with several, but unequal, sharp scratch marks, revealing typically two but up to three secondary claws in front of the large primary one (Seilacher, 1970, 1992a). The group includes *Rusophycus dispar* (Fig. 13.5a), a typical Lower Cambrian (Series 2) ichnospecies known from Sweden and Poland, and *C. salomonis* (Fig. 13.5c), a Middle Cambrian (Series 3) ichnospecies from Jordan (Mángano *et al.*, 2007). *Cruziana barbata–Rusophycus barbatus* (Fig. 13.5d), known from the Middle Cambrian of Spain, Poland, Turkey, and China, are also in the *dispar* group.

The *semiplicata* group is not based on a claw formula because endopodal scratch marks are commonly too small; prominent exopodal "brushings" defining external lobes flanked by marginal thin ridges represent the diagnostic features (Crimes, 1969, 1970a; Seilacher, 1970, 1992a). *Cruziana semiplicata* (Fig. 13.5k), a common ichnospecies in Furongian–Tremadocian rocks, is the most typical ichnotaxa of the group, having been recorded in Argentina, Eastern Canada, Wales, Spain, Poland, and Oman (Seilacher, 1970, 1992a). *Cruziana semiplicata*, characterized by lateral exopodal brushings and typically trifid endopodal marks, is most likely paleobiologically related to olenids (Crimes, 1970a, b; Orłowski *et al.*, 1970; Fortey and Seilacher, 1997; Żylińska, 1999), although Bergström (1973, 1976) proposed selenopleuraceans as possible tracemakers. Other ichnospecies included in this group are *C. aegyptica, R. aegypticus*, *C. arizonensis* (Fig. 13.5e), *C. torworthi*, *R. leifeirikssoni* (Fig. 13.5f), *R. moyensis* (Fig. 13.5i), and *R. polonicus* (Fig. 13.5h). *Cruziana aegyptica*, and *R. aegypticus* occur in Middle Cambrian rocks of Jordan (Mángano *et al.*, 2007), probably extending into the Lower Cambrian in its type locality in Egypt (Seilacher, 1990b), while *C. arizonensis* is Middle Cambrian (Seilacher, 1992a). The stratigraphic range of *C. torworthi*, *R. moyensis*, and *R. polonicus* is roughly coincident with that of *C. semiplicata*. *Rusophycus leifeirikssoni* was originally recorded from Furongian–Tremadocian rocks of Eastern Canada (Bergström, 1976; Fillion and Pickerill, 1990), but is also known from older units (Lower to Middle Cambrian) in Argentina (Mángano and Buatois, 2003b).

Together with the *semiplicata* group, the *rugosa* group displays well-constrained stratigraphic distribution, and a distinctive and easy to identify morphology. The *rugosa* group is characterized by typically seven to ten, but up to twelve subequal claws; exopodial markings are absent (Seilacher, 1970, 1992a). The group includes *C. rugosa rugosa*, *C. rugosa goldfussi*, and *C. rugosa furcifera* (Fig. 13.5k), which occur in Arenigian–Llanvirnian rocks and, therefore, are useful to place the Tremadocian–Arenigian boundary. However, an overlap between some of the ichnotaxa of the *rugosa* group and *C. semiplicata* has been noted in the upper Tremadocian in some regions (Baldwin, 1975, 1977; Mángano and Buatois, 2003a). In addition, Seilacher (1992a) indicated that the *rugosa* group could extend into the Caradocian in quartzite facies in Bolivia. Recent biostratigraphic work by Egenhoff *et al.* (2007) confirmed the Caradocian age of the *rugosa*-bearing strata. Although the presence of *C. rugosa furcifera*, *C. rugosa goldfussi*, and *C. rugosa rugosa* in Lower Cambrian (Series 2) rocks of Eastern Canada has been reported (Magwood and Pemberton, 1990), specimens were subsequently assigned to a new ichnospecies, *C. pectinata*, upon reanalysis (Seilacher, 1994). The distinctive multiple and sharp scratch marks of the *rugosa* group generated a debate concerning their origin, with some authors suggesting production by multi-clawed endopodites (Seilacher, 1970, 1992a; Baldwin, 1977; Mángano and Buatois, 2003a)

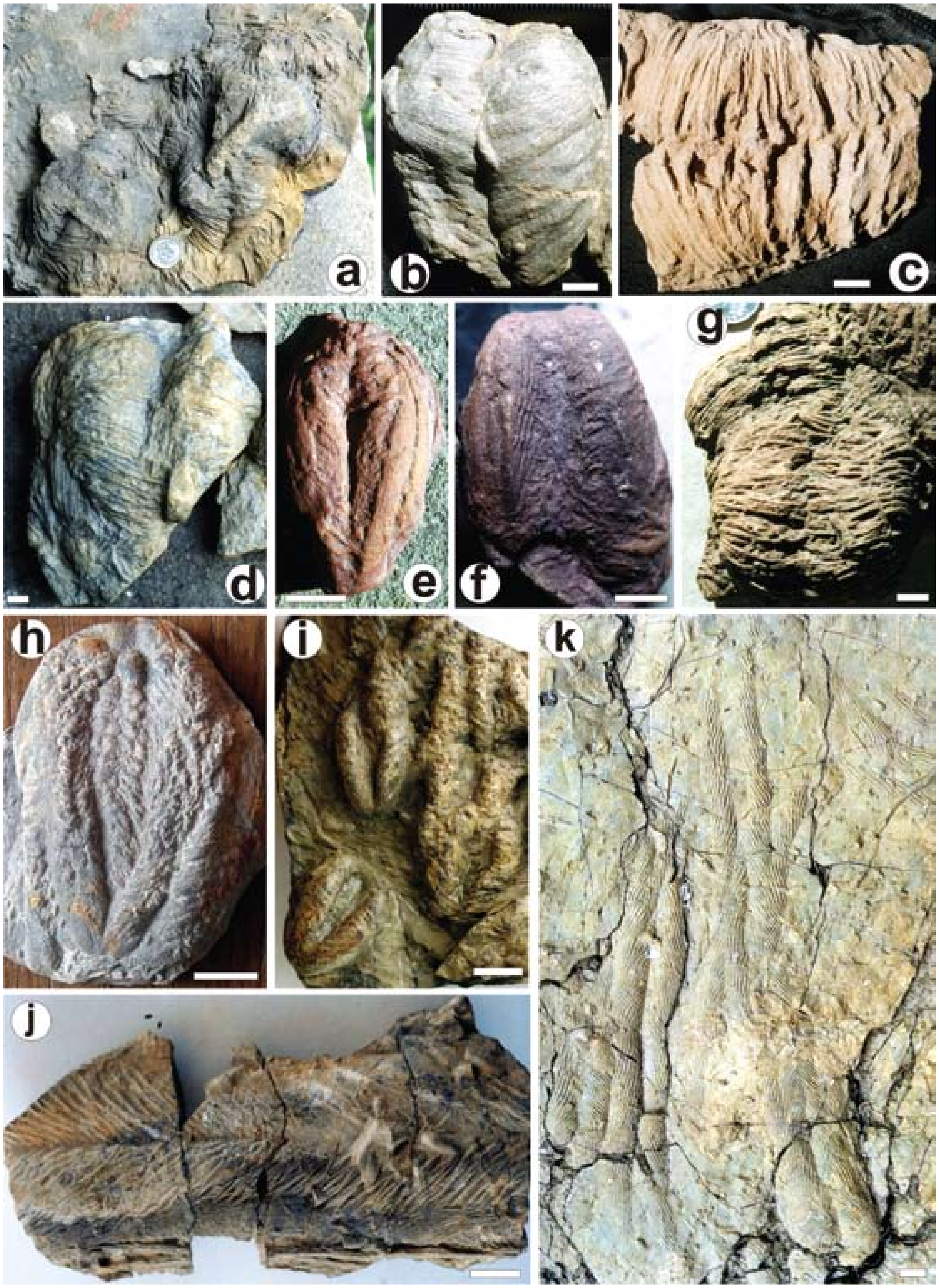


Figure 13.5 Cambrian to Lower Ordovician *Cruziana* and *Rusophycus*. (a) *Rusophycus dispar* forming clusters. Lower Cambrian, Mickwitzia Sandstone, Västergötland, Sweden. Coin is 1.9 cm. See Jensen (1997). (b) *Cruziana fasciculata* displaying sets of at least five endopodal fine scratch marks. Lower Cambrian, Herrería Sandstone, Boñar, Spain. See Seilacher (1970). (c) *Cruziana salomonis* showing scratch marks produced by strong proverse front legs (left) and weaker retroverse rear legs (right). Middle Cambrian, Burj Formation, Zerka Main, Jordan. See Seilacher (1990b) and Mángano *et al*. (2007). (d) *Cruziana barbata* with prominent front leg markings. Middle Cambrian, Obersfar Quartzite, Boñar, Spain. See Seilacher (1970). (e) *Rusophycus arizonensis (= Cruziana-arizonensis)*. Endopodal scratch marks are bordered and partially covered by exopodal scratch marks. Middle Cambrian, Tapeats Sandstone, Kaibab Trail, Grand Canyon, Arizona, United States. See Seilacher (1970). (f) *Rusophycus leifeirikssoni*. Posterior view showing axial groove and two lobes covered by coarse endopodal marks and thin exopodal marks. Lower to Middle Cambrian, Campanario Formation, Angosto del Morro de Chucalezna, Quebrada de Humahuaca, northwest Argentina. See Mángano and Buatois (2003b). (g) *Rusophycus latus* showing prominent endopodal scratch marks. Lower Ordovician, Scopes Range Beds, west of Bilpa, New South Wales, Australia. See Webby (1983). (h) *Rusophycus polonicus* with well-preserved coxal impressions between endopodal lobes. Upper Cambrian, Wiśniówka Sandstone Formation, Wielka Wiśniówka, Holy Cross Mountains, Poland. See Orłowski *et al*. (1970). (i) *Rusophycus moyensis* displaying central area and lobes covered by well-developed endopodal scratch marks. Upper Cambrian to Tremadocian, Alfarcito Member, Santa Rosita Formation, Angosto del Morro de Chucalezna, Quebrada de Humahuaca, northwest Argentina. See Mángano *et al*. (2002c). (j) *Cruziana semiplicata* displaying marginal furrows, exopodal external lobes with delicate scratch marks oriented subparallel to the axis, and endopodal lobes with scratch marks at an acute angle with respect to axis. Tremadocian, Guayoc Chico Group, Angosto del Moreno, northwest Argentina. See Mángano and Buatois (2003a). (k) *Cruziana rugosa furcifera* showing sharp, regular scratch marks forming a highly variable V-angle. Arenigian-Llanvirnian, Mojotoro Formation, Quebrada del Gallinato, northwest Argentina. See Mángano *et al*. (2001b). All scale bars are 1 cm.

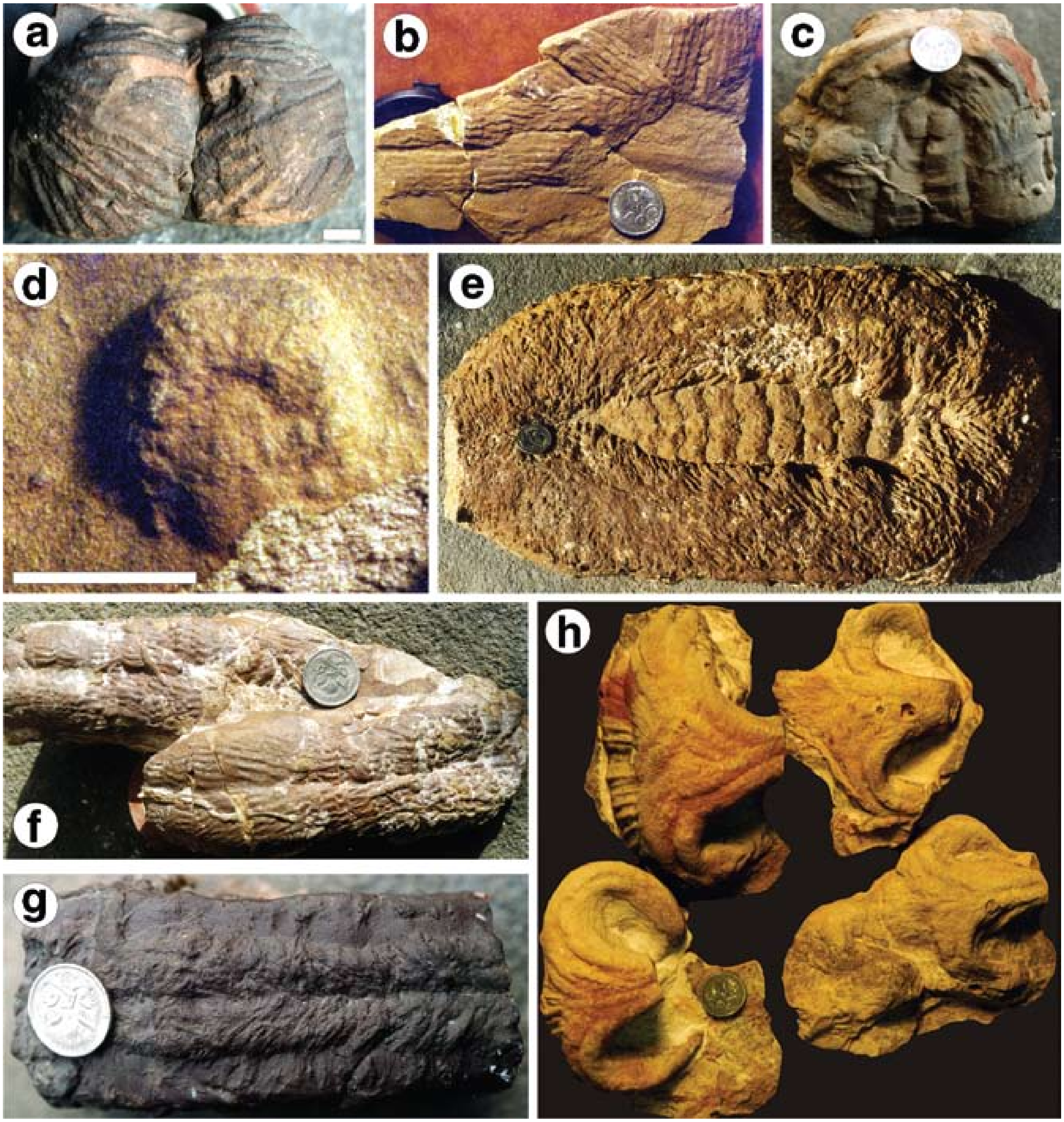


Figure 13.6 Upper Ordovician to Lower Silurian *Cruziana* and *Rusophycus*. (a) *Cruziana petraea* with rounded and subequal scratch marks. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. See Seilacher (1970). (b) *Cruziana flammosa* with flame-like front leg scratch marks. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. See Seilacher (1970). (c) *Rusophycus almadenensis* (= *Cruziana-almadenensis*) displaying radiating palm-tree scratch pattern. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. See Seilacher (1970). (d) *Rusophycus perucca* (= *Cruziana perucca*) showing typical deep wig-like structures as a result of front leg action. Upper Ordovician, Conularia Sandstone, northwest of Mudawwara, Jordan. See Seilacher (1970). (e) *Rusophycus radialis* (= *Cruziana radialis*) characterized by large size, radial scratch pattern, and well-developed coxal impressions. Upper Ordovician, Mithaka Formation, Toko Range, Queensland, Australia. See Draper (1980). (f) *Cruziana acacencis sandalina* displaying typical Turk sandal-shape Lower Silurian, Acacus Sandstone, Sebhā Ghāt, Libya. See Seilacher (1996). (g) *Cruziana quadrata* displaying its diagnostic rectangular cross section and oblique multiple scratch marks on endopodal lobes. Lower Silurian, Acacus Sandstone, Wadi Tanezzuft, Libya. See Seilacher (1970). (h) *Cruziana ancora ibex* showing anchor-shaped extension. Lower Silurian, Fada Oasis, Chad. See Seilacher (1970). All scale bars are 1 cm. All coins are 1.9 cm.

Box 13.1 *Cruziana* stratigraphy in the lower Paleozoic of northern Africa

The potential of *Cruziana* stratigraphy is particularly evident in the case of unfossiliferous sandstones. Ordovician–Silurian outcrops of the Kufra Basin in remote areas of the Sahara, southeast Libya, have been particularly appropriate for applying this tool. Nearshore prograding sandstone wedges advanced from south to north interfingering with anoxic shelf black shale. The black shale has been dated based on graptolites, but correlation with the sandstone wedges is complicated due to the absence of body fossils in these coarser-grained tongues. However, the presence of several *Cruziana* ichnospecies in the sandstone facies allows dating of the clastic wedges and correlation with their distal equivalents. The southernmost succession, exposed close to the boundary with Chad, contains elements of the *rugosa* group, namely *C. rugosa goldfussi* and *C. rugosa furcifera*, suggesting an Arenigian–Llanvirnian age for the Hawaz Formation. The overlying Memouniat Formation lacks trace fossils and probably records deposition in fluvial environments. Towards the north, a coarsening-upward succession is exposed, recording the vertical transition from black shale of the Tanezzuft Formation into the Akakus Sandstone. The presence of *Cruziana acacensis* indicates a Lower Silurian age for the sandstone wedge. Further north, the slightly younger *C. quadrata* and *C. pedroana* are present in the next overlying sandstone wedges. Interestingly, the only ichnosubspecies of *C. acacensis* recorded in the area is *C. acacensi plana*, a simpler variant that is assumed to be older than the most complex ichnosubspecies (*C. acacensis sandalina*, *C. acacensis retroversa*, and *C. acacensis laevigata*), which occur upward into the Acacus Sandstone, but in the Murzuk Basin of western Libya. Overall, the integration of *Cruziana* stratigraphy with graptolite data allows reconstructing the northward diachronic progradation of nearshore clastic wedges into shelf settings.

References: Seilacher (1996); Seilacher *et al*. (2002).

and others favoring comb-like exopodites (Bergström, 1973; Crimes and Marcos, 1976). Based on geographic distribution and size, the most likely tracemakers are asaphacean trilobites (Bergström, 1973, 1976; Fillion and Pickerill, 1990; Mángano *et al*., 2001b; Neto de Carvalho, 2006).

Although *Cruziana* stratigraphy allows relative dating of sandstones lacking body fossils (Box. 13.1), it remains an underexplored paradigm. There are some possible reasons for this. First, this methodology requires a careful evaluation of fine morphological details, including determination of the “claw formula”. Poorly preserved material or a small sample (that fails to represent the ethological variability of the ichnotaxon) are common problems. However, this may be overcome with critical analysis based on adequate sampling and avoiding determinations or proposal of new ichnotaxa based on fragmentary material. Second, anomalies within the model have created doubts about the validity of the proposed biostratigraphic scheme. In some cases (e.g. the *rugosa* group in Lower Cambrian rocks), subsequent re-analysis and solving of the anomaly has reinforced the model (Seilacher, 1994). In others (e.g. *rugosa* group in Caradocian rocks), additional research led to the extension of the originally proposed stratigraphic range of key *Cruziana* ichnospecies (e.g. Mángano and Buatois, 2003a; Egenhoff *et al*., 2007). Third, several *Cruziana* ichnospecies are only known from their type localities or from a few localities, whose age in some cases has probed to be incorrect (e.g. *C. salomonis*, see Mángano *et al*., 2007). To complicate matters, independent biostratigraphic evidence (e.g. body fossils and radiometric dating) is commonly absent in many of these localities. Finally, identification of *Cruziana* ichnospecies and ichnosubspecies requires a fair amount of background understanding about trilobite behavior and anatomy (Seilacher, 1970, 1985, 1992a; Bergström, 1973). In any case, specific technical expertise is required with any fossil group of biostratigraphic significance and, therefore, trace fossils are not an exception. Undoubtedly, there is a need for further studies, particularly in areas where independent paleontological evidence based on body fossils or radiometric dating may allow testing and further developing of the *Cruziana* stratigraphy paradigm.

13.3 ARTHROPHYCID STRATIGRAPHY

There is yet another group of trace fossils (*Arthrophycus*, *Daedalus*, and *Phycodes*), included in the ichnofamily Arthrophycidae, which has been proposed as yielding biostratigraphic significance (Seilacher, 2000). Although these trace fossils cannot be confidently assigned to a particular group of organisms, the different ichnotaxa included in this ichnofamily share regular transverse ridges and a teichichnoid spreite.

In particular, the ichnogenus *Arthrophycus* is abundant and widespread in Ordovician and Silurian strata, specifically in shallow-marine epeiric quartzites and quartzose sandstones. According to Seilacher (2000), *Arthrophycus* has a distinct stratigraphic range and can be used as a biostratigraphic index in Ordovician–Silurian rocks. Five ichnospecies are known at present: *A minimus*, *A. brongniartii* (= *A. linearis*), *A. alleghaniensis*, *A. lateralis*, and *A. parallelus* (Mángano *et al*., 2005b; Brandt *et al*., 2010). *Arthrophycus minimus* consists of shallow, small, long, regularly annulated hypichnial elements displaying subcircular to squarish cross-section and a ventral median groove; palmate, fan-like structures and scribbling patterns are absent, but a few side branches may occur (Mángano *et al*., 2005b) (Fig. 13.7a). *Arthrophycus minimus* is known in Upper Cambrian (Furongian) to Lower Ordovician rocks and displays

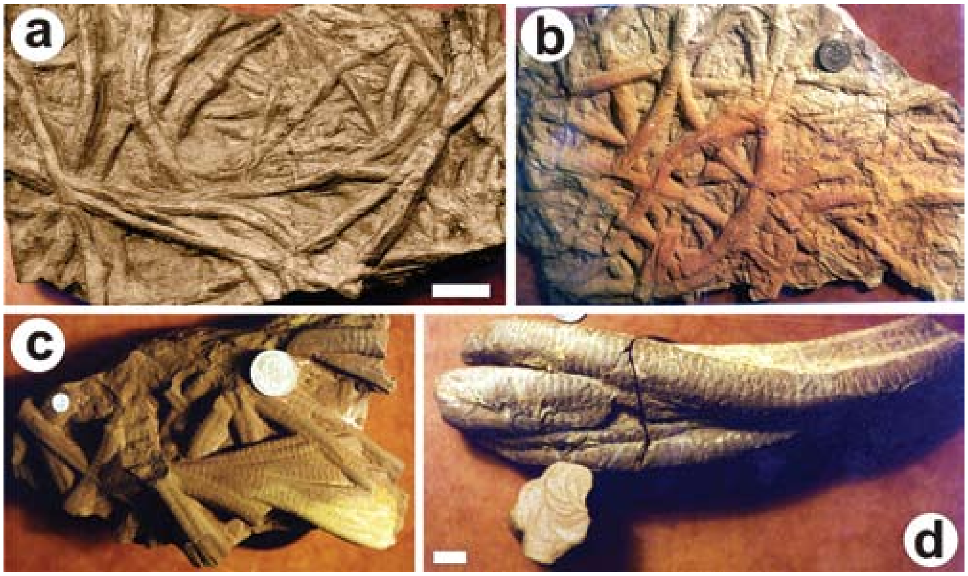


Figure 13.7 Typical *Arthrophycus* ichnospecies used in biostratigraphy. (a) *Arthrophycus minimus*. Upper Cambrian–Lower Ordovician, Santa Rosita Formation, Angosto del Morro de Chucalezna, northwest Argentina. Scale bar is 1 cm. See Mángano *et al.* (2005b). (b) *Arthrophycus brongniartii* (= *A. linearis*) *retrusiva*. Lower Silurian, Acacus Sandstone, Acacus Mountains, Libya. Coin is 1.9 cm. See Seilacher (2000). (c) *Arthrophycus alleghaniensis*. Lower Silurian, Medina Sandstone, Rochester, United States. Coin is 1.9 cm. See Seilacher (2000). (d) *Arthrophycus lateralis*. Lower Silurian, Acacus Sandstone, Takharkhuri Pass, Libya. Polished slab (lower left) shows spreiten pattern. Scale bar is 1 cm. See Seilacher (2000).

an exploratory behavioral pattern that is simpler than that of the younger *Arthrophycus* ichnospecies, which is consistent with its basal position within the arthrophycid lineage (Mángano *et al.*, 2005b). *Arthrophycus brongniartii* consists of shallow, straight to gently curved elements having no or few side branches (Seilacher, 2000; Rindsberg and Martin, 2003) (Fig 13.7b). This ichnospecies ranges from the Lower Ordovician to the Lower Silurian. *Arthrophycus alleghaniensis* comprises three-dimensional palmate bundles of tunnels typically displaying vertically retrusive spreite (Fig 13.7c), and *A. lateralis* consists of fan-shaped structures, in which branches bend only to one side having a horizontal protrusive spreite (Seilacher, 2000) (Fig 13.7d). Both ichnospecies are only known from the Lower Silurian. Finally, *A. parallelus* consists of elongate tunnels with well-developed annulations, showing a parallel to sub-parallel orientation (Brandt *et al.*, 2010). This ichnospecies has been introduced by Brandt *et al.* (2010) based on Carboniferous specimens and represents the youngest confident occurrence of this ichnogenus.

The ichnogenus *Daedalus* also seems to have biostratigraphic potential. While the ichnospecies *D. labechei*, *D. halli*, and *D. desglandi* are apparently restricted to the Lower Ordovician, *D. multiplex* is only known from the Middle Ordovician, and *D. verticalis* and *D. archimedes* occur in the Lower Silurian (Seilacher, 2000). According to Seilacher (2000), some ichnospecies of *Phycodes* may be useful in biostratigraphy. *Phycodes circinatum* is widespread in the Tremadocian, while *P. fusiforme* is only known from the Upper Arenigian. *Phycodes parallelum* ranges from the Upper Arenigian to the Lower Llanvirnian, and *P. flabellum* is only present in the Caradocian–Ashgillian.

In short, as in the case of *Cruziana* stratigraphy, the Arthrophycid stratigraphy provides an alternative to date and correlate lower Paleozoic quartzites and quartzose sandstones that commonly lack body fossils. The amount of evidence supporting the scheme is uneven. Some ichnospecies are widespread, while others are only known from one or two localities. We can certainly consider that this paradigm is still in a state of flux. Further fieldwork will most likely adjust and add to the original ichnostratigraphic proposal.

13.4 OTHER INVERTEBRATE ICHNOTAXA

Besides those ichnotaxa apparently restricted to the Lower Cambrian and those included in the *Cruziana* and arthrophycid stratigraphy, there are a few other invertebrate ichnofossils that seem to have a more restricted stratigraphic distribution. One of these ichnogenera is *Climactichnites* (Fig. 13.8a) and its associated resting trace *Musculopodus*, which are only known from the Upper Cambrian (Yochelson and Fedonkin, 1993; Getty and Hagadorn, 2008, 2009).

Heimdallia (Fig. 13.8b) is apparently restricted to Upper Ordovician–Devonian strata, mostly in nearshore settings, *H. chatwini* being the most typical ichnospecies (e.g. Bradshaw, 1981; Trewin and McNamara, 1995; Hunter and Lomas, 2003; Bradshaw and Harmsen, 2007). A potential Lower Ordovician occurrence of *H. chatwini* (Fillion and Pickerill, 1990) requires further analysis. Another ichnospecies, *H. zigzag*, occurs in the Lower Silurian (Seilacher and Alidou, 1988; Seilacher 2007b). A slightly younger representative, *Heimdallia mullaghmori*, is known from the Lower Carboniferous (Buckman, 1996).

The ichnogenus *Dictyodora* also displays a restricted stratigraphic distribution, which is of biostratigraphic significance (Seilacher 1967a; Benton and Trewin, 1980; Uchman, 2004a). *Dictyodora simplex* is Cambrian–Ordovician, while *D. scotica* and *D. tenuis* are Ordovician–Silurian. Others ichnospecies display more restricted ranges, such as the Ordovician *D. zimmermanni*, the Silurian *D. silurica*, and the Early Carboniferous *D. liebeana* (Fig. 13.8c).

Some graphoglyptids have narrower stratigraphic ranges than less complex ichnotaxa (Uchman, 2004a). For example,

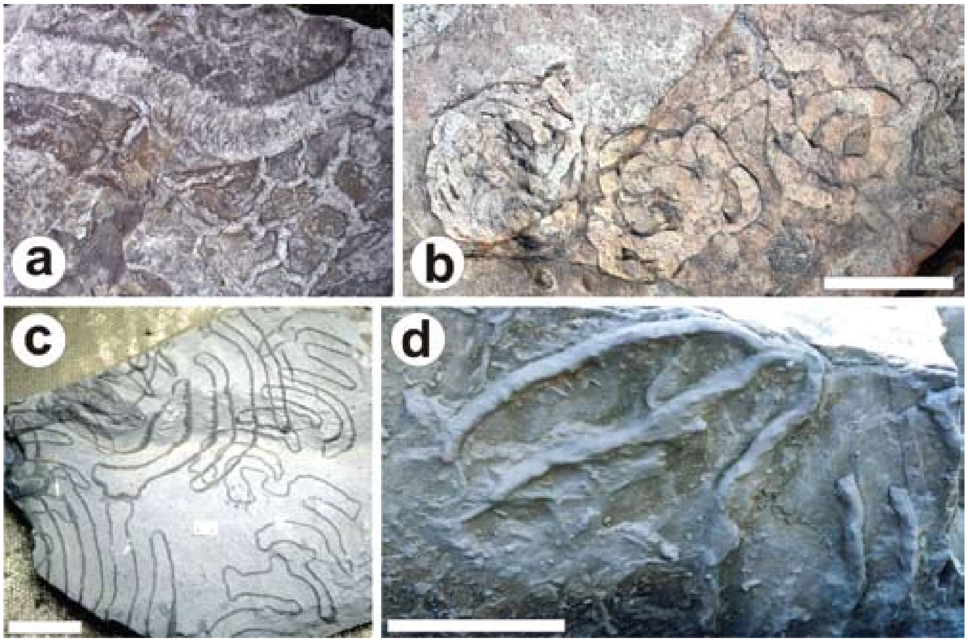


Figure 13.8 Other invertebrate trace fossils showing restricted stratigraphic ranges. (a) *Climactichnites wilsoni* cross-cutting desiccation cracks. Upper Cambrian, Cairnside Formation, Postdam Group, slab exhibited at the Fossil Garden at Buisson Point Archaeological Park, Melocheville, Quebec, Canada. Coin (upper center) is 2.4 cm. (b) *Heimdallia chatwini*. Ordovician, Peninsula Formation, Table Mountain Group, Matjiesgloof Farm, South Africa. Scale bar is 10 cm. (c) *Dictyodora liebeana*. Lower Carboniferous, Cabo de Favaritz Beds, Menorca, Spain. Scale bar is 3 cm. (d) *Glockerichnus alata*. Lower to Middle Eocene, Tarcau Sandstone, Teherau Valley, Romania. Scale bar is 10 cm.

Glockerichnus alata (Fig. 13.8d) is only known from the Eocene, while *Rotundusichnium zumayense* occurs in Maastrichtian–Eocene. However, most of graphoglyptid ichnotaxa have longer stratigraphic ranges, essentially from the Cretaceous to the Neogene (Uchman, 2003, 2004a).

Crustacean burrows having bilobate segments with scratch marks were originally referred to a new ichnospecies, *Cruziana seilacheri* (Zonneveld *et al.*, 2002), but belong in some of the ichnogenera currently available for burrow systems, most likely *Spongeliomorpha* (Knaust, 2007). This form is at present only known from the Middle Triassic.

Genise (2004) reviewed the stratigraphic range of insect trace fossils in paleosols. Most of these ichnotaxa range from the Paleogene. Of these, *Eatonichnus* is only known from the Paleocene–Eocene, and *Teisseirei* from the Eocene–Oligocene. Although the temporal resolution of these ichnotaxa is too crude, the presence of some of these insect trace fossils may be useful to differentiate Cenozoic paleosols from older terrestrial strata (Genise *et al.*, 2000).

The stratigraphic distribution of macro- and microborings has been reviewed by Bromley (2004), and Glaub and Vogel (2004). Bromley (2004) concluded that the temporal ranges of borings are too long to allow their use in biostratigraphy. However, first-appearance data may have some applications in biostratigraphy. More restricted temporal ranges are displayed by bioclaustrations (Tapanila, 2005; Tapanila and Ekdale, 2007). Although some of the most abundant forms (e.g. *Tremichnus*) have long temporal ranges, other less-widespread ichnogenera (e.g. *Catellocaula*, *Diorygma*, *Hicetes*, *Klemmatoica*, and *Torquaysalpinx*) seem to be restricted to one to four stages, a resolution unparalleled by any other ichnotaxa. Because many of these forms are poorly known, further documentation of these ichnotaxa may be necessary to test their biostratigraphic significance.

13.5 TETRAPOD TRACKWAYS

Tetrapod trackways are known since the early Middle Devonian (Niedźwiedzki *et al.*, 2010), being particularly abundant in marginal-marine to continental deposits since the Carboniferous (Lucas, 2007). This group of trace fossils has been extensively used in biostratigraphy. In fact, the tradition of using trace fossils in biostratigraphy is more firmly entrenched among vertebrate ichnologists than among invertebrate ichnologists. Lucas (2007) provided an exhaustive review of tetrapod trackway biostratigraphy, addressing a series of limiting factors that complicate use of vertebrate footprints in this field.

As in the case of invertebrate ichnology, some of these problems are connected with taxonomy (see Section 2.6). The uneven quality of footprint ichnotaxonomy complicates the reliability of biostratigraphic zonations. Ichnotaxa based on extramorphological features result from a splitting approach to taxonomy. Biostratigraphic zonations based on this approach give the false appearance of stratigraphic resolution because they include a large number of biozones, which are, in fact, unsound and simple artifacts of poor taxonomic practice. Zonations based on better defined ichnotaxa are sound, albeit with limited resolution. This is because vertebrate ichnogenera do not correspond to tetrapod genera, but to higher-rank taxonomic levels (e.g. families and groups), and the most precise biostratigraphic schemes are based on genus- or species-level taxa (e.g. Baird, 1980; Carrano and Wilson, 2001; Lucas, 2007). Lucas (2007) also noted that, as in the case of invertebrate trace fossils, facies restrictions limit the utility of tetrapod footprints.

Despite all these problems, tetrapod trackways are effectively used in biostratigraphy, and Lucas (2007) recognized several global time intervals based on the footprint record. The recently discovered early Middle Devonian tetrapod trackways from

Poland (Niedźwiedzki *et al*., 2010) predate the oldest tetrapod body fossils which are from the Upper Devonian (Ahlberg, 1991). The Late Devonian interval is characterized by trackways attributed to ichthyostegalians, which is consistent with the skeletal record (Warren and Wakefield, 1972; Rogers, 1990; Stössel, 1995; Clack, 2002, 2005). However, the trackway record is poor and no index taxa have been defined, restricting biostratigraphic utility (Lucas, 2007).

The Carboniferous trackway record is very rich, although mostly restricted to Laurussia. Lucas (2007) pointed out that taxonomic problems due to oversplitting complicate biostratigraphic schemes, but that three time intervals can be recognized: Early Carboniferous (Mississippian), Middle Carboniferous (roughly Westphalian), and Late Carboniferous (approximately Stephanian). The Early Carboniferous interval is mostly based on trackways from Nova Scotia (e.g. Sarjeant and Mossman, 1978; Hunt *et al*., 2004b; Lucas *et al*., 2004b) and, to a lesser extent, England (e.g. Scarboro and Tucker, 1995). Typical trackways are produced by temnospondyls and stem amniotes (captorhinomorphs), including the ichnogenera *Peratodactylopus*, *Megapezia*, *Baropezia*, *Hylopus*, and *Palaeosauropus*, although the latter three also occur in younger Carboniferous rocks (Lucas, 2007). Middle Carboniferous trackways are known essentially from Nova Scotia, eastern and western United States, Germany, France, and the Czech Republic (e.g. Sarjeant and Mossman, 1978; Cotton *et al*., 1995). This interval is dominated by stem amniotes (captorhinomorphs) trackways (although temnospondyl footprints occur also), and is referred to as the *Pseudobradypus* biochron (Lucas, 2007). Other ichnogenera include *Notalacerta*, *Cincosaurus*, *Matthewichnus*, *Anthracopus*, *Salichnium*, and *Quadropedia*. The producers of Lower and Middle Carboniferous trackways are essentially the same, and distinction between these two global time intervals is therefore problematic. Upper Carboniferous footprints have been recorded in eastern and western United States, Germany, France, Italy, England, and Spain (e.g. Haubold and Sarjeant, 1973; Gand, 1975; Soler-Gijón and Moratalla, 2001). Lucas (2007) noted that this interval is characterized by the first appearance of *Batrachichnus*, *Ichniotherium*, *Dromopus*, *Gilmoreichnus*, and *Dimetropus*, marking the beginning of the *Dromopus* biochron, highlighting the consistency between the track and body-fossil record.

The Permian tetrapod trackway record is more widespread, including localities in Europe, South Africa, South America, and North America, and encompasses two intervals (Lucas and Hunt, 2006; Lucas, 2007). The Early Permian interval is represented by the continuation of the *Dromopus* biochron, and has been extensively recorded in southern and western United States, Canada, and Europe (e.g. Lucas *et al*., 1999, 2004b; Haubold and Lucas, 2001; Avanzini *et al*., 2001). Trackmakers are temnospondyls, "diadectomorphs", seymouriamorphs, procolophonids, and basal synapsids (pelycosaurs). Dominant ichnotaxa include *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Dromopus* (Fig. 13.9a), *Varanopus*, *Hyloidichnus*, *Ichniotherium*, *Dimetropus* (Fig. 13.9b), and *Gilmoreichnus* (Lucas, 2007). The Late Permian interval is illustrated by tetrapod footprints in Europe and South Africa (e.g. Smith, 1993), and has been referred to as the *Rhychosauroides* biochron (Lucas, 2007). According to this author, paraeiasaurs and dicynodonts are the most important trackmakers, with *Pachypes*, *Dicynodontipus*, and *Rhychosauroides* being characteristic ichnogenera. Interestingly, there seems to be a gap in the trackway record that is roughly equivalent to the Guadalupian (Middle Permian), and longer than the Olson's gap of the body-fossil record (Lucas, 2004).

The Triassic tetrapod trackway record is essentially worldwide and contains many ichnotaxa with biostratigraphic potential. Demathieu (1977, 1994) proposed three main intervals, from the Early to the Late Triassic, and Lucas (2007) added a fourth zone for the earliest Triassic. The lowermost interval is of Induan age (earliest Triassic) and is characterized by dicynodont tracks (e.g. Retallack, 1996). The second zone comprises the Olenekian–early Anisian (Early Triassic to early Middle Triassic), and is known as the Chirothere assemblage, which is dominated by archosaur trackways (e.g. Demathieu and Demathieu, 2004). *Chirotherium* is the most common ichnogenus; *Isochirotherium*, *Rotodactylus*, *Brachychirotherium*, and *Synaptichnium* are present locally (e.g. Demathieu, 1977, 1984; Avanzini and Lockley, 2002; King *et al*., 2005). The late Middle Triassic interval is known as the Dinosauromorph assemblage (Lucas, 2007). Although chirothere footprints (e.g. *Brachychirotherium*) are also present, they are rare and the interval is distinguished from the Chirothere assemblage by the appearance of tridactyl bipedal trackways that have been attributed to dinosaur or dinosaur-like organisms (Demathieu, 1989; Haubold, 1999) (see Section 14.1.5). The Late Triassic interval is represented by the Dinosaur assemblage (Lucas, 2007). It is characterized by the higher diversity in dinosaur-like and dinosaur footprints, such as *Tetrasauropus*, *Pseudotetrasuropus*, *Grallator* (Fig. 13.9c), and *Atreipus*. Attempts have been made to further subdivide this interval (e.g. Olsen, 1980; Haubold, 1986; Lockley, 1993; Olsen and Huber, 1998; Lockley and Hunt, 1994, 1995).

The Jurassic tetrapod-footprint record is remarkably widespread, with dinosaur trackways found in all continents except Antarctica (Lucas, 2007). This author recognized two intervals within the Jurassic based on dinosaur trackways. The Early Jurassic interval is dominated by non-avian theropod footprints. This interval is characterized by and the appearance of a number of ichnotaxa (e.g. *Eubrontes*, *Anomoepus*, and *Ameghinichnus*) and the absence of some ichnogenera typical of the Triassic (e.g. *Brachychirotherium*). Of these, *Eubrontes* is the most abundant, and Lucas (2007) has referred to the base of this interval as the *Eubrontes* datum, stressing the biostratigraphic importance of this ichnogenus (e.g. Lockley *et al*., 2004). However, this is not without problems because *Eubrontes* has been recorded in Upper Triassic rocks, probably reflecting the early appearance of large theropods (Lucas *et al*., 2005). Lockley and Hunt (1995) noted that, although *Grallator* occurs in both Triassic and Jurassic rocks, it tends to be smaller in the Triassic. The Middle–Late Jurassic interval is characterized by a less sparse record and an increase in the size of tracks (Farlow, 1992).

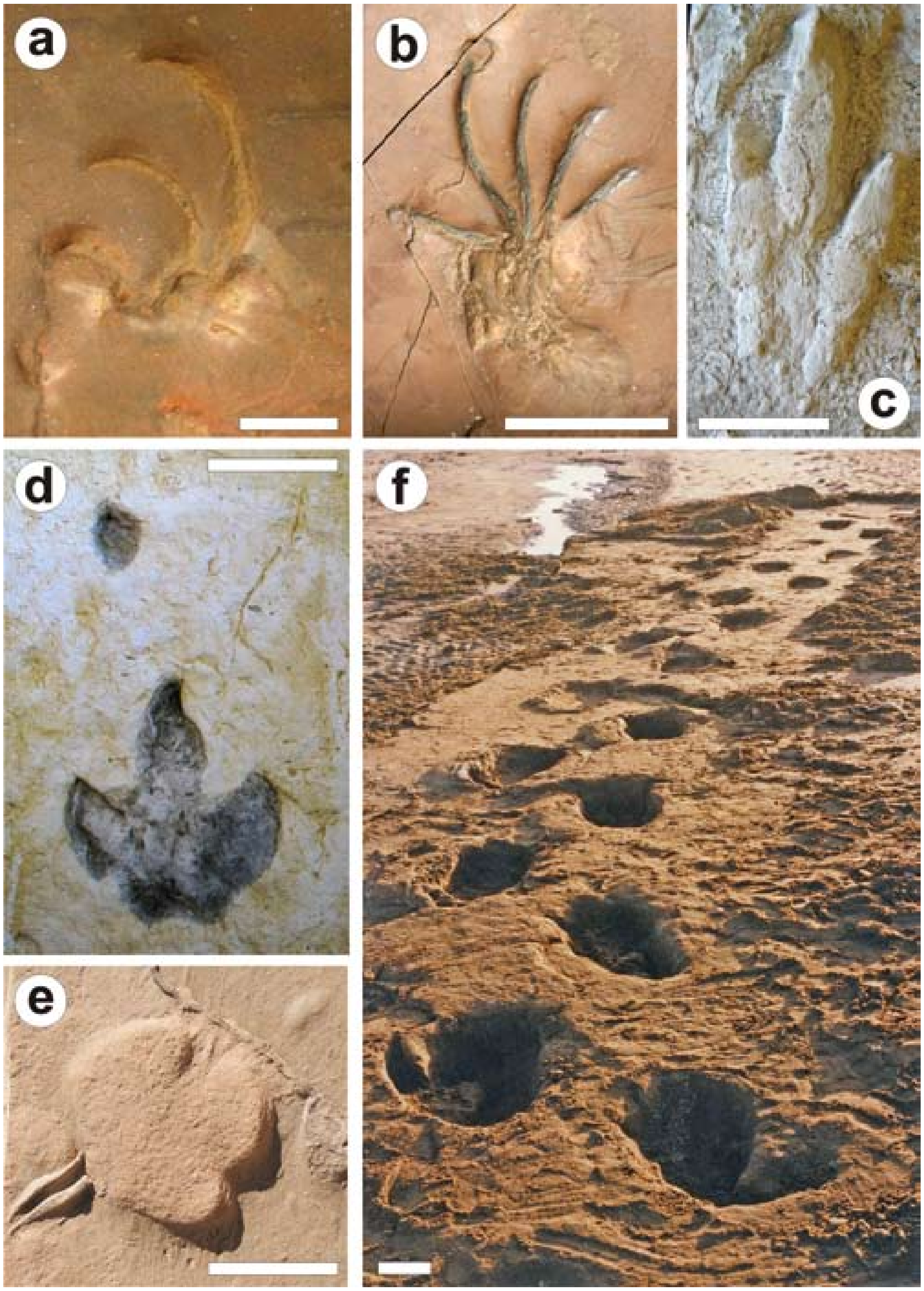


Figure 13.9 Vertebrate trackways showing restricted stratigraphic ranges and commonly used in biostratigraphy. (a) *Dromopus agilis*. Lower Permian, Hueco Formation, Robledo Mountains, New Mexico, United States. Scale bar is 1 cm. See Hunt *et al*. (2005). (b) *Dimetropus leisnerianus*. Lower Permian, Hueco Formation, Robledo Mountains, New Mexico, United States. Scale bar is 5 cm. See Hunt *et al*. (2005). (c) *Grallator sulcatus*. Upper Triassic, Brunswick Formation, Clark Quarry, near Milford, New Jersey, United States. Scale bar is 5 cm. See Olsen *et al*. (1998). (d) *Caririchnium leonardii*. Lower Cretaceous, Dakota Group, Dinosaur Ridge, Colorado, United States. Scale bar is 10 cm. See Lockley (1987). (e) *Macrauchenichnus rector*. Miocene, Toro Negro Formation, Quebrada de la Troya, near Vinchina, western Argentina. Scale bar is 10 cm. See Krapovickas *et al*. (2009). (f) *Neomegatherichnium pehuencoensis*. Upper Pleistocene, Pehuen-Co, southeastern coast of Buenos Aires Province, Argentina. Scale bar is 10 cm. See Aramayo and Manera de Bianco (1996, 2009).

Theropod (e.g. *Carmelopodus* and *Megalosauripus*), sauropod (e.g. *Gigantosauropus* and *Parabrontopodus*, *Breviparopus*), and ornithopod (e.g. *Dinehichnus*) trackways occur (Ishigaki, 1989; Lockley and Hunt, 1995; Lockley and Meyer, 2000; Lucas, 2007). Possible refinements in the Jurassic biostratigraphic scheme have been further proposed in other studies (e.g. Lockley, 1998; Lockley and Meyer, 2000).

As with the Jurassic record, the Cretaceous footprint record is global in nature, with tracksites known from every continent, including Antarctica (Olivero *et al*., 2007). The record is overwhelmingly dominated by dinosaur tracks, but bird, pterosaur, and, more rarely, mammal trackways also occur (Lucas, 2007). According to this author, the main difference with respect to the Jurassic record is the abundance of large ornithopod trackways in the Cretaceous. Two global intervals have been identified, Early Cretaceous and Late Cretaceous. The Early Cretaceous tends to be dominated by sauropod trackways, including the ichnogenera *Parabrontopodus* and *Brontopodus*, particularly in southern United States. Nevertheless, ornithopod trackways occur also, with *Iguanodontipus* and *Caririchnium* (Fig. 13.9d) being typical ichnotaxon. Bird tracks are also abundant in the Early Cretaceous, commonly associated with lake-margin environments, and including the ichnogenera *Ignotormis* and *Aquatilavipes* (Lockley *et al*., 1992; Lockley and Rainforth, 2002). The Late Cretaceous dinosaur-track record differs from the Early Cretaceous one in the lower number of sauropod tracks and in the appearance of ceratopsian, tyrannosaurid, and hadrosaurid footprints (Lucas, 2007). Bird tracks are also abundant and include the ichnogenera *Yacoraitichnus* and *Magnoavipes* (Lockley and Rainforth, 2002).

Although mammal body fossils provide a high-resolution biostratigraphy for the Cenozoic, the mammal-track record still remains poorly explored (Lucas, 2007). To further complicate things, trackways produced by amphibians, reptiles, and birds are too uncommon to be used in biostratigraphy. Lucas (2007) recognized two global intervals, Paleogene and Neogene based on the track record. The Paleogene track interval is sparse, and characterized by the abundance of basal ungulates (e.g. Sarjeant and Langston, 1994; McCrea *et al*., 2004). Some Paleogene ichnotaxa include the crocodile trackway *Albertasuchipes* and two ichnotaxon attributed to creodont mammals (*Sarjeantipes*, *Quirtipes*) (Sarjeant *et al*., 2002; McCrea *et al*., 2004). The Neogene track interval is richer, and dominated by derived ungulates (e.g. Aramayo and Manera de Bianco, 1987a, b, 1996, 2009; Sarjeant and Reynolds, 1999; Lucas *et al*., 2002; Krapovickas *et al*., 2009). Some Neogene ichnotaxa attributed to mammals are *Macrauchenichnus* (Fig. 13.9e), *Venatoripes*, *Megatherichnum*, *Neomegatherichnum*, *Eumacrauchenichnus*, and *Odocoileinichnum* (e.g. Aramayo and Manera de Bianco, 1987a, b, 1996, 2009; Krapovickas *et al*., 2009).

In short, the review by Lucas (2007) indicated that global biochronology based on tetrapod trackways resolves geological time approximately 20–50% as well as the body-fossil record. This resolution is even better than that of invertebrate trace fossils used in biostratigraphy (e.g. *Cruziana* and *Rusophycus* ichnospecies). In addition, because resolution based on skeletal remains is uneven through geological time, the temporal resolution of tetrapod footprints may be as good as that of body fossils for time intervals characterized by a meager bone record (e.g. Carboniferous). As in the case of invertebrate trace fossils, tetrapod footprints are particularly useful in the absence of skeletal remains. The fact that trackways are commonly found in facies lacking body fossils underscores the potential of footprints to fill stratigraphic gaps and to provide biostratigraphic information (e.g. Lockley, 1991).

14 Trace fossils in evolutionary paleoecology

> There is nothing like the Cambrian until the Cambrian.
>
> Andrew Knoll
> *Life on a Young Planet: The First Three Billion Years of Evolution on Earth* (2004)

> Some of these ideas were already touched upon by Darwin, such as the notion that burrowing organisms have a proportionally large impact on their environment, which is now formalized in the concept of ecosystem engineering. Other ideas were unforeseen, such as the role that bioturbation had during the Cambrian explosion. This establishes a strong link between Darwin's bioturbation book and On the Origin of Species, a connection that would have certainly astounded the author.
>
> Filip Meysman, Jack Middelburg, and Carlo Heip
> "Bioturbation: a fresh look at Darwin's last idea" (2006)

> Timing is the complex part of simplicity.
>
> Keith Jarrett
> *The Art of Improvisation* (2005)

Because ichnological analysis commonly emphasizes the long temporal range of most ichnotaxa (see Section 1.2.8), trace fossils have been traditionally overlooked as a source of information in macroevolution. However, comparisons of ichnofaunas through geological time do reveal the changing ecology of organism–substrate interactions. The use of trace fossils in evolutionary paleoecology represents a relatively new trend in ichnology that is providing important information for our understanding of patterns and processes in the history of life. In particular, Bambach (1983) understood the history of life as a process of colonization that implies the exploitation of empty or underutilized ecospace (see also Bambach *et al.*, 2007). Trace fossils may provide crucial evidence for the recognition of spatial and temporal patterns and processes associated with paleoecological breakthroughs (e.g. Seilacher, 1956, 1974, 1977b; Crimes, 1994, 2001; Buatois and Mángano, 1993b; Buatois *et al.*, 1998c, 2005; Orr, 2001; Mángano and Droser, 2004; Uchman, 2004a; Carmona *et al.*, 2004; Jensen *et al.*, 2005; Seilacher *et al.*, 2005; Mángano and Buatois, 2007).

Droser *et al.* (1997) proposed a hierarchy of paleoecological levels that allow for the ranking of ecological changes through geological time. First-level changes, the highest level, indicate colonization of a new ecosystem (e.g. terrestrialization), and fourth-level changes, at the other end, indicate turnover at the community level. This scheme provides a useful way to frame ichnological data having implications in evolutionary paleoecology (e.g. Mángano and Droser, 2004). Additionally, we make extensive use of the ichnoguild concept (see Section 5.4) in order to evaluate ecospace colonization in specific ecosystems through geological time. In many instances, trace-fossil evidence demonstrates much greater evidence of ecological change than that revealed by body fossils alone. The distribution of biogenic structures through geological time reveals a process of colonization resulting from the exploitation of empty or underutilized ecospace. Secular trends include an increase in the diversity of biogenic structures, increase in the intensity of bioturbation, addition of new invaders, environmental expansion, and faunal turnovers. In this chapter, we summarize the significance of trace-fossil information in evolutionary paleoecology. In order to do so, we first turn our attention to a number of evolutionary events, such as the Cambrian explosion, the Ordovician radiation, and the different mass extinctions. Then, we will address how animal–substrate interactions in various ecosystems have changed through geological time.

14.1 EVOLUTIONARY EVENTS

14.1.1 THE EARLY RECORD OF COMPLEX LIFE

The question about the earliest ichnological evidence of complex life (i.e. metazoans) is one of the most controversial in the science of organism–sediment interactions. The history of research is plagued with frequent reinterpretations, resulting from both the continuous scrutiny of Precambrian structures and the specific complexities of Precambrian paleobiology. The issue is of utmost relevance to understand the origin of metazoans, particularly in the absence of consensus on the affinities of many Neoproterozoic body fossils (Glaessner, 1984; Seilacher, 1989; Narbonne, 2005).

Bergström (1990) and Crimes (1994) cleverly summarized the unfortunate fate of previous candidates for the "oldest trace fossil" award. Either structures are inorganic, the rocks are younger than originally thought, or the structures are biogenic but younger than the host rock, among other less likely alternatives. For example, structures interpreted by Hofmann (1967) as new ichnotaxa, *Rhysonetron lahtii* and *R. byei*, from Lower Proterozoic rocks (2.0 Ga) in Canada, were subsequently reinterpreted by the same author as inorganic (Hofmann, 1971). Supposed burrow systems described by Clemmey (1976) in Mesoproterozoic (1.0 Ga) rocks of Zambia later were reinterpreted as traces of modern termites (Cloud *et al.*, 1980).

More recently, two new candidates have been proposed. Seilacher *et al.* (1998) documented sinusoidal and branched structures (the so-called "Chorhat worm burrows") in rocks from India that were considered as Middle Proterozoic in age (1.1 Ga). The reception was rather mixed and the actual age of the rocks became a controversial issue in itself (Azmi, 1998; Bagla, 2000; Kumar *et al.*, 2000). Finally, two independent teams dated the rocks as 1.6 Ga (Rasmussen *et al.*, 2002a; Ray *et al.*, 2002), which would push far back in time the origin of metazoans. Considering that one has to wait for more than 1.0 Ga (well into the Ediacaran) to see truly convincing examples of trace fossils, this finding became problematic at best. Either the structures are inorganic and the gap is removed, or we are forced to admit that the first attempt of metazoan life was a failed experiment with a probable extinction event during Snowball Earth times. Unsurprisingly, the biogenic nature of the structures was subject to further scrutiny and the present view is more parsimonious: the structures are not trace fossils (Budd and Jensen, 2000, 2004; Conway Morris, 2002; Jensen, 2003; Hofmann, 2005; Seilacher, 2007a). The second challenging example consists of supposed body fossils (Ediacaran-like), sea anemone burrows (*Bergaueria*), and vermiform traces described in rocks dated between 1.2 and 2.0 Ga from Western Australia (Rasmussen *et al.*, 2002b; Bengtsön *et al.*, 2007). However, they have been reinterpreted as pseudofossils (Conway Morris, 2002; Jensen, 2003; Budd and Jensen, 2004).

Crimes (1994) considered the possibility of trace fossils in pre-Ediacaran rocks highly unlikely. The oldest convincing trace fossils come, in fact, from Ediacaran strata that postdate the Marinoan Ice Age (Jensen, 2003). Recently, possible trails have been reported from 565 My-old deep-water deposits of Mistaken Point, Newfoundland, eastern Canada (Liu *et al.*, 2010). Overall, the trace-fossil record is consistent with at least some of the more recent estimations based on molecular clocks, which suggest an Ediacaran origin for bilaterians (Peterson, 2005; Rokas *et al.*, 2005; Bromham, 2006; Peterson *et al.*, 2008).

14.1.2 EDIACARAN ECOSYSTEMS

Ediacaran rocks are characterized by a rather unusual suite of structures, containing a wealth of wrinkled surfaces, ripple patches, palimpsest ripples, and elephant skin structures, all suggestive of sediment stabilization by microbial binding (Seilacher and Pflüger, 1994; Seilacher, 1999; Gehling *et al.*, 2005; Dornbos *et al.*, 2006; Droser *et al.*, 2006; Bottjer and Clapham, 2006; Mángano and Buatois, 2007). In all probability, microbial mats were critical components in Ediacaran ecosystems. Benthic communities developed in direct association with resistant matgrounds setting up an anactualistic scenario for early marine ecosystems (Seilacher, 1999). Four major categories of organism–microbial mat interactions were established during the Ediacaran: mat encrusters (attached to the microbial mats), mat scratchers (organisms grazing on the microbial mats), mat stickers (organisms growing inside of the mats), and undermat miners (those who constructed tunnels below the mat). Mat encrusters (e.g. *Charniodiscus*) and mat stickers (e.g. *Cloudina*) are essentially represented by body fossils. On the other hand, evidence of the activity of undermat miners and mat scratchers is preserved in the ichnological record. Interestingly, undermat miners seem to be more common in lowermost Cambrian deep-marine deposits than in Ediacaran rocks, being represented by the ichnogenus *Oldhamia* (see Section 14.1.3).

Trace fossils produced by mat scratchers can be further subdivided into two main groups: those reflecting the activity of worm-like metazoans and those recording the interaction of vendozoans with the matground (Mángano and Buatois, 2007). The most abundant trace fossils in Ediacaran rocks are mat grazers that belong to this first group (Gehling, 1999; Seilacher *et al.*, 2005; Jensen *et al.*, 2006). These are represented by very simple feeding trace fossils, and nonspecialized grazing trails (e.g. *Helminthoidichnites*, *Helminthopsis*, *Gordia*) preserved on corrugated surfaces. Buatois and Mángano (2003a, 2004) placed these structures in the *Helminthopsis* ichnoguild, which consists of transitory, near-surface to very shallow-tier, mat-grazer structures produced by vagile vermiform animals that exploit organic matter concentrated within microbial mats below a thin veneer of sediment (Fig. 14.1a–d). Contrary to common belief, these simple trails are not emplaced on the surface, but rather within the sediment (Seilacher, 1999). However, caution should be exercised because some filamentous body fossils can easily be confused with grazing trails (Jensen *et al.*, 2006). In addition, the giant protist *Gromia sphaerica* has been observed producing trails on the modern sea bottom (Matz *et al.*, 2008). However, these structures are commonly quite straight and shorter than most grazing trails attributed to bilaterians. Segmented burrows reflecting peristaltic locomotion are less common, but may be represented by *Torrowangea* (Narbonne and Aitken, 1990; Seilacher *et al.*, 2005). Because of the controversial nature of most of the Ediacaran body fossils, these trace fossils represent the clearest evidence of triploblastic organisms in the Neoproterozoic (Seilacher, 1989).

In recent years, evidence accumulated to demonstrate a direct link between Ediacaran trace fossils and their producers. Ediacaran shallow-marine deposits of the White Sea and south Australia contain serially repeated resting traces of *Dickinsonia* and the related genus *Yorgia* (Ivantsov and Malakhovskaya, 2002; Fedonkin, 2003; Gehling *et al.*, 2005). The body fossils *Yorgia waggoneri* and *Dickinsonia tenuis* were found in direct association with their trace fossils (Ivantsov and Malakhovskaya, 2002). The absence of preserved trails linking the resting traces suggests that the substrate did not record any locomotion disrupting the biomats (Gehling *et al.*, 2005). Recently, Sperling and Vinther (2010) suggested that these trace fossils indicate that *Dickinsonia* externally digested the mat using its entire lower sole. In addition, these authors noted that the ability of *Dickinsonia* to move militates against an algal, fungal, or sponge affinity, and that the combined locomotion and feeding mode suggest affinities with placozoans. However, a different interpretation has been proposed by McIlroy *et al.* (2009) who, based on experimental work,

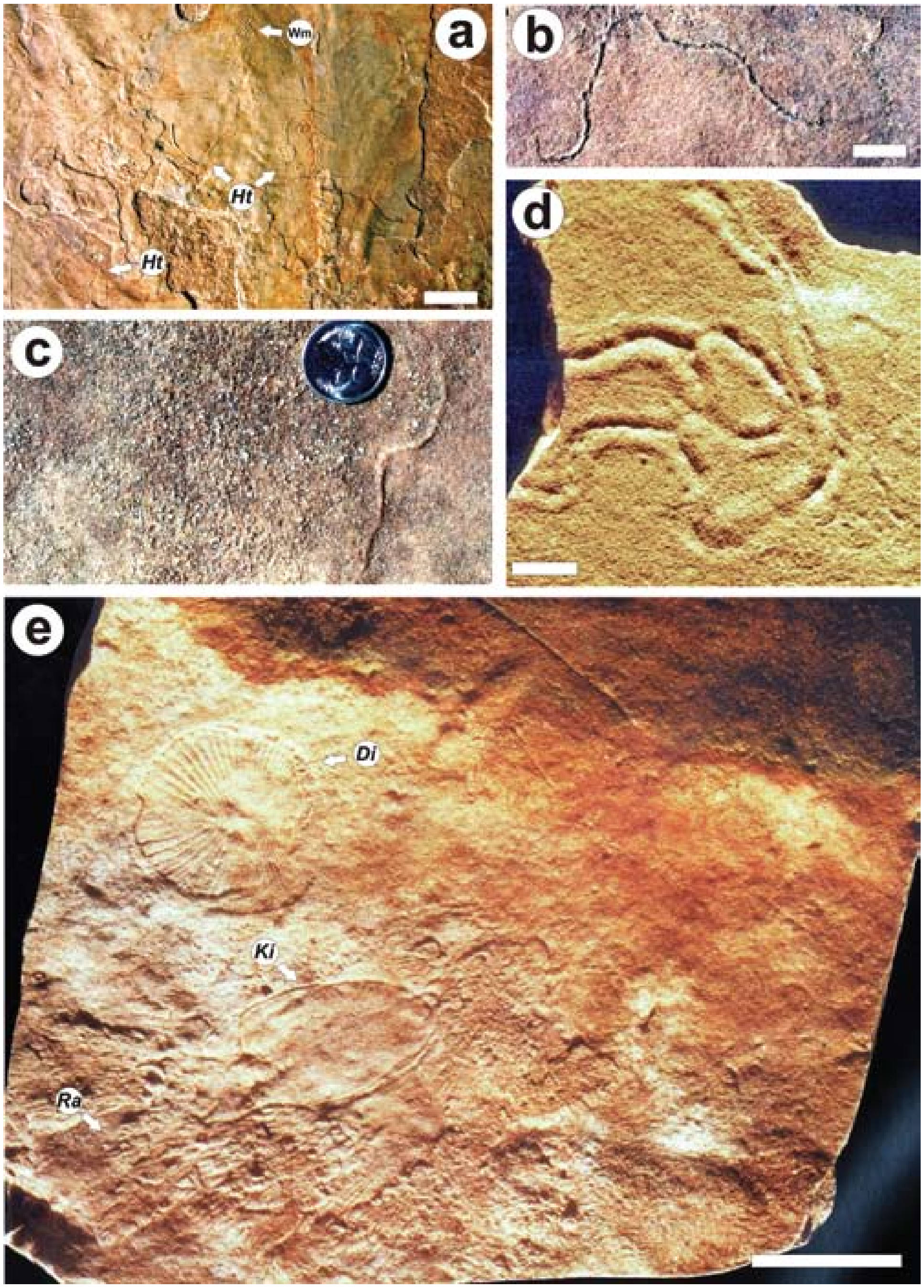


Figure 14.1 Representative trace fossils from the Ediacaran. (a) *Helminthoidichnites tenuis* (*Ht*) associated with wrinkle marks (Wm) suggestive of microbial mats. Arondegas Formation, Vanrhynsdorp Group, Arondegas Farm, South Africa. Scale bar is 1 cm. See Buatois *et al*. (2007c). (b) *Helminthopsis tenuis*. Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Scale bar is 1 cm. See Gehling *et al*. (2005). (c) *Helminthopsis tenuis* in unusually coarse-grained sandstone Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Coin is 1.9 cm. See Gehling *et al*. (2005). (d) *Archaeonassa fossulata*. Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Scale bar is 1 cm. (e) Radular marks attributed to the ichnogenus *Radulichnus* (*Ra*) in direct association with the producer, the protomollusck *Kimberella quadrata* (*Ki*). Note also the presence of *Dickinsonia* (*Di*). Ediacara Member, Rawnsley Quartzite, Pound Subgroup, Flinders Ranges, southern Australia. Scale bar is 5 cm. See Seilacher (2008).

suggested that the passive movement of dead organisms upon a microbial mat may have produced multiple impressions of body tissues mimicking a trace fossil.

Another match between producer and trace fossil is illustrated by the postulated primitive molluscan *Kimberella* (Fedonkin and Waggoner, 1997; but see Budd and Jensen, 2003, for a more basal phylogenetic position) and the scratches produced on microbial mats by its paired radular teeth (Seilacher, 1997; Fedonkin, 2003; Seilacher *et al*., 2005; Gehling *et al*., 2005; Fedonkin *et al*., 2007). Analysis of small specimens of

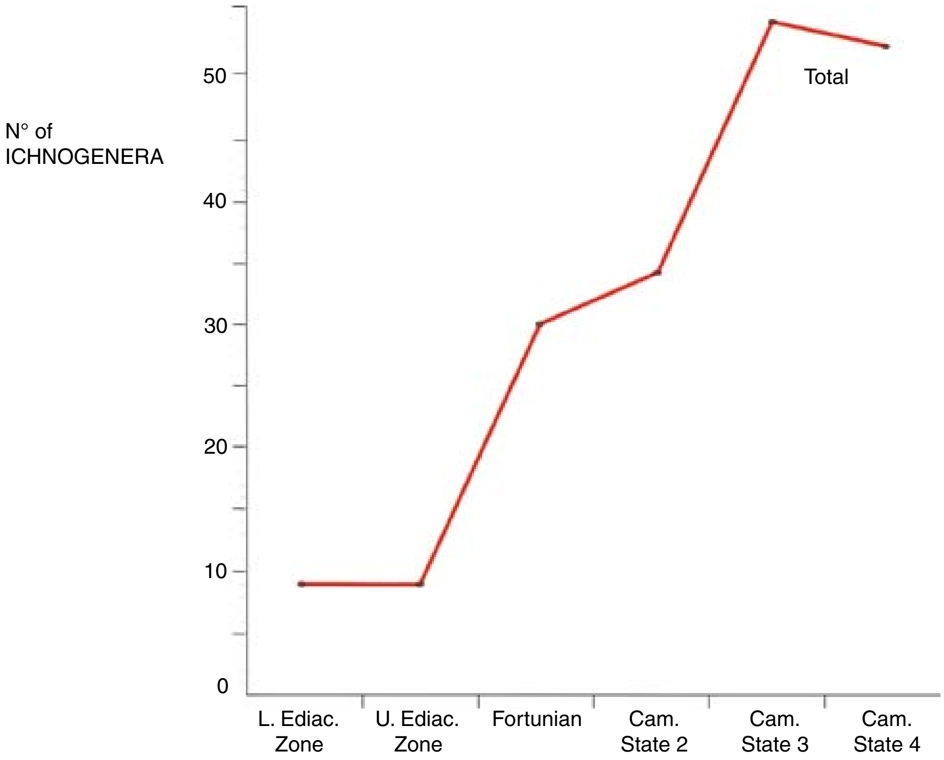


Figure 14.2 Ichnodiversity changes through the Ediacaran–Cambrian. No formal stratigraphic division is accepted yet for the Ediacaran, but two stratigraphic zones have been used here based on work by Jensen (2003). Although ichnodiversity levels remained more or less the same in these two zones, the upper Ediacaran zone is characterized by the appearance of more complex forms, such as *Treptichnus*, *Streptichnus*, and three-lobate trace fossils similar to *Curvolithus*. However, other forms present in the lower Ediacaran zone (e.g. *Radulichnus*, *Nenoxites*, Dickinsonid trace fossils) have not been recorded in the upper Ediacaran zone. Note sharp increase of trace-fossil diversity at the beginning of the Cambrian (Fortunian) and at the beginning of the Cambrian Series 2 (base of Cambrian Stage 3). The ichnodiversity curves were compiled at the ichnogenus level because the taxonomy is more firmly established than for ichnospecies.

Kimberella, and the fan-like arrangement of scratch marks indicate that the animal must have used a proboscis-like device to rasp on the microbial mat (Gehling *et al.*, 2005) (Fig. 14.1e).

The previous summary was essentially based on shallow-marine strata (e.g. Flinders Ranges, Australia, White Sea, Russia, Namibia, and South Africa) and, therefore, provides evidence on nearshore to offshore ecosystems. However, ichnological information is also available from deep-marine deposits (e.g. North Carolina, Mackenzie Mountains, Canada and central Spain), indicating that deep-sea bottoms were colonized by benthic animals already in Ediacaran times (Narbonne and Aitken, 1990; Vidal *et al.*, 1994; MacNaughton *et al.*, 2000; Orr, 2001; Crimes, 2001; Seilacher *et al.*, 2005; Liu *et al.*, 2010). In fact, the oldest trace fossils are known from deep-marine deposits rather than shallow-water deposits (Liu *et al.*, 2010). The colonization of the deep sea records a first-level ecological change. Ediacaran deep-marine ichnofaunas are poorly diverse and are dominated by nonspecialized grazing trails (e.g. *Helminthopsis*, *Helminthoidichnites*) associated with structures indicative of microbial mats (see Section 14.2.2). The body-fossil record further supports colonization of deep-sea bottoms during the terminal Proterozoic (Narbonne, 1998, 2005; Narbonne and Gehling, 2003; Clapham *et al.*, 2003; Grazhdankin, 2004).

Recent studies in Ediacaran ichnofaunas are changing our view of ichnodiversity levels by the end of the Proterozoic (Fig. 14.2). Previous studies listed a large number of ichnotaxa for the Ediacaran period (e.g. Runnegar, 1992a; Crimes, 1994). However, the emerging view is that Neoproterozoic ichnofaunas are of limited diversity and complexity (Jensen, 2003; Seilacher *et al.*, 2003, 2005; Mángano and Buatois, 2004c, 2007; Jensen *et al.*, 2005, 2006; Droser *et al.*, 2005, 2006). This shift reflects a reinterpretation of the trace-fossil nature of most ichnogenera that were considered exclusive of the Ediacaran (Group 1 of Alpert, 1977) (Haines, 2000; Gehling *et al.*, 2000, 2005; Jensen, 2003; Seilacher *et al.*, 2003, 2005; Jensen *et al.*, 2006). Supposedly guided meandering trails, such as *Yelovichnus* and *Palaeopascichnus*, have been reinterpreted either as algal remains (Haines, 2000) or body fossils of xenophyophorean protozoans (Seilacher *et al.*, 2003, 2005) or tubicolous animals (Shen *et al.*, 2007) (but see Zhuravlev *et al.*, 2009). *Harlaniella*, a rope-like structure regarded as a trace fossil, is now considered a body fossil related to *Palaeopascichnus*

(Jensen, 2003; Jensen *et al.*, 2006). The subcircular blob *Intrites* is now regarded as a body fossil of uncertain affinities (Gehling *et al.*, 2000). In particular, Jensen *et al.* (2006) provided a detailed table summarizing current re-evaluations of Ediacaran ichnofossils.

Problems also become evident with other ichnotaxa that occur through all or most of the Phanerozoic, and whose supposed presence in the Neoproterozoic has been pointed out in several compilations. For example, unquestionable specimens of vertical burrows, such as *Skolithos* or *Diplocraterion*, have not been documented from Ediacaran strata (Seilacher *et al.*, 2005; Jensen *et al.*, 2006). The presence of branched burrow systems in Ediacaran rocks is controversial. *Chondrites* has been mentioned in Ediacaran strata (e.g. Jenkins, 1995). However, these structures are commonly preserved as furrows that lack the characteristic burrow fill. More recently, they have been reinterpreted as poorly preserved specimens of body fossils or as overlap of unbranched trace fossils (Seilacher *et al.*, 2005; Jensen *et al.*, 2006). The radial structure *Mawsonites* is no longer considered a trace fossil (Runnegar, 1992b; Seilacher *et al.*, 2005; Jensen *et al.*, 2006). However, very shallow, three-dimensional burrow systems (*Treptichnus* and *Streptichnus*) occur in the uppermost Ediacaran, recording incipient exploitation of the infaunal ecospace and a slight increase in trace fossil complexity (Jensen *et al.*, 2000; Jensen and Runnegar, 2005). In addition, an increase in size seems to have occurred by the end of the Neoproterozoic as suggested by the presence of large horizontal trace fossils in Ediacaran rocks (Buatois *et al.*, 2007c).

14.1.3 THE CAMBRIAN EXPLOSION

The Ediacaran–Cambrian boundary constitutes a major divide in the history of life on Earth (Knoll *et al.*, 2006). Ediacaran biotas were dominated by soft-bodied organisms that are considered at least in part to be unrelated to modern metazoan faunas (Seilacher, 1992b; Seilacher *et al.*, 2003; Narbonne, 2004, 2005). On the other hand, the rapid development of almost all modern groups of animals, including the rise of skeletal faunas, took place during the Cambrian, in a major evolutionary event known as the Cambrian explosion (Conway Morris, 2000; Erwin, 2001; Droser and Li, 2001; Budd, 2003; Valentine, 2004; Marshall, 2006). Our understanding of the Cambrian explosion has implications for several key topics, including the origin of metazoan bodyplans, the role of developmental genetics, the validity of molecular clocks, and the influence of paleoenvironmental factors on macroevolution (Conway Morris, 2000). Although most evolutionary studies dealing with the Ediacaran–Cambrian transition have been based on the analysis of body fossils, the ichnological record provides an independent line of evidence to calibrate and evaluate the Cambrian explosion (Mángano and Buatois, 2007). This is of paramount importance because there is still no agreement whether the Cambrian explosion is a real evolutionary event or a preservational artifact that reflects an increase in fossilization potential (Valentine, 2004). It is evident that the Cambrian was a unique time in the history of life. Paraphrasing Andrew Knoll, it is also fair to say that there is nothing like the Cambrian after the Cambrian.

The diversity of Neoproterozoic ichnofaunas is generally low, and behavioral complexity is also limited (see Section 14.1.2). By the Fortunian (lowermost Cambrian), this picture changed with the appearance of much more diverse and complex ichnofaunas, particularly in shallow-marine environments (Fig. 14.2). Another increase in trace-fossil diversity again mostly in shallow-marine settings took place by the beginning of Cambrian Stage 3 (Fig. 14.2). Relatively diverse ichnofaunas composed of arthropod trackways, such as *Diplichnites* (Fig. 14.3a) and *Dimorphichnus*, the arthropod resting trace *Rusophycus*, complex grazing trace fossils (e.g. *Psammichnites*), the sinusoidal trail *Cochlichnus* (Fig. 14.3b), bilobate locomotion trace fossils (e.g. *Didymaulichnus*), branched feeding burrows of deposit feeders, including *Treptichnus pedum* (Fig. 14.3c), and complex feeding patterns included in the ichnogenus *Oldhamia* are known worldwide in lowermost Cambrian strata (Buatois and Mángano, 2004b, and references therein). Systematic guided meanders, such as those present in *Psammichnites saltensis* (Fig. 14.3d) and the elaborate feeding morphologies displayed by various ichnospecies of *Oldhamia* (Fig. 14.3e) reveal the onset of sophisticated grazing strategies that were notably absent during the Ediacaran (Seilacher *et al.*, 2005). Also, the large size of earliest Cambrian trace fossils (e.g. *Psammichnites*) contrasts with the typical small size of most Ediacaran trace fossils. In contrast to the rather monotonous aspect of Ediacaran ichnofaunas (see Section 14.1.2), Fortunian shallow-marine ichnofaunas display more varied behavioral patterns. This fact undoubtedly reflects the appearance of a number of body plans of soft-bodied organisms, which cannot be fully evaluated based on the analysis of the body fossil record alone.

Lowermost Cambrian trace fossils are typically oriented parallel to the bedding plane, and, therefore, they do not significantly disturb the primary sedimentary fabric (McIlroy and Logan, 1999; Buatois and Mángano, 2004b; Mángano and Buatois, 2004c, 2006). Fortunian trace fossils mostly reflect shallow to very shallow infaunal feeding activities of mobile, bilaterian metazoans. As a consequence of being restricted to bedding planes, the degree of bioturbation is only slightly higher than that of Ediacaran deposits. As in the case of Ediacaran rocks, there is a conspicuous absence of *Skolithos* pipe rock in Fortunian strata (Mángano and Buatois, 2004c, 2007). Vertically oriented trace fossils are only represented by shallow specimens of *Gyrolithes* (Droser *et al.*, 2002, 2004). This limited extent and depth of bioturbation resulted in the widespread development of relatively firm substrates and the virtual absence of a mixed layer within the substrate (Droser *et al.*, 2002, 2004; Dornbos *et al.*, 2004, 2005; Jensen *et al.*, 2005; Mángano *et al.*, 2007).

In contrast to Fortunian ichnofaunas, Cambrian Stage 2 trace-fossil assemblages are characterized by the appearance of vertical dwelling structures (*Skolithos*, *Diplocraterion*, and *Arenicolites*) of suspension feeders and passive predators, reflecting the onset of deep bioturbation, and the establishment

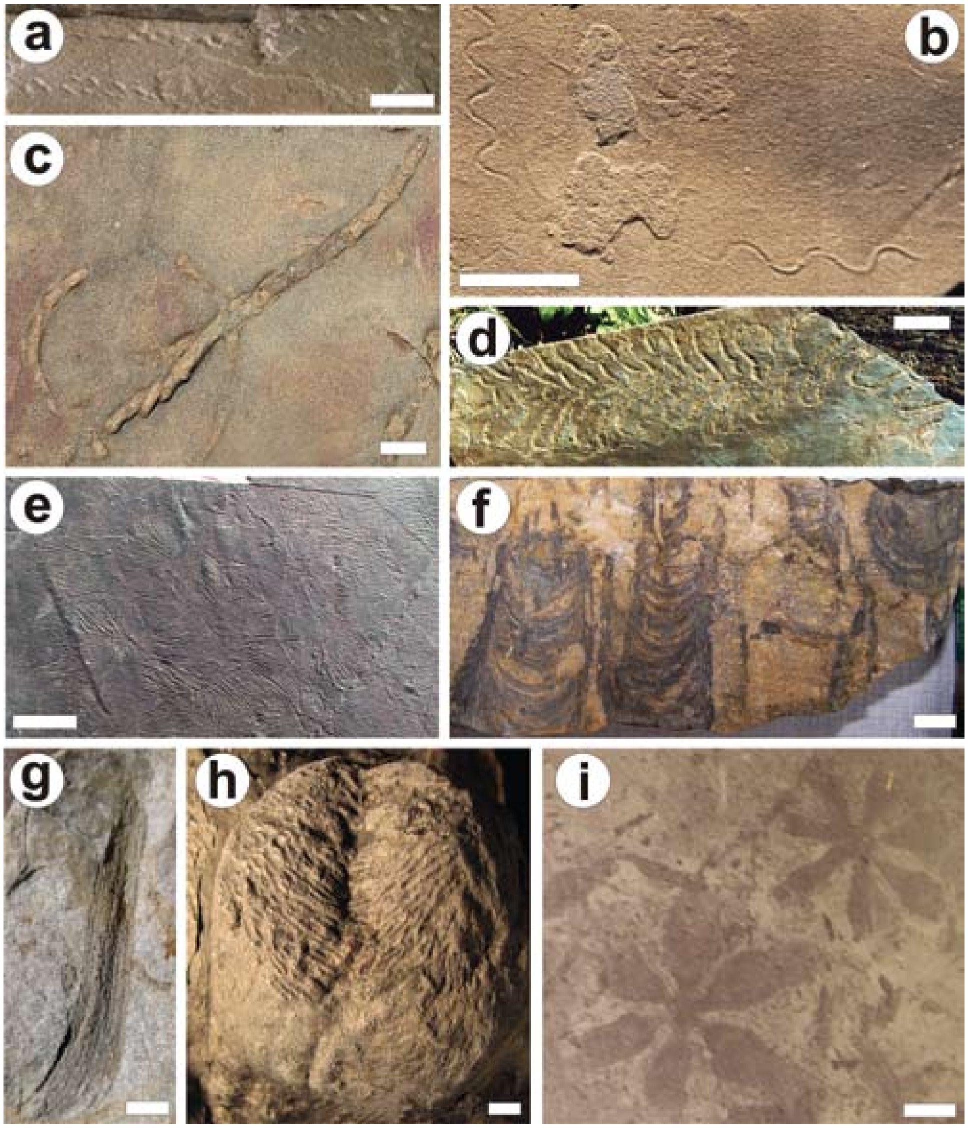


Figure 14.3 Trace-fossil variability and the Cambrian explosion. Note the wide variety of morphological patterns attained by the Early Cambrian. (a) *Diplichnites* isp. Puncoviscana Formation, San Antonio de los Cobres, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (b) *Cochlichnus anguineus*. Puncoviscana Formation, San Antonio de los Cobres, northwest Argentina. Scale bar is 1 cm. See Buatois and Mángano (2003a). (c) *Treptichnus pedum*. Klipbak Formations, Brandkop Subgroup, Gannabos Farm, South Africa. Scale bar is 1 cm. See Buatois *et al.* (2007c). (d) *Psammichnites saltensis*. Puncoviscana Formation, Cachi, northwest Argentina. Scale bar is 2 cm. See Buatois and Mángano (2004b). (e) *Oldhamia alata*. Puncoviscana Formation, el Mollar, Quebrada del Toro, northwest Argentina. Scale bar is 1 cm. See Seilacher *et al.* (2005). (f) *Diplocraterion parallelum*. Dividalen Group, Imobekken, northern Norway. Scale bar is 2 cm. See Bromley and Hanken (1991). (g) *Syringomorpha nilssoni* in an erratic block, Kiersgoube Pastz, Berlin, Germany. Scale bar is 1 cm. (h) *Rusophycus jenningsi*. Lake Louise Formation, Gog Group, Lake O'Hara, Canadian Rockies. (i) *Dactyloidites asteroides*. Metawee Slate Formation, vicinity of Middle Granville, New York State, northeastern United States. Scale bar is 1 cm.

of the *Skolithos* ichnofacies in high-energy settings (Fig. 14.3f). These vertical burrows may occur in prolific densities forming *Skolithos* pipe rock (Droser, 1991). Additionally, the J-shaped spreite trace fossil *Syringomorpha* (Fig. 14.3g) may occur in similar settings, forming distinct ichnofabrics (Mángano and Buatois, 2004b) (see Box 5.1). While Fortunian ichnofaunas were emplaced very close to the sediment–water interface, younger Lower Cambrian ichnofaunas reflect burrowing depths in the order of tens of centimeter, revealing an exponential increase in the depth of bioturbation of suspension-feeding organisms (Mángano and Buatois, 2004c, 2007). Also, detailed ichnological analysis in shallow-marine environments reveals a more complex tiering structure with the development of multiple guilds (Mángano and Buatois, 2004b). This increase in depth of bioturbation is not exclusive of high-energy nearshore areas, but also of lower-energy settings, where deep *Rusophycus*, such as *R. jenningsi* (Fig. 14.3h) and *R. dispar*, became common. In any case, the tiering structure is much simpler than that in younger ichnofaunas. During the Cambrian Stages 2 to 3, matgrounds became rare due to the onset of vertical bioturbation, and were replaced by mixgrounds in an event referred to as the "Agronomic Revolution" (Seilacher and Pfluger, 1994; Seilacher, 1999). This dramatic change at the biosphere scale was conducive to a remarkable change in the way living organisms interacted with the substrate ("Cambrian Substrate Revolution" of Bottjer *et al.*, 2000). Also, archaeocyathid reefs containing high densities of *Trypanites* are present in Lower Cambrian hardgrounds, revealing bioerosion by a macroboring biota (James *et al.*, 1977) (see Section 14.2.3). Additionally, increasing levels of predation were implicated in an arms race, spurring the development of complex predatory–prey interactions, and spurring evolutionary innovations (Vermeij, 1987). The role of predation as a triggering factor in the thorough exploitation of the infaunal ecospace has been a matter of debate. Evaluating extrinsic and intrinsic factors at the onset of the Cambrian explosion and the Agronomic Revolution is not easy (Marshall, 2006). In any case, evidence of predation has been detected in some Lower Cambrian deep burrowing *Rusophycus* directly associated with *Palaeophycus* (Jensen, 1990).

In addition to the noted changes in substrate conditions and predation intensity, it has recently been emphasized that the increased complexity and heterogeneity of marine environments may have played a major role as a driving force of evolutionary changes across the Ediacaran–Cambrian boundary (Plotnick, 2007; Plotnick *et al*., 2010). The distribution of environmental signals in the marine ecosystem that an organism can potentially respond to has been termed its "information landscape". It has been hypothesized that a coevolutionary increase in the information content of the marine environment and in the ability of animals to obtain and process this information took place during the Cambrian explosion. According to this view, these facts may have resulted in the development of mobile bilaterians with macroscopic sense organs. This evolutionary event has been referred to as the "Cambrian Information Revolution" (Plotnick *et al*., 2010). The trace-fossil record of this revolution is most likely expressed by the appearance of grazing trails and feeding burrows, displaying more sophisticated strategies to exploit resources in an heterogeneous landscape (e.g. Gámez Vintaned *et al*., 2006) (Fig. 14.3d–e, and i).

The presence of multiple trophic guilds, and a well-established suspension-feeding infauna represented by abundant pipe rock in Cambrian Stages 2 to 3 strata provide evidence of a significant change in complexity of shallow-marine benthic communities, suggesting a coupling between plankton and benthos (Mángano and Buatois, 2004b, 2006, 2007; Mángano *et al*., 2007). Butterfield (2001) suggested that the appearance of filter-feeding mesozooplankton were crucial in metazoan evolution. In fact, the addition of mesozooplankton to the trophic web may have acted as a trigger not only for the evolution of large metazoa, but also for the advent of the Agronomic Revolution. By repacking unicellular phytoplankton as nutrient-rich larger particles, zooplankton provides a more concentrated and exploitable resource for the benthos (Butterfield, 2001). This significant increase in the delivery of labile, nutrient-rich particles into the sediment may be behind the most significant change in the history of benthic ecology: the shift from matgrounds to mixgrounds. Mángano and Buatois (2004c, 2007) noted that ichnological evidence suggests that the presence of metazoa able to exploit the endobenthic environment preceded the establishment of a modern endobenthic ecological structure (i.e. mixground ecology). According to the decoupling hypothesis, the Cambrian evolutionary event consists of two phases: diversification of body plans during the Fortunian and a subsequent infaunalization and ecological shift during Cambrian Stages 2 and 3. Therefore, the Agronomic Revolution is not strictly coincident with the Ediacaran–Cambrian boundary. Although the body fossil record indicates the appearance of most of the major clades at the Cambrian Stage 3, the presence of rich ichnofaunas revealing diverse body plans during the Fortunian indicates the existence of a fuse time previous to what is commonly referred to as the Cambrian explosion (Mángano and Buatois, 2006).

Lower Cambrian ichnofaunas display segregation into two distinct environmentally related trace-fossil associations: shallow- and deep-marine (e.g. Buatois and Mángano, 2004b). Shallow-marine ichnofaunas are relatively diverse and complex (Box 14.1), but deep-marine trace-fossil assemblages essentially

Box 14.1 The Lower Cambrian Mickitzia Sandstone of Sweden and the Cambrian explosion

The Mickitzia Sandstone of Sweden contains one of the best documented Lower Cambrian ichnofaunas, and is essential to understanding the level of complexity reached by shallow-marine benthic communities at this early stage of metazoan evolution. Acritarch data indicate that this unit ranges in age from Cambrian Stage 3 to Stage 4. Forty one different ichnotaxa have been documented. The most outstanding feature of this ichnofauna is the wide variety of morphological and ethological types (Fig. 14.4a–e). The Mickitzia ichnofauna includes plug-shaped dwelling or resting burrows of actinarians (*Bergaueria perata*), sinusoidal grazing trails of nematodes or annelids (*Cochlichnus* isp.), arthropod locomotion (*Cruziana problematica* and *Cruziana rusoformis*, and *Cruziana* cf. *rusoformis*), resting (*Rusophycus dispar, Rusophycus jenningsi*, *Rusophycus eutendorfensis*), and dwelling (*Cheiichnus gothicus*) trace fossils commonly with distinctive scratch marks, vertical dwelling burrows (*Diplocraterion parallelum*, *Skolithos linearis*), concentrically filled conical vertical dwelling burrows of polychaetes (*Rosselia socialis*), spiral-shaped dwelling burrows of polychaetes (*Gyrolithes polonicus*), J-shaped vertical feeding burrows (*Syringomorpha nilssoni*), simple grazing trails of worm-like organisms (*Helminthoidichnites tenuis*), simple horizontal dwelling burrows of worm-like organisms (*Palaeophycus imbricatus*, *Palaeophycus tubularis*, *Palaeophycus tubularis*), annulated burrows (*Fustiglyphus* isp.), irregular feeding networks (*Olenichnus* isp.), branched feeding burrows of worm-like organisms, including priapulids (*Phycodes* cf. *curvipalmatum*, *Phycodes palmatus*, *Treptichnus bifurcus*, *Treptichnus pedum*), spreite simple feeding burrows possibly produced by annelids, priapulids, or trilobites (*Teichichnus ovillus* and *Trichophycus venosus*), spreite U-shaped feeding burrows (*Rhizocorallium jenense*), radiating feeding burrows (*Scotolithos mirabilis*), and spreite lobate feeding burrows (*Zoophycos* isp.). The Mickitzia ichnofauna displays a sharp contrast with their Ediacaran counterparts of shallow-marine environments, which are remarkably less diverse and much simpler. Characterization of the Mickitzia ichnofauna illustrates the profound ecological and evolutionary changes resulting from the Cambrian explosion and the Agronomic Revolution.

Reference: Jensen (1997); Jensen and Bergström (2000).

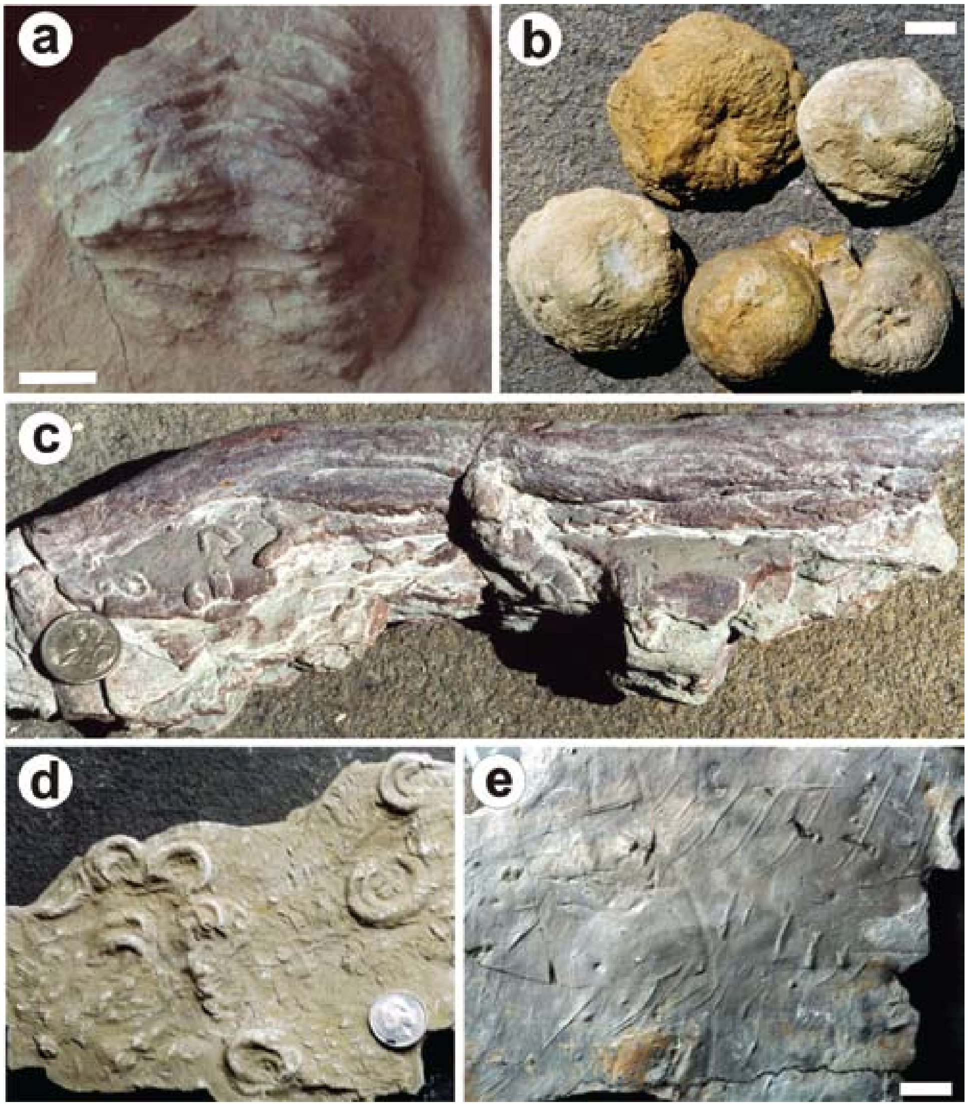


Figure 14.4 Selected trace fossils from the Lower Cambrian Mickitzia Sandstone, Västergötland, Sweden. See Jensen (1997). (a) *Rusophycus dispar*. Scale bar is 1 cm. (b) *Cheiichnus gothicus*. Scale bar is 2 cm. (c) *Trichophycus venosus*. Coin is 1.9 cm. (d) *Gyrolithes polonicus*. Coin is 1.9 cm. (e) *Dimorphichnus obliquus*. Scale bar is 2 cm.

consist of simple grazing trails, arthropod trackways, and different ichnospecies of the specialized undermat miner feeding structure *Oldhamia* (Buatois and Mángano, 2003a). This association indicates that microbial matground ecology persisted in the deep sea during the Early Cambrian, representing a Proterozoic "hangover" (see Section 14.2.2). This idea is consistent with the notion of archaic relics taking refuge in the deep sea (e.g. Conway Morris, 1989). *Oldhamia* flourished in Early Cambrian deep-marine environments, experiencing a remarkable behavioral diversification as revealed by a great diversity of ichnospecies (Seilacher *et al.*, 2005). *Oldhamia*-dominated assemblages in microbial-mat ecosystems persisted in the deep sea after the rise of vertical bioturbation in shallow seas, suggesting a gradual closure of a taphonomic window during the Ediacaran–Cambrian transition (Buatois and Mángano, 2004b). This is consistent with the recognition of Ediacara-type body fossils in Cambrian strata (Gehling *et al.*, 1998; Jensen *et al.*, 1998; Crimes and McIlroy, 1999; Hagadorn *et al.*, 2000; Shu *et al.*, 2006).

In addition to fully marine environments, Lower Cambrian ichnofaunas have been documented from marginal-marine settings (e.g. Mángano and Buatois, 2004b; Baldwin *et al.*, 2004; Mángano *et al.*, 2007), revealing that representatives of the Cambrian evolutionary fauna were able to colonize brackish-water environments (see Section 14.2.5). Although the scarcity of land plants was probably a major limiting factor in colonization of marginal-marine systems, documentation of Cambrian cryptospores suggests the presence of plants with one or more life-cycle phases on land (Strother and Beck, 2000; Strother, 2000). In contrast to complex modern estuarine food webs, Cambrian web chains in marginal-marine ecosystems were mostly marine-based, with acritarchs and algae being primary producers. However, a nascent terrestrial flora may have played a role in these ancient food webs (Mángano and

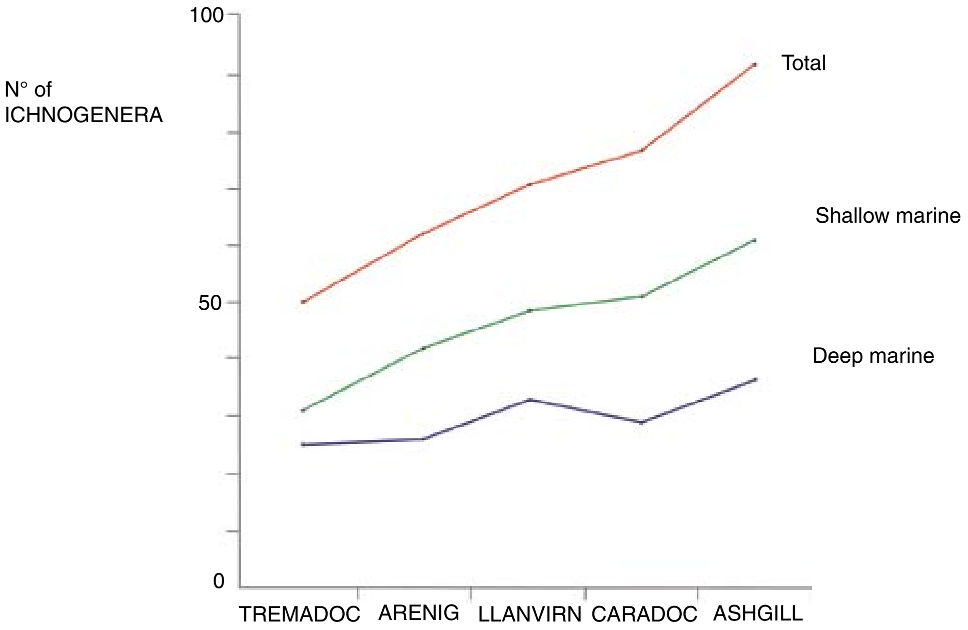


Figure 14.5 Ichnodiversity changes through the Ordovician (after Mángano and Droser, 2004). The ichnodiversity curves were compiled at the ichnogenus level. The ichnogeneric compilation was plotted as "range-through" data. Total curve includes not only shallow- and deep-marine ichnofossils but also continental trace fossils and boring ichnotaxa. The shallow-marine curve does not include borings.

Buatois, 2004b). Although tiering structure remains simple in marginal-marine environments, ichnoguild analysis reflects an incipient exploitation of food resources, recording the activity of a benthos that developed in the aftermath of the Agronomic Revolution (Mángano *et al.*, 2007).

14.1.4 THE ORDOVICIAN RADIATION

As in the case of the Cambrian explosion, most of our knowledge of the Ordovician radiation comes from the body-fossil record (e.g. Sepkoski, 1995; Sheehan, 2001; Droser and Finnegan, 2003). Some studies, however, have focused on the information potential of ichnological data (Mángano and Droser, 2004). In contrast to previous views, analysis of ichnodiversity indicates a continuous increase in ichnogeneric diversity through the Ordovician, with the number of shallow-marine ichnogenera doubling from the Tremadocian to the Ashgill (Mángano and Droser, 2004) (Fig. 14.5). This increase parallels substantial changes in the nature of biofabrics (Kidwell and Brenchley, 1994; Li and Droser, 1999; Droser and Li, 2001) and compositional turnovers by the dominant bioturbators of shallow-water environments.

Lower Ordovician ichnofaunas from shallow-marine siliciclastic deposits tend to be dominated by trilobite trace fossils, which record a significant turnover in peri-Gondwanan settings. Elements of the *Cruziana semiplicata* group (Upper Cambrian–Tremadocian) are replaced by elements of the *Cruziana rugosa* group by the Late Tremadocian (see Section 13.2). This change in ichnotaxonomic composition parallels the replacement of olenid-dominated communities by saphid-dominated communities (Waisfeld *et al.*, 1999, 2003). Other common components of the *Cruziana* ichnofacies in Lower Ordovician strata are vermiform structures such as *Planolites*, *Palaeophycus*, *Trichophycus*, *Treptichnus*, *Teichichnus*, and *Phycodes*.

Middle to Late Ordovician shallow-marine siliciclastic ichnofaunas commonly display more ethological variability. Although still relatively abundant, trilobite trace fossils are rarely the dominant component in open-marine clastic deposits, most likely reflecting the development of multiple tiers and the establishment of a well-developed mixed layer (Droser *et al.*, 2004). Mángano and Droser (2004) noted that the dominant patterns include branched, spreiten burrow systems (e.g. *Phycodes* and *Trichophycus*), branched, annulated burrow systems (e.g. *Arthrophycus*), branched burrow mazes and boxworks (e.g. *Thalassinoides*), dumbbell-shaped traces (e.g. *Arthraria*), and chevronate structures (e.g. *Protovirgularia*). Most of these behavioral architectures were present in Cambrian and Lower Ordovician rocks already, but generally were subordinate in abundance and diversity to trilobite and other arthropod trace fossils.

In general, the tiering structure of Ordovician shallow-marine siliciclastic resident communities is more complex than that of Cambrian biotas. On the other hand, the post-depositional suite, which commonly reflects the work of opportunistic organisms, seems to be less sensitive to evolutionary events, being mostly recorded by vertical suspension feeder structures, such as *Skolithos*, *Arenicolites*, and *Diplocraterion* (Mángano and Buatois, 2003a).

In contrast to siliciclastic shallow-marine settings, carbonate softgrounds do not show a significant increase in ichnodiversity through the Ordovician, but rather reveal increased ecospace utilization and tiering complexity (Droser and Bottjer, 1989; Mángano and Droser, 2004). Colonization of carbonate substrates may have lagged behind that of siliciclastic deposits. Ichnofabric evidence indicates an onshore–offshore pattern. Intense bioturbation first developed in shallow-water environments and only later in the offshore (Droser and Bottjer, 1989). Inner-shelf carbonates of the Great Basin in the western United States reveal two major increases in the extent and depth of bioturbation during the early Paleozoic: the first one between pre-trilobite and trilobite-bearing Cambrian rocks, and the second between the Middle and Late Ordovician (Droser and Bottjer, 1989).

The Ordovician increase in bioturbation seems to have resulted, in part, from an increase in the size of discrete structures (Droser and Bottjer, 1989). Although *Thalassinoides* is present in Cambrian and Lower Ordovician rocks, specimens are typically small, architecturally simpler, and commonly form two-dimensional networks (e.g. Myrow, 1995). In contrast, Middle to Upper Ordovician *Thalassinoides* burrow systems tend to be larger and deeper, and display classic "T" and "Y" branching (Sheehan and Schiefelbein, 1984). These *Thalassinoides* burrow systems resemble modern structures produced by decapod crustaceans recording extensive reworking with severe obliteration of primary structures (Sheehan and Schiefelbein, 1984; Droser and Bottjer, 1989; Carmona *et al*., 2004). In spite of this general trend, *Thalassinoides* burrows from Upper Cambrian–Tremadocian lagoonal carbonates in the Argentinean Precordillera display unquestionable three-dimensional morphology, suggesting an earlier origin of boxwork architecture (Cañas, 1995; Mángano and Buatois, 2003a). Although Ordovician *Thalassinoides* has typical boxwork architecture, unquestioned scratch mark ornamentation has not been recorded in early Paleozoic galleries (Carmona *et al*., 2004). Furthermore, early Paleozoic examples largely predate the first occurrence of decapod crustacean body fossils in the Devonian (Schram *et al*., 1978). Therefore, these burrow systems were most likely produced by other malacostracans (e.g. phyllocarids) or unrelated clades (e.g. enteropneusts) as a result of behavioral convergence (Carmona *et al*., 2004). In addition to those changes operating in carbonate softgrounds, significant changes in the evolution of macroboring organisms occurred in shallow-water hardgrounds during the Ordovician, resulting in the so-called Ordovician Bioerosion Revolution (Wilson and Palmer, 2006) (see Section 14.2.3).

The Ordovician radiation was not restricted to shallow-marine environments, but also represents a breakthrough in the deep sea, where ichnofaunas attained a much more modern aspect in comparison with their Ediacaran–Cambrian counterparts marking the real onset of the *Nereites* ichnofacies (see Section 14.2.2). Further changes took place in marginal-marine (see Section 14.2.5) and continental (see Section 14.2.6) ecosystems, revealing the environmental breadth of the Ordovician radiation.

14.1.5 THE ORIGIN OF DINOSAURS

The oldest skeletal remains of dinosaurs are known from the Late Triassic (e.g. Sereno and Novas, 1992). However, Early and Middle Triassic trackways attributed to dinosaurs have been mentioned in the literature. Wills and Sarjeant (1970) documented several trackways from Lower Triassic borehole cores in England which were attributed to small coelurosaur dinosaurs. However, subsequent reviews reinterpreted these structures as ripple marks, mud rip-up clasts, and possible limulid trackways (Thulborn, 1990; King and Benton, 1996). Sarjeant (1967) documented a Middle Triassic tracksite from England, which included footprints attributed to small theropods and prosauropods. Subsequent work by King and Benton (1996) placed them in the archosaur trackway *Chirotherium*, while Sarjeant (1996) reinterpreted some of them as *Chirotherium* and others as crocodilian trackways.

The strongest ichnological evidence for an earlier origin of dinosaurs comes from the Middle Triassic of continental Europe and Argentina. In France, Demathieu (1989) described trackways that have a strong similarity with *Grallator*, a dinosaur trackway recorded in Late Triassic and Jurassic rocks. Lockley and Meyer (2000) concluded that these are either the oldest dinosaur trackways or they were produced by non-dinosaurian archosaurs. In Germany, Haubold and Klein (2000, 2002) documented tridactyl pedes of bipeds (*Grallator*) and quadrupeds (*Atreipus*), which were regarded as having been produced by early dinosaurs and dinosauriforms, respectively. Avanzini (2002) described isolated small tridactyl imprints from Italy and attributed them to dinosauromorphs. Middle Triassic rocks of western Argentina contain large tridactyl footprints attributed to theropods (Arcucci *et al*., 1995; Forster *et al*., 1995; Marsicano *et al*., 2004). A recent analysis by Marsicano *et al*. (2007) documented a more diverse track assemblage, but indicated that no synapomorphies are preserved in the three-toed footprints that might allow discrimination among theropods, basal saurischians, and basal ornithischian groups as trackmakers. In any case, the trace-fossil record seems to suggest a Middle Triassic history of dinosaurs, predating the earliest occurrence of body fossils (Marsicano *et al*., 2007) (Fig. 14.6).

14.1.6 MASS EXTINCTIONS

The potential of trace fossils to explain mass-extinction events has been realized only recently (e.g. Twitchett and Wignall, 1996; Twitchett and Barras, 2004). Of the "Big Five" mass extinctions, research has focused on the end-Permian (e.g. Twitchett and Wignall, 1996; Twitchett, 1999; Pruss and Bottjer, 2004; Wetzel *et al*., 2007) and end-Cretaceous (e.g. Ekdale and Bromley, 1984b; Savrda 1993; Rodríguez-Tovar, 2005; Rodríguez-Tovar and Uchman, 2006, 2008) events. A more limited ichnological dataset is available for the end-Ordovician, Late Devonian, and end-Triassic events.

Estimations indicate that approximately 85% of marine species went extinct during the Late Ordovician event as a result of a brief glacial episode (Brenchley *et al*. 2001; Sheehan 2001), although the ecological impact was comparatively low (McGhee *et al*., 2004). Only a few ichnological studies have been devoted to this mass extinction (McCann, 1990; Herringshaw and Davies, 2008). Information from shallow-marine strata of the Welsh Basin indicates overall low degrees of bioturbation and trace-fossil diversity during the Late Ordovician–Early Silurian transition, but no other clear patterns are apparent (Herringshaw and Davies, 2008). Examination of deep-marine deposits in the same basin reveals a sharp decrease in ichnodiversity across the Ordovician–Silurian boundary (McCann, 1990).

During the Late Devonian (Frasnian–Famennian) mass extinction approximately 70% of species disappeared, with the

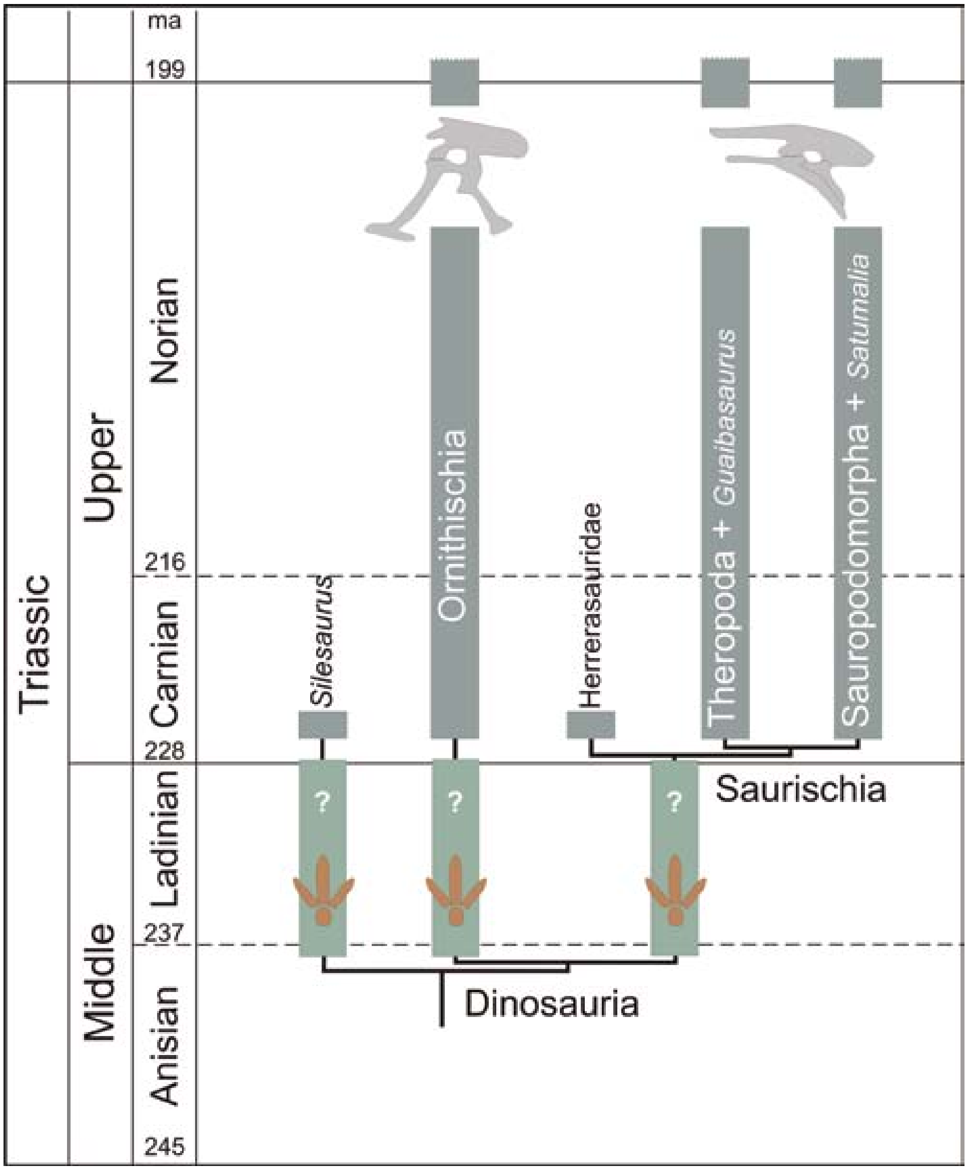


Figure 14.6 Calibrated phylogeny of early dinosaurs and its sister taxon taking into account not only the body-fossil record, but also the trace-fossil record. Addition of ichnological data implies the extension of the early diversification of dinosaurs and/or their closest relatives into the Middle Triassic. Based on Marsicano *et al*. (2007).

event affecting both marine and terrestrial organisms (McGhee, 1996). Global oceanic anoxia, global cooling, and multiple impacts of asteroids or comets have been proposed as potential causes (McGhee, 1996, 2001). Ichnological analysis of this event is still in its infancy and only one study has been published so far (Morrow and Hasiotis, 2007). Preliminary information indicates that the crisis is associated with a drop in ichnodiversity, reduction in bioturbation intensity, decreased depth of bioturbation, and decreased burrow size. A protracted post-extinction recovery is apparently marked by an increase in trace-fossil diversity by the middle Famennian, including *Cruziana* and *Rusophycus*. However, evaluation of environmental and facies controls needs to be addressed in more detail in this study. The suggested trends were based on a shallowing-upward succession from slope to offshore environments. Therefore, the appearance of trilobite burrows and the associated increase in ichnodiversity noted by these authors may simply reflect shallowing and the establishment of an offshore community rather than a true post-extinction recovery.

The end-Permian mass extinction was the largest of the entire Phanerozoic, and it has been estimated that up to 96% of species became extinct, (Raup, 1979; Hallan and Wignall, 1997; Benton, 2003; Erwin, 2006). This mass extinction displays the highest ecological severity in both marine and continental environments (McGhee *et al*., 2004). Global anoxia has been suggested as the most likely cause of the extinction in the oceans (Hallam and Wignall, 1997; Wignall, 2001). Release of large volumes of volcanic carbon dioxide may have triggered a super-greenhouse climate, making large areas of Pangea uninhabitable. In turn, global warming may have affected global ocean circulation patterns by decreasing the generation of dense cold deep waters, resulting in stagnation and anoxia (Wignall, 2001). In recent years, trace-fossil information has been used to analyze the patterns of extinction and recovery across the critical

Permian–Triassic interval, and a more robust ichnological dataset is now available for this event (e.g. Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004; Pruss and Bottjer, 2004; Wetzel et al., 2007; Zonneveld *et al.*, 2007, 2010; Beatty *et al.*, 2008; Fraiser and Bottjer, 2009). Comparative ichnological analyses through the pre-extinction, post-extinction aftermath, and recovery phases are particularly useful for evaluating the endobenthic response to the end-Permian mass extinction event in shallow-marine settings (Twitchett and Barras, 2004). Pre-extinction deposits are intensely bioturbated and contain a wide variety of ichnotaxa. In contrast, ichnofaunas from the lowermost Triassic (immediate post-extinction aftermath) are typically monospecific and consist of small *Planolites*, indicating environmental stress in connection with a widespread anoxic event. Available information indicates that there was a stepwise appearance of ichnogenera through the Early Triassic, signaling the phase of recovery. Parallel to this increase in ichnodiversity, an increase in burrow size and depth of bioturbation has been noted. In addition, proliferation of microbial mat structures during the post-extinction aftermath provides further evidence of suppressed bioturbation and environmental stress (Pruss *et al.*, 2004, 2005; Mata and Bottjer, 2009). It has been suggested that there may have been a faster recovery at higher latitudes, as indicated by the presence of higher ichnodiversity levels (Beatty *et al.*, 2008; Zonneveld *et al.*, 2010). In addition, Wetzel *et al.* (2007) documented a deep-marine ichnofauna in Upper Triassic rocks of Oman, which displays unusually high diversity in contrast to age-equivalent deep-sea assemblages worldwide. According to these authors, some of these refuge habitats may have been located in warm-water, low-latitude shelf and continental-margin environments, allowing recolonization of the deep-sea floor after the Permian-Triassic mass extinction.

The end-Triassic mass extinction accounts for an approximately 76% loss in species diversity and is ranked third in terms of ecological severity, affecting both marine and continental communities (Raup, 1992; Tanner *et al.*, 2004; McGhee *et al.*, 2004). In comparison, less research has been done on this mass extinction and its causes are poorly understood, with hypotheses ranging from widespread eruptions of flood basalts to the release of methane hydrates and bolide impact-induced environmental degradation (Tanner *et al.*, 2004). Although ichnological aspects of this event have not been analyzed in the same detail as those of the end-Permian event, there is a growing volume of information suggesting changes in vertebrate and invertebrate ichnofaunas. The tetrapod footprint record indicates that large theropod dinosaurs appeared less than 10 000 years after the Triassic–Jurassic boundary and that dinosaur communities became dominant less than 100 000 years after the boundary (Olsen *et al.*, 1987). Marine invertebrate ichnofaunas of the pre-extinction Late Triassic are diverse, while lowermost Jurassic (Hettangian) deposits are characterized by low ichnodiversity, low bioturbation intensity, small burrow diameters, and an absence of deep-tier structures, illustrating the immediate post-extinction aftermath (Barras and Twitchett, 2007). A stepwise appearance of ichnogenera characterizes recovery times. Ichnological evidence seems to be consistent with an episode of marine anoxia (Barras and Twitchett, 2007).

The end-Cretaceous extinction accounts for 40–76% species loss, affecting both marine and terrestrial communities (Jablonski, 1995; Hallam and Wignall, 1997; Norris, 2001; Wolfe and Russell, 2001). This extinction most clearly illustrates the decoupling of taxonomic and ecological severity, being the least severe of the "Big Five" in terms of taxonomic diversity, but the second from an ecological standpoint (McGhee *et al.*, 2004). Most researchers favor the impact of a large bolide impact as the triggering cause of the extinction (Alvarez *et al.*, 1980; Kauffman and Hart, 1996), although other mechanisms, such as massive volcanism, have also been proposed (e.g. Keller, 2001, 2003). Ichnological research on the Cretaceous–Tertiary mass extinction focused on three different aspects: paleoenvironmental interpretation of the associated deposits, the nature of benthic colonization after the extinction, and changes in the types and intensity of arthropod–plant interactions. The first set of studies took place inland of the Gulf of Mexico, in Alabama (Savrda, 1993) and northeastern Mexico (Ekdale and Stinnesbeck, 1998). Both studies questioned the catastrophic nature of the deposits which were attributed to a tsunami. In the case of Alabama, ichnological and sedimentological analysis supports transgressive deposition in an estuarine incised valley (Savrda, 1993), while deposits in Mexico are intensely bioturbated, suggesting slow sedimentation rather than a catastrophic event (Ekdale and Stinnesbeck, 1998). The second set of studies was performed in Europe, more precisely in several sections in Denmark (Ekdale and Bromley, 1984b) and Spain (Rodríguez-Tovar, 2005; Rodríguez-Tovar and Uchman, 2004a, b; 2006, 2008; Rodríguez-Tovar *et al.*, 2006). In general, these studies documented intense bioturbation in earliest Danian strata, suggesting rapid substrate colonization and re-establishment of infaunal communities after the extinction event, and, therefore, arguing against the idea of a major restructuring of the infaunal benthic community. Also, it has been noted that deep burrowing may have transported Danian forams into the underlying Maastrichtian deposits, complicating positioning of the boundary (Rodríguez-Tovar and Uchman, 2006). Finally, evidence of insect traces preserved in fossil plants allowed an evaluation of the impact of the mass extinction in continental environments (e.g. Labandeira *et al.*, 2002a, b). These studies suggested a sudden and sustained drop in many categories of plant–insect interactions at the Cretaceous–Tertiary boundary. Similar levels of interactions to those of the latest Cretaceous were not attained until the Paleocene–Eocene boundary (Wilf *et al.*, 2001; Labandeira *et al.*, 2002a, b). Those categories of interactions that were most affected correspond to specialized associations in which monophagy defines plant–host specificity (Labandeira *et al.*, 2002a).

Also, ichnofaunas from various environments were differentially impacted by mass extinctions. Shallow-marine communities were the most affected. In contrast, the impact was lower on marginal-marine brackish-water faunas (Buatois *et al.*, 2005). Brackish-water faunas consist of opportunistic organisms that flourish under extreme conditions, and are able to rapidly colonize environments after a major disturbance, as it is the case of a mass extinction. Deep-water ichnofaunas have not been strongly affected by mass extinctions either (Uchman, 2004a). No major deep-water crisis has been associated with any of the "Big Five" mass extinctions. However, Uchman (2003) noted reduced diversity and abundance of graphoglyptids associated with the end-Ordovician and end-Cretaceous mass extinctions.

14.2 ANIMAL–SUBSTRATE INTERACTIONS AND ECOSYSTEMS THROUGH TIME

14.2.1 COLONIZATION OF SHALLOW-MARINE ENVIRONMENTS

Because nearshore to offshore-shelf strata typically contain a high diversity of body fossils, shallow-marine environments have been the focus of most studies in marine evolutionary paleoecology. Some of the most influential research on this topic was performed by Sepkoski (1981, 1991, 1992, 1997). In these studies, Sepkoski recognized the existence of three main evolutionary faunas in the Phanerozoic: the Cambrian, Paleozoic, and Modern evolutionary faunas. Each evolutionary fauna had a unique set of higher taxa and displays higher diversity and more ecological complexity than the previous one. This increase in ecological complexity has been further demonstrated through the analysis of Bambachian megaguilds (Bambach, 1983; Bambach *et al*., 2007; Bush *et al*., 2007). Although further studies based on more refined techniques and more extensive databases have questioned some aspects of this model (e.g. Alroy *et al*., 2001, 2008), this scheme has proved to be quite relevant to our understanding of ecological aspects of the history of life. Trace-fossil information is consistent with the body-fossil record of evolutionary faunas.

The Cambrian evolutionary fauna was dominated by trilobites, with inarticulate brachiopods, hyolithids, monoplacophorans, eocrinoids, and hexactinellid sponges as other components (Sepkoski, 1981). Deposit, detritus, and suspension feeders were the main trophic types, with predation being a relatively minor component (Sepkoski, 1981; Bambach, 1983; Burzin *et al*., 2000; Sheehan, 2001). The ecological structure of communities in this evolutionary fauna was relatively simple. Thirty modes of life (see Section 3.1) have been recognized for Lower to Middle Cambrian faunas, representing roughly one-third of the modes of life used by recent faunas (Bambach *et al*., 2007). Of these 30 modes of life, 19 were recorded based on skeletal faunas and the other 11 based on the analysis of soft-bodied animals preserved in Konservat-Lagerstätten. Overall, the Cambrian evolutionary fauna represents the occupation of 11 megaguilds (*sensu* Bambach, 1983). The Cambrian evolutionary fauna began in the Early Cambrian, increased in diversity during the Cambrian, gradually diminished in importance after the Ordovician, and was severely affected by the end-Permian mass extinction.

Of the typical components of the Cambrian evolutionary fauna, only trilobites and other arthropods are important trace-fossil producers, being inarticulate brachiopods makers of *Lingulichnus*. The increase and subsequent decrease in dominance and diversity of arthropod- and particularly trilobite-produced trace fossils certainly follows the trend displayed by the Cambrian evolutionary fauna (see Sections 14.1.3 and 14.1.4). Also, tiering analysis based on the study of ichnofaunas indicates relatively simple community structures and limited utilization of the infaunal ecospace. Deposit-feeding ichnoguilds are mostly shallow tier, while deep-tier ichnoguilds of suspension feeders are restricted to high-energy nearshore zones. Bambach (1993) has proposed that the paucity of deep deposit-feeding burrowers in offshore to deeper-water settings indicates limited amounts of food buried in the sediment. Limited durophagous predation is also suggested by the trace-fossil record, as illustrated by the scarcity of bored shells (see Section 14.2.3). Based on the existence of graphoglyptids in shallow-water deposits, it may be argued that farming and trapping strategies had already developed during the Cambrian, and later migrated into the deep sea (see Section 14.2.2). Because these sophisticated strategies are usually employed as a response to scarce food resources, this pattern seems to be consistent with comparatively limited food in shallow seas during the Cambrian (Buatois and Mángano, 2003b).

The Paleozoic evolutionary fauna was dominated by articulate brachiopods, rugose and tabulate corals, and crinoids; stenolaemate bryozoans, graptolites, and cephalopods were common also (Sepkoski, 1981). The benthos experienced a diversification in deposit feeders, detritus feeders, suspension feeders, and grazers, while suspension feeders and predators diversified in the pelagic setting (Bambach, 1983; Sheehan, 2001). Predation levels also increased and the ecological structure of the communities became more complex. As a result of the Ordovician radiation, the number of modes of life utilized by skeletal organisms increased to a total of 30 by the Late Ordovician; the scarcity of Konservat-Lagerstätten precludes analysis of soft-bodied faunas (Bambach *et al*., 2007; but see Van Ray *et al*., 2010). Of the 20 potential Bambachian megaguilds, 14 were filled by the Paleozoic fauna (Sheehan, 2001). The Paleozoic evolutionary fauna began in the Early Cambrian, but attained its maximum diversity in the Ordovician. Diversity was maintained during the Paleozoic and, although the fauna persisted into the Mesozoic and the Cenozoic, it was significantly affected by the end-Permian mass extinction, showing a rapid decline (Sepkoski, 1981).

The ichnological expression of the Paleozoic evolutionary fauna is mostly reflected by an increase in ichnodiversity and tiering complexity, as well as by an increase in degree and depth of bioturbation. As previously discussed, the number of shallow-marine ichnogenera doubled as a result of the Ordovician radiation (see Section 14.1.4). The tiering structure of ichnofaunas becomes more complex, both by the addition of deeper tiers and by the addition of a wider variety of behavioral patterns in previously occupied tiers, mostly in the case of offshore deposit-feeding faunas (Mángano and Droser, 2004; Mángano and Buatois, 2011). Interestingly, recent studies suggest that infaunalization by deposit feeders in offshore siliciclastic environments was most likely diachronic, with mid tiers being colonized first in Laurentia and Baltica, and subsequently in Gondwana (Mángano and Buatois, 2011). An overall increase in the depth of bioturbation seems to have occurred since the Ordovician and well into the Devonian (Larson and Rhoads, 1983). Bioturbation depths of 5–6 cm were common, locally with depths up to 30 cm (Bambach, 1993). Preliminary data suggest that these levels persisted into the Triassic (Aigner, 1985). Increased burrowing depths by deposit feeders have been linked to an increase in the amount of buried food (Bambach, 1993). In contrast, *Skolithos* pipe rock, a product of deep-tier suspension feeders which was widespread during the Cambrian, become less common through the Paleozoic (Droser, 1991; Desjardins *et al*., 2010a). Although the reasons for this decline are unclear, increased disturbance of the substrate by deposit feeders may have impacted negatively on passive suspension feeders (Thayer, 1979; Miller and Byers, 1984) (see Section 6.6). In fact, the diversification of sediment bulldozers has been deemed responsible for the decline throughout the Phanerozoic of suspension feeders living in soft sediments (Thayer, 1979). Other potential factors involved in the decline of large sessile suspension-feeders may have been the radiation of predators (McIlroy and Garton, 2004) and greater spatial competition for the infaunal ecospace (Desjardins *et al*., 2010a). Ichnological evidence of increased durophagous predation in the Paleozoic evolutionary fauna is indicated by a higher abundance of predatory holes. Overall, bioerosion increased significantly in both diversity and intensity (see Section 14.2.3).

The Modern evolutionary fauna is dominated by mollusks (bivalves and gastropods), echinoids, crustaceans, and different vertebrates; gymnolaemate bryozoans, demosponges, and ammonites are also members of this fauna (Sepkoski, 1981). A significant diversification occurs in the pelagic realm. The evolutionary innovations that took place during the Mesozoic have been referred to as “the Mesozoic marine revolution” by Vermeij (1987). This event led to a major restructuring of shallow-marine benthic communities. Some of these changes involved the acquisition of additional ecological guilds that were not present in the Cambrian and Paleozoic evolutionary faunas, particularly with respect to the exploitation of the deep infaunal ecospace (Thayer, 1983; Bambach, 1983). The intensification of grazing and the diversification of durophagous predators were conducive to increases in prey sturdiness and the frequency of shell repair (Vermeij, 1987; Kelley and Hansen, 2001) (see Section 14.2.3). The number of modes of life utilized increased up to present levels (Bambach *et al*., 2007). All 20 Bambachian megaguilds were filled (Sheehan, 2001). Overall, the body-fossil record shows that by the late Cenozoic, marine paleocommunities have a much greater representation of infaunal organisms and higher proportion of motile animals than mid-Paleozoic communities (Bush *et al*., 2007). The Modern evolutionary fauna began in the early Paleozoic, becoming dominant after the end-Permian mass extinction (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985).

The advent of the Modern evolutionary fauna is clearly reflected by the ichnological record (e.g. Carmona *et al*., 2008). This is obvious not only from the composition of the ichnofaunas, but also from the complexity of tiering structure and intensity and depth of bioturbation. The imprint of malacostracan crustaceans is evidenced by the dominance of a wide variety of burrow systems produced by these organisms, such as *Thalassinoides*, *Ophiomorpha*, *Spongeliomorpha*, and, to a lesser extent, *Pholeus*, *Psilonichnus*, *Sinusichnus*, and *Maiakarichnus* (Carmona *et al*., 2004; Verde and Martínez, 2004; Curran, 2007; Buatois *et al*., 2009a). To this list we should add the double helicoidal burrow *Lapispira*, also possibly produced by decapod crustaceans (Lanes *et al*., 2007). Crustacean burrows become dominant not only in offshore to shelf environments, but also in nearshore settings. In fact, *Ophiomorpha* replaced *Skolithos* as the dominant component of the *Skolithos* ichnofacies in post-Paleozoic strata (Droser and Bottjer, 1993). Another typical component of the Modern evolutionary fauna reflected in the trace-fossil record is irregular echinoid burrows, namely *Scolicia* and *Bichordites*, which are known since the Jurassic (Smith and Crimes, 1983). To this list we may add a number of post-Paleozoic morphologically complex ichnogenera (e.g. *Paradictyodora*, *Patagonichnus*) that are probably produced by unknown soft-bodied organisms (Olivero *et al*., 2004; Olivero and López-Cabrera, 2005). The complex tiering structure commonly revealed by these ichnofaunas shows the development of a finely partitioned infaunal niche and an increase in degree of bioturbation. This is particularly obvious in the case of Neogene shallow-marine ichnofaunas, which typically display complex tiering patterns and a wide variety of ichnoguilds (e.g. Buatois *et al*., 2003; Carmona *et al*., 2008). Depth of bioturbation reached a maximum, with crustacean burrows colonizing the deep infaunal ecospace and reaching several meters below the sediment–water interface. Increased intensity of predation is revealed by the larger proportion of shells showing evidence of drilling holes produced by gastropods and breakage by crabs (Vermeij, 1987; Bambach, 1993). In addition, a remarkable increase in the diversity of bioerosion structures due to predation resulted from the Mesozoic marine revolution (see Section 14.2.3). Increased infaunalization and predation may also reflect an increase in the biomass of marine consumers (Bambach, 1993).

It has been suggested that evolutionary innovations commonly started in shallow water and subsequently migrated or expanded into deeper water. In fact, this pattern is also revealed by the evolutionary faunas themselves (Sepkoski and Miller, 1985) (see Sections 14.2.2 and 14.2.4). Also, the intensity of bioturbation first increased in shallow-water settings and only occurred later in the offshore (Droser and Bottjer, 1989). In addition, some ichnogenera seem to display an offshore–onshore trend. In the case of expansion, an ichnogenus that occurs for the first time in shallow water subsequently extends its environmental range into deeper water without loss of onshore representatives. In contrast, retreat involves migration into deeper water with loss of onshore representatives (Botjjer *et al*., 1988; Stanley and Pickerill, 1993). For example, the ichnogenus *Zoophycos* is common in Paleozoic shallow-marine deposits. However, it migrated into deeper water throughout the Mesozoic, essentially disappearing from nearshore areas by the Cenozoic, providing an example of retraction (Bottjer *et al*., 1988). Another example of retraction into deep-water settings has been suggested for the ichnogenus *Fustiglyphus* (Stanley and Pickerill, 1993). The ichnogenus *Ophiomorpha*, restricted to shallow-marine environments during the late Paleozoic and early Mesozoic, expanded into deep water during the late Mesozoic (Bottjer *et al*, 1988; Tchoumatchenco and Uchman, 2001). *Scolicia* may have originated in shallow-marine settings, but expanded into deep water by the end of the Cretaceous, displaying an optimization of grazing patterns (Seilacher, 1986). Other ichnogenera, such as *Asteriacites*, seem to exhibit less straightforward distribution patterns (Mikuláš, 1992).

14.2.2 COLONIZATION OF THE DEEP SEA

The colonization of the deep sea was one of the first evolutionary processes addressed from an ichnological perspective (e.g. Seilacher, 1974, 1977b; Crimes, 1974). More recently, it has been discussed in detail in a number of papers (e.g. Orr, 2001; Uchman, 2003, 2004a). In particular, Uchman (2004a) provided a comprehensive analysis of the Phaneozoic history of deep-sea trace fossils supported by an extensive database. There is general agreement in that: (1) complex behavioral patterns initially evolved in shallow water, and subsequently migrated into the deep sea (Crimes and Anderson, 1985; Crimes and Fedonkin, 1994; Jensen and Mens, 1999), and (2) that there has been an increase in complexity and diversity of trace fossils throughout the Phanerozoic (Crimes, 1974; Seilacher, 1974, 1977b; Crimes and Crossley, 1991; Uchman, 2003, 2004a).

The earliest record of deep-marine trace fossils is Ediacaran, as indicated by poorly diverse, nonspecialized grazing trails (e.g. *Helminthopsis*, *Helminthoidichnites*) in connection with microbial mats (MacNaughton *et al*., 2000; Liu *et al*., 2010) (Fig. 14.7). These strategies linked to exploitation of microbial mats persisted well into the Cambrian with the addition of arthropod trackways (e.g. *Diplichnites*) and more sophisticated feeding strategies represented by different *Oldhamia* ichnospecies (Buatois and Mángano, 2003a) (Fig. 14.7).

Deep-marine ecosystems underwent significant changes by the end of the Cambrian, probably as a result of increased competition for ecospace and/or resources within shallow-marine ecosystems that forced animals into deeper-water settings (Crimes *et al*., 1992; Crimes, 2001; Orr, 2001; Mángano and Droser, 2004; Buatois *et al*., 2009b). The main lineages of deep-marine trace fossils (i.e. rosette, meandering, networks, and spirals) were established in deep-sea environments by the Early Ordovician, recording the first appearance of the *Nereites* ichnofacies (Orr, 2001; Mángano and Droser, 2004; Uchman, 2004a; Buatois *et al*., 2009b) (Fig. 14.7). Lower to Middle Ordovician deep-marine ichnofaunas seem to be moderately diverse, and fodinichnia commonly dominates rather than graphoglyptids (e.g. Orr, 1996). A significant diversity increase occurred in the Upper Ordovician–Lower Silurian, with ichnofaunas recording higher proportions of graphoglyptids (McCann, 1990; Orr, 2001; Mángano and Droser, 2004; Uchman, 2003, 2004a). In short, ichnological evidence records the advent of a deep-marine ecosystem of modern aspect during the Ordovician, representing a second-level change (*sensu* Droser *et al*., 1997). Interestingly, most of the Cambrian–Ordovician deep-marine trace fossils represent the activity of shallow-tier organisms. However, Orr (2003) documented Ordovician deep-marine ichnofabrics that record the activity of a climax suite that may have penetrated at least 40 cm into the substrate. Other examples of deep bioturbation (e.g. Pickerill and Williams, 1989) may have been produced by the activity of doomed pioneers transported from shallow- to deep-marine environments via turbidity currents (Waldron, 1992; Allison and Briggs, 1994).

Uchman (2004a) noted that Ordovician to Carboniferous deep-marine ichnofaunas were compositionally similar, typically containing *Dictyodora*, several ichnospecies of *Nereites*, and *Megagrapton*, among other ichnotaxa. In particular, *Dictyodora* records a clear evolutionary trend from the Upper Ordovician to the Carboniferous, as revealed by an increase in the height of the wall, and an improvement in feeding efficiency (Seilacher, 1967a; Benton, 1982). This pattern suggests a strategy of underground mining progressively deeper into the sediment through time (Seilacher, 1967a; Benton and Trewin, 1980; Benton, 1982; Seilacher-Drexler and Seilacher, 1999; Mángano and Droser, 2004).

A subsequent ichnodiversity peak is recorded in the Early Carboniferous (Orr, 2001; Uchman, 2004a). However, the rest of the Carboniferous experienced a constant decrease in ichnodiversity, culminating in overall low-ichnodiversity levels during the Permian to the Middle Jurassic (for an exception see Wetzel *et al*., 2007) (see Section 14.1.6). Uchman (2004a) linked the decrease in ichnodiversity during the Late Carboniferous–Permian to the deep-seawater temperature decrease resulting from the Gondwanan glaciations. He also noted that some typical earlier Paleozoic ichnotaxa disappeared from the fossil record (e.g. *Dictyodora* and *Spirodesmos*).

Significant innovations had taken place in the deep sea by the Late Jurassic–Early Cretaceous, when trace fossils produced by irregular echinoids (*Scolicia*) and large decapod crustaceans (*Ophiomorpha*) occurred for the first time (Tchoumatchenco and Uchman, 2001). These are efficient bioturbators and their arrival at deep-sea bottoms was conducive to intensive plowing of the sediment, deepening of the redox boundary, and expansion into deeper tiers (Uchman, 2004a). This author regarded this event as somewhat analogous to the Agronomic Revolution of Cambrian times (see Section 14.1.3). Also, an ichnodiversity peak is detected by the Late Jurassic–Early Cretaceous, followed by a remarkable decrease during the Albian, most likely as a result of widespread anoxia.

The maximum ichnodiversity peak is reached during the Eocene, accompanied by the largest contribution of graphoglyptids to global diversity (Uchman, 2003, 2004a). The Eocene optimum in graphoglyptid diversity has been linked to the advent of oligotrophic conditions in the oceans linked to global warming (Tunis and Uchman, 1996a, b). However, recent research on

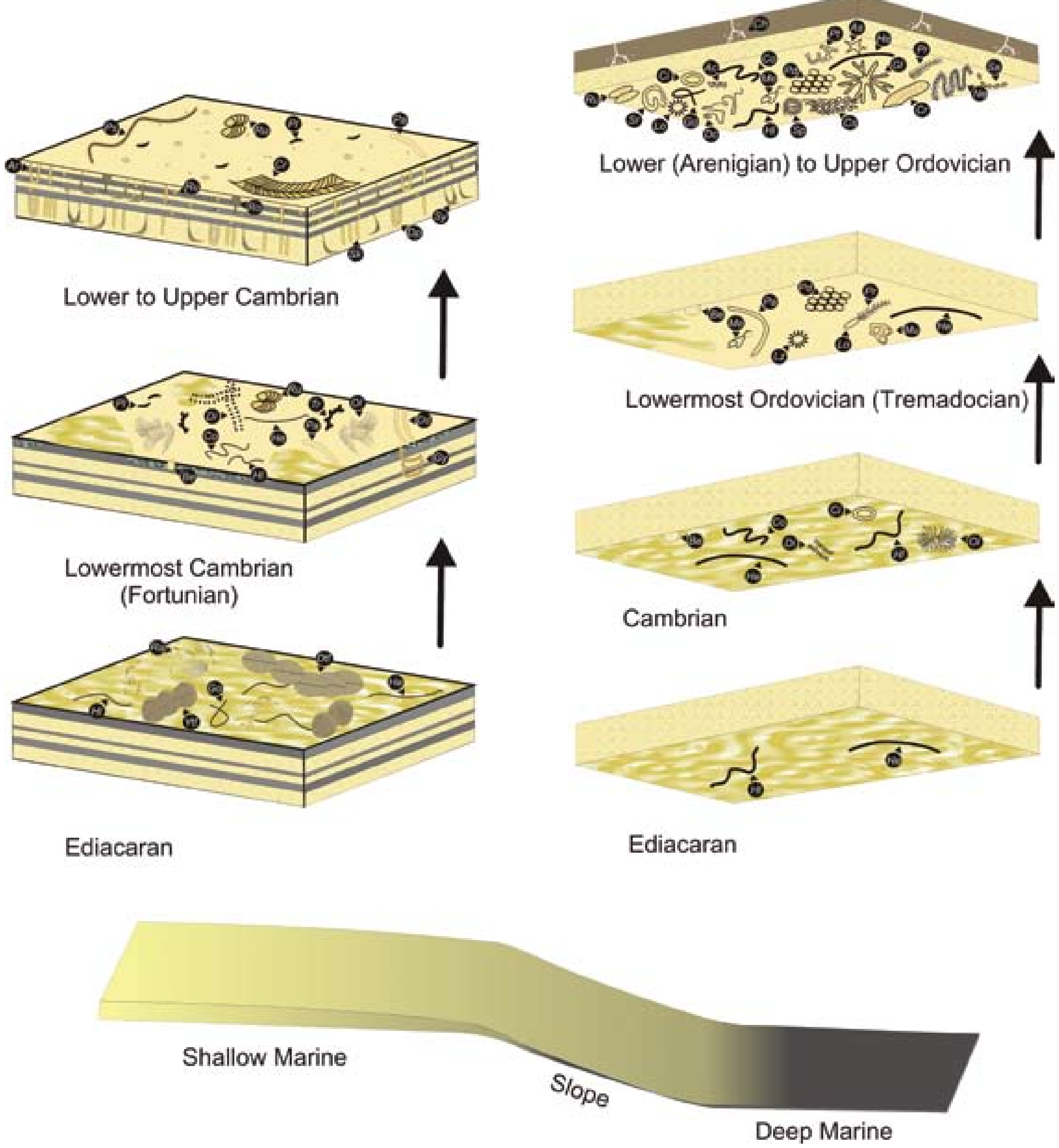


Figure 14.7 Early history of deep-sea colonization in comparison with evolutionary events in the shallow-marine realm. Colonization of deep-sea bottoms was delayed with respect to that of shallow-marine environments. By the Ediacaran, typical shallow-marine ichnofaunas consist of nonspecialized grazing trails, such as *Helminthopsis* (*Hl*), *Helminthoidichnites* (*He*), and *Gordia* (*Go*), the rasping trace *Radulichnus* (*Ra*), and trace fossils produced by *Dickinsonia* (*D*tf) and *Yorgia* (*Y*tf). Coeval deep-marine deposits contain less diverse ichnofaunas, essentially consisting of *Helminthopsis* (*Hl*) and *Helminthoidichnites* (*He*). Microbial mats are widespread in both settings. Lowermost Cambrian (Fortunian) shallow-marine deposits reflect a remarkable increase in ichnodiversity, and are dominated by branched burrows, typically *Treptichnus* (*Tr*), arthropod trace fossils such as *Diplichnites* (*Di*), *Rusophycus* (*Ru*), and *Diplopodichnus* (*Do*), the spiral-shaped burrow *Gyrolithes* (*Gy*), the plug-shaped burrow *Bergaueria* (*Be*), and simple burrows such as *Palaeophycus* (*Pa*) and *Planolites* (*Pl*). *Cochlichnus* (*Co*), *Helminthopsis* (*Hl*), and *Helminthoidichnites* (*He*) are also common. Some ichnospecies of *Oldhamia* (*Ol*) may occur in shallow-marine settings. Microbial matgrounds display a more patchy distribution. Later in the Early Cambrian other ichnotaxa become typical in shallow-marine environments. These include a wide variety of vertical burrows abundant in high-energy environments, such as *Skolithos* (*Sk*), *Diplocraterion* (*Dp*), *Arenicolites* (*Ar*), *Rosselia* (*Ro*), and *Syringomorpha* (*Sy*), together with other ichnogenera more typical of lower-energy settings, including *Psammichnites* (*Ps*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Rusophycus* (*Ru*), and *Cruziana* (*Cr*). Microbial mats became restricted to stressed settings, being rare in fully marine settings later in the Cambrian. Cambrian deep-marine ichnofaunas remained poorly diverse. Different ichnospecies of *Oldhamia* (*Ol*) are dominant, together with unspecialized grazing trails such as *Helminthoidichnites* (*He*), *Helmintopsis* (*Hl*), *Cochlichnus* (*Co*), the feeding trace *Circulichnis* (*Ci*), arthropod trackways such as *Diplichnites* (*Di*), and the plug-shaped burrow *Bergaueria* (*Be*). Matgrounds persisted in the deep sea during the Cambrian. Lowermost Ordovician (Tremadocian) deep-marine ichnofaunas are characterized by branched feeding burrows, typically *Multina* (*Mu*), simple trace fossils such as *Palaeophycus* (*Pa*) and *Helminthoidichnites* (*He*), and the bivalve locomotion trace *Protovirgularia* (*Pr*). Graphoglyptids also occur, including *Megagrapton* (*Me*), *Paleodictyon* (*Pd*), and *Lorenzinia* (*Lo*), although they do not seem to be abundant. The plug-shaped burrow *Bergaueria* (*Be*) persisted in this setting. Later in the Ordovician, a remarkable increase in trace-fossil diversity took place in deep-sea environments. These ichnofaunas consist of a wide variety of forms, including the graphoglyptids *Megagrapton* (*Me*), *Paleodictyon* (*Pd*), *Protopaleodictyon* (*Pt*), *Cosmorhaphe* (*Cs*), *Spirorhaphe* (*Sp*), *Acanthorhaphe* (*Ac*), *Glockerichnus* (*Gl*), and *Lorenzinia* (*Lo*). Other ichnotaxa include *Chondrites* (*Ch*), *Spirophycus* (*Sr*), *Dictyodora* (*Dc*), *Helminthoidichnites* (*He*), *Protovirgularia* (*Pr*), *Cruziana* (*Cr*), *Rusophycus* (*Ru*), *Nereites* (*Ne*), *Asteriacites* (*As*), *Cochlichnus* (*Co*), *Circulichnis* (*Ci*), *Helminthopsis* (*Hl*), *Gordia* (*Go*), and *Saerichnites* (*Sa*). Microbial mats show a remarkably patchy distribution. Modified from Mángano and Buatois (2007), and Buatois *et al*. (2009b).

ichnofaunas from Tierra del Fuego, southern Argentina, demonstrated a diversity peak accompanied by a cooling trend (López-Cabrera *et al.*, 2008). Accordingly, these authors suggested a link between diversification of graphoglyptids and constancy of relative oligotrophy, rather than temperature per se.

Most graphoglyptid ichnotaxa have their first occurrence in Upper Cretaceous–Eocene rocks (Uchman, 2003). Also, since the Late Cretaceous graphoglyptids displayed an accelerated evolution with farming becoming a widespread strategy in the deep sea (Seilacher, 1977b; Uchman, 2004a). After the Eocene, no new graphoglyptid ichnotaxa have been recorded (Uchman, 2004a). By the Oligocene, parallel to a decrease in water temperatures, ichnodiversity displayed a dramatic decrease, most likely linked to the Eocene–Oligocene boundary crisis, which negatively impacted on other groups, such as foraminiferans, dinoflagellates, and nanoplankton. No increase in ichnodiversity was recorded during climatic amelioration in the Miocene (Uchman, 2004a).

14.2.3 COLONIZATION OF HARD SUBSTRATES

Examination of trends displayed by marine bioerosion structures allows an understanding of evolutionary changes in marine hard substrate communities, including the role of drilling predation (e.g. Kowalewski *et al.*, 1998, 1999; Harper *et al.*, 1999; Perry and Bertling, 2000; Taylor and Wilson, 2003; Bromley, 2004; Glaub, 2004; Wilson, 2007; Tapanila, 2005, 2008). The oldest trace fossils known are microborings reported from Archean (3500 ma) pillow lavas from South Africa (Furnes *et al.*, 2004). These structures record microbial etching of glass along fractures and indicate biologically mediated corrosion. The presence of organic carbon in the margins of the microborings and isotopically low $\delta^{13}C$ values of carbonate in the glassy rims of the pillow support microbial fractionation and a biogenic origin for these structures. Bioerosion evidence is therefore consistent with an early origin of thermophilic microbes around deep-sea hydrothermal vents. Paleo- to Mesoproterozoic stromatolites were bored by cyanobacteria (Zhang and Golubic, 1987). Microbioerosion due to cyanobacteria has been also reported from Neoproterozoic oolites and pisolite grains (Knoll *et al.*, 1986).

Although bioerosion became more important during the Cambrian, borings provide evidence of incipient predation during the Ediacaran. Predatory holes (assigned to the ichnogenus *Oichnus*) in the tubular shell *Cloudina* suggest that shell-drilling predation may have been already present in the Ediacaran, representing the oldest evidence of macrobioerosion (Bengtsön and Yue, 1992; Hua *et al.*, 2003). The intensity of bioerosion increased as a result of the Cambrian explosion, but borings were very simple and diversity remained low with only *Trypanites* and *Oichnus* recorded (Wilson, 2007). High densities of *Trypanites* are present in Lower Cambrian archaeocyathid reefs, revealing domichnial bioerosion by a macroboring biota (James *et al.*, 1977; Kobluk *et al.*, 1978). The round hole *Oichnus* is present in Cambrian shells, representing increased predation levels, albeit significantly lower that those displayed by younger faunas (Matthews and Missarzhevsky, 1975; Conway Morris and Bengtson, 1994; Bromley, 2004). Bitten trilobites provide further evidence of predation in the Cambrian (Babcock, 1993; Pratt, 1998).

A significant rise in bioeroders probably occurred by the end of the Middle Ordovician (Kobluk *et al.*, 1978; Ekdale and Bromley, 2001b; Wilson and Palmer, 2001, 2006; Benner *et al.*, 2004), and has recently been referred to as "the Ordovician Bioerosion Revolution" by Wilson and Palmer (2006). This event is not only reflected in bioerosion domiciles but also in bioclaustrations (Tapanila, 2008). Early to Middle Ordovician bioerosion was dominated by simple borings such as *Trypanites* and *Palaeosabella*, although clavate borings (*Gastrochaenolites*), which are attributed to bivalves in younger rocks, have been recorded (Ekdale and Bromley, 2001; Ekdale *et al.*, 2002; Benner *et al.*, 2004). Late Ordovician hardground communities also included sponge borings (*Cicatricula*), bryozoan etchings (*Ropalonaria*), and bivalve borings (*Petroxestes*) (Wilson and Palmer, 2006; Wilson, 2007). The oldest record of green algae microborings (*Reticulina*) is known from the Ordovician, while that of red algae microborings (*Palaeoconchocelis*) is from the Silurian (Glaub and Vogel, 2004).

A subsequent increase in the diversity of macroborings had occurred by the Devonian ("Middle Paleozoic Marine Revolution" of Wilson, 2007, also referred to as a precursor of the "Mesozoic Marine Revolution" by Signor and Brett, 1984). Some of the bioerosion ichnotaxa which appeared by this time (e.g. *Entobia*, *Rogerella*, *Caulostrepsis*, *Talpina*) became dominant throughout the rest of the Phanerozoic (Bromley, 2004; Wilson, 2007). By the Carboniferous, the first *Gastrochaenolites* confidently attributed to bivalves has been recorded (Wilson and Palmer, 1998). Notably, diversification of macroborings and bioclaustrations is decoupled because the latter shows a decrease in diversity by the Late Devonian, most likely as a result of a decline in the host coralline taxa (Tapanila, 2005; Tapanila and Ekdale, 2007).

By the Jurassic, the Mesozoic Marine Revolution (Vermeij, 1977) is marked by an increase in the diversity, abundance, and size of macrobioerosion structures (Bromley, 2004; Wilson, 2007). An increase in diversity by the beginning of the Mesozoic is also evidenced by microborings (Glaub and Vogel, 2004). In addition, this event was characterized by the rise of boring echinoids and an increase in the abundance of sponge borings (Taylor and Wilson, 2003). A large number of ichnotaxa occurs for the first time in the Mesozoic, including the echinoid bite trace *Gnathichnus*, the echinoid boring *Circolites*, the cirriped etching scar *Centrichnus*, the bryozoan etching trace *Leptichnus*, and the bivalve wood boring *Teredolites*.

These evolutionary changes have a direct influence on the nature of some substrate-controlled ichnofacies. The *Teredolites* ichnofacies has not been recorded prior to the Cretaceous. In addition, the Jurassic represents a pivotal point for hardground ichnofacies because it marks the appearance of the *Gnathichnus* ichnofacies (Gibert *et al.*, 2007). Also, sponge and bivalve borings became common after the Jurassic, resulting in the appearance of the so-called *Entobia* association (Bromley and Asgaard, 1993a; Gibert *et al.*, 1998). Interestingly, Tapanila (2008) noted that, with the exception of echinoids, no new classes of organisms adopted an endolithic strategy during the Mesozoic Marine Revolution. By the beginning of the Cenozoic, a change is reflected in the dominant microbioeroding ichnotaxa, with the appearance of new ichnogenera whose oldest record is Paleogene (Glaub and Vogel, 2004).

14.2.4 COLONIZATION OF TIDAL FLATS

Tidal flats are geologically ephemeral systems, and at a given geographic region rarely last longer than 10^4 years as a result of transgressions and regressions (Reise, 1985). In contrast to the long-term temporal instability, tidal flats are, on a daily basis, highly predictable and controlled by tidal cyclicity. Tidal flats usually are regarded as harsh, heterogeneous, physically controlled environments (see Section 7.2). From a biological perspective, tidal flats are highly heterogeneous systems in which interspecific interactions are poorly regulated and open to numerous possibilities. Accordingly, ecological and environmental attributes of tidal-flat communities, together with the high genetic variability in populations inhabiting unstable environments, may have provided the appropriate ground for major steps in evolution (Reise, 1985).

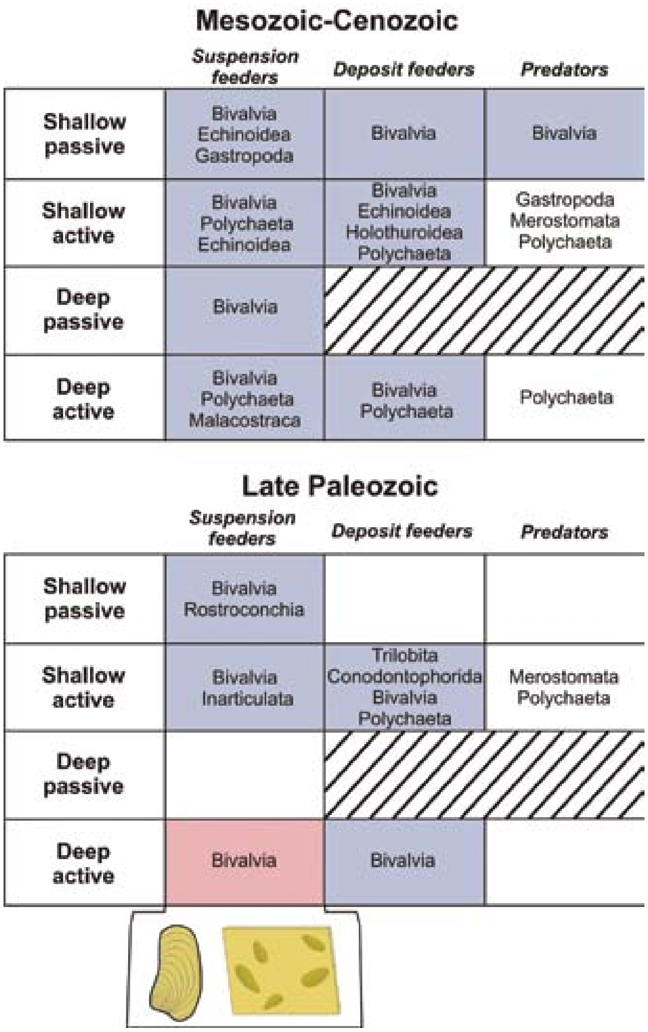
Comparison of tidal-flat ichnofaunas through time helps to address the problem of onshore replacement and offshore migration of benthic faunas, and provides ground data to evaluate the notion that tidal flats may have served as sites of evolutionary innovations (Mángano *et al.*, 2002a). The earliest records of trace fossils in intertidal deposits are from the earliest Early Cambrian (Fortunian), and consist of monospecific occurrences of *Treptichnus pedum* (Buatois *et al.*, 2007c; Almond *et al.*, 2008). Younger early Paleozoic tidal-flat ichnofaunas are dominated by trilobite and other arthropod trace fossils (e.g. Durand, 1985; Astini *et al.*, 2000; Mángano *et al.*, 2001b; Mángano and Buatois, 2004b). Some aspects of early Paleozoic tidal flats are anactualistic in nature (Mángano and Buatois, 2004b). While modern tidal flats are characterized by abundant food supply derived from multiple sources, including terrestrially-derived organic particles, early Paleozoic intertidal trophic webs were almost entirely based on the organically rich marine source and significant autochthonous production. Modern intertidal organisms are exposed to a double set of predators: preyed on by marine organisms during submergence and by terrestrial organisms during emergence. Contrastingly, early Paleozoic intertidal environments may have functioned as refugia in the absence of continental predators, only being under the pressure of marine predators (Mángano and Buatois, 2004b). Another anactualistic aspect, particularly for Cambrian tidal flats, is the common presence of microbial matgrounds (Hagadorn *et al.*, 2002; Hagadorn and Belt, 2008). Tidal-flat deposits contain a wide variety of microbially induced structures that allowed preservation of medusa body fossils, and a peculiar suite of trace fossils consisting of the giant mollusk-like trail *Climactichnites*, its associated resting trace *Musculopodus*, and the arthropod trackway *Protichnites* (Yochelson and Fedonkin, 1993; Hagadorn *et al.*, 2002; Hagadorn and Belt, 2008; Seilacher, 2008; Getty and Hagadorn, 2008, 2009).

Although the picture that emerges from these early Paleozoic tidal flats is significantly different, they may have resembled modern ones in their ecological role as sites of reproduction and protection. Arthropod incursions in early Paleozoic tidal flats, recorded by the presence of *Rusophycus*, *Cruziana*, and *Dimorphichnus*, provide direct evidence of an early colonization of intertidal environments, and show that representatives of the Cambrian evolutionary fauna were not restricted to offshore settings, but were able to colonize very shallow-water environments. *Skolithos* and *Syringomorpha* pipe rock occurs in high-energy sand-flat areas. Depth and extent of bioturbation reveal colonization of a relatively deep-infaunal ecospace by endobenthic organisms at least in lower-intertidal areas, suggesting a significant landward expansion of the Agronomic Revolution (Mángano and Buatois, 2004b).

Molluscan trace fossils, in particular those of bivalves, are important components in late Paleozoic tidal-flat deposits (e.g. Rindsberg, 1994; Mángano *et al.*, 2002a; Mángano and Buatois, 2004a). Late Paleozoic intertidal ichnofaunas are remarkably different from those recorded in early Paleozoic tidal flats in that trilobite-dominated faunas were replaced by bivalve-dominated communities. Sepkoski and Miller (1985) documented onshore–offshore patterns of evolutionary faunas. Based on the analysis of body-fossil communities, these authors detected a replacement of trilobite-rich communities by mollusk-rich communities in shallow-water niches throughout the Paleozoic. Ichnological analysis of Paleozoic tidal-flat ichnofaunas provides further support to this model, and underscores the importance of tidal flats as nurseries of evolutionary innovations (Mángano *et al.*, 2002a). Bivalves, in contrast to articulate brachiopods, were particularly adaptable to physically unstable, stressful nearshore settings (Steele-Petrovic, 1979). The striking ecological segregation between articulate brachiopods and bivalves may indicate a higher tolerance of bivalves to unstable environments (Olszewski, 1996).

Analysis of late Paleozoic tidal-flat ichnofaunas also reflects patterns of colonization of the infaunal ecospace by bivalves. Presence of large specimens of *Lockeia siliquaria* in Carboniferous intertidal sandstone suggests relatively deep-bivalve burrowing below the sediment–water interface (Mángano *et al.*, 1998). These burrows have been attributed to the anomalodesmatan *Wilkingia*, also present in the same deposits, most likely illustrating siphon-feeding in the late Paleozoic, preceding the subsequent Mesozoic radiation of siphon-feeding infaunal bivalves (Mángano *et al.*, 1998) (Fig. 14.8). Although the deep-infaunal ecospace was colonized, late Paleozoic intertidal ichnofaunas contain a high diversity of shallow-tier trace fossils, suggesting that deep burrowers did not obliterate shallowly emplaced structures.

Mesozoic and Cenozoic tidal-flat ichnofaunas are quite different from their Paleozoic equivalents, but they share many similarities with Recent examples. Post-Paleozoic tidal-flat deposits tend to be dominated by deep- to mid-tier crustacean burrows together with a wide variety of polychaete and bivalve



Mesozoic-Cenozoic

	Suspension feeders	*Deposit feeders*	*Predators*
Shallow passive	Bivalvia Echinoidea Gastropoda	Bivalvia	Bivalvia
Shallow active	Bivalvia Polychaeta Echinoidea	Bivalvia Echinoidea Holothuroidea Polychaeta	Gastropoda Merostomata Polychaeta
Deep passive	Bivalvia	▨	▨
Deep active	Bivalvia Polychaeta Malacostraca	Bivalvia Polychaeta	Polychaeta

Late Paleozoic

	Suspension feeders	*Deposit feeders*	*Predators*
Shallow passive	Bivalvia Rostroconchia		
Shallow active	Bivalvia Inarticulata	Trilobita Conodontophorida Bivalvia Polychaeta	Merostomata Polychaeta
Deep passive		▨	▨
Deep active	Bivalvia	Bivalvia	

Figure 14.8 Evolutionary innovations in tidal flats. Boxes illustrate Bambachian megaguilds for infaunal ecospace based on body fossils after Bambach (1983). According to body-fossil information, no suspension feeders occupied deep tiers before the Mesozoic marine revolution. However, ichnological information (deep *Lockeia siliquaria*) indicates that suspension- feeding bivalves colonized the deep-infaunal ecospace in tidal-flat settings by the late Paleozoic. This prompted re-evaluation of associated body fossils, suggesting that the potential producer, the anomalodesmatan *Wilkingia*, was an efficient siphonate burrower (Mángano *et al*., 1998).

trace fossils (Mángano *et al*., 2002a). This seems to be the case in most modern tidal flats, where these groups dominate (e.g. Howard and Dörjes, 1972; Curran and Martin, 2003). In addition, crustaceans and polychaetes produce large quantities of argillaceous fecal pellets, and they are therefore important agents of biosedimentation and modifiers of substrate properties (Pryor, 1975; Bromley, 1990, 1996; Curran and Martin, 2003). In contrast to late Paleozoic tidal-flat ichnofaunas, Mesozoic to Cenozoic ichnofaunas are biased towards deeper tiers. Burrowing activities of crustaceans may have caused significant sediment reworking and obliteration of shallower tiers. Overall, post-Paleozoic tidal flats exhibit only moderate levels of ichnodiversity. This trend likely represents a taphonomic artifact resulting from the dominance of deep infaunal crustaceans in Mesozoic and Cenozoic tidal-flat ecosystems. Establishment of crustacean-dominated communities in tidal-flat ecosystems may have played a significant role in the offshore expansion of bivalves during the Mesozoic (Mángano *et al*., 2002a).

14.2.5 COLONIZATION OF BRACKISH-WATER ENVIRONMENTS

The invasion of marginal-marine environments represents the appearance of an ecosystem and, therefore, qualifies as a first-level paleoecological event *sensu* Droser *et al*. (1997). The ichnological aspects of the colonization history of brackish-water environments have been recently explored (Buatois *et al*., 2005). According to these authors, brackish-water ichnofaunas show an increase in ichnodiversity, an increase in the intensity of bioturbation, the addition of new invaders, environmental expansion, and faunal replacements through the Phanerozoic. The colonization of marginal-marine, brackish-water environments by fully marine organisms was a long-term process, but did not occur at a constant rate. Five major colonization phases have been proposed: Ediacaran–Ordovician, Silurian–Carboniferous, Permian–Triassic, Jurassic–Paleogene, and Neogene–Recent (Buatois *et al*., 2005) (Fig. 14.9).

The first phase (Ediacaran–Ordovician) is a prelude to the major invasion that occurred during the rest of the Paleozoic. Although Ediacaran trace fossils have been recorded for the most part in open-marine strata, at least in one case, biogenic structures were described from deposits formed in a coastal environment subjected to rapid changes in salinity, as well as in sedimentation rate and turbidity (Netto and Martini da Rosa, 2001). This ichnofauna may represent one of the earliest attempts of benthic organisms to survive under marginal-marine conditions. As a result of the Cambrian explosion, a new array of characters invaded brackish-water settings. Among these, arthropods, including trilobites, trilobitomorphs, and eurypterids, were among the most successful (Selley, 1970; Mikuláš, 1995; Braddy and Almond, 1999; Webber and Braddy, 2004; Mángano and Buatois, 2003a). In Cambrian–Ordovician estuaries and embayments, trace fossils of trilobites and other arthropods occur in fine-grained deposits of low-energy zones, while high- to moderate-energy sandstones, such as those forming subtidal bars, are dominated by vertical burrows (e.g. *Skolithos*) (e.g. Martin, 1993; Mángano *et al*., 2001b; Mángano and Buatois, 2003a; Baldwin *et al*., 2004). Most of the lower Paleozoic ichnofaunas recorded in marginal-marine deposits are from tide-dominated estuaries, where salinity stress was probably attenuated by tidal mixing. Also, environmental expansion is recorded through the early Paleozoic. Cambrian trace fossils seem to be restricted to the outer regions of estuaries, but Ordovician ichnofaunas reveal a slight landward expansion, also being present in more central zones of the estuaries (Mángano and Droser, 2004). In any case, intensity of bioturbation and ichnodiversity levels remained relatively low.

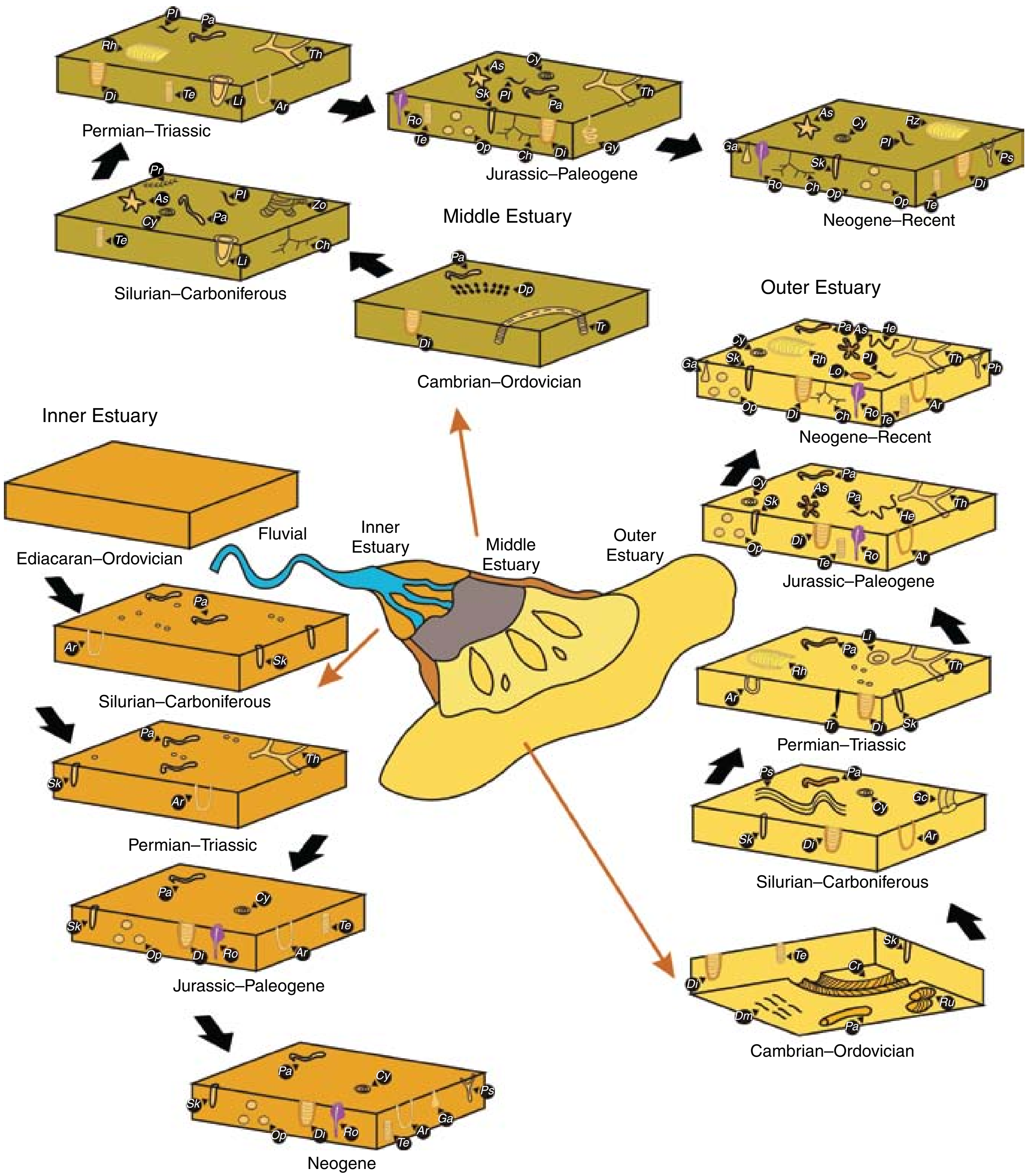


Figure 14.9 Colonization of brackish-water environments through geological time. The inner-estuary zone was essentially barren of biogenic structures during the Ediacaran–Ordovician. During the Silurian–Carboniferous, facies-crossing ichnotaxa, such as *Arenicolites* (*Ar*), *Palaeophycus* (*Pa*), and *Skolithos* (*Sk*), occur. Inner-estuarine Permian–Triassic deposits are characterized by the addition of the crustacean burrow *Thalassinoides* (*Th*). An increase in ichnodiversity in this environment took place during the Jurassic–Paleogene with the addition of a number of ichnotaxa, including *Ophiomorpha* (*Op*), *Rosselia* (*Ro*), *Teichichnus* (*Te*), *Cylindrichnus* (*Cy*), and *Diplocraterion* (*Di*). Neogene inner-estuarine ichnofaunas are similar to those from the Jurassic–Paleogene, but may contain *Psilonichnus* (*Ps*) and *Gastrochaenolites* (*Ga*) as well. Cambrian–Ordovician middle-estuarine deposits are typically sparsely burrowed, and contain *Diplichnites* (*Dp*), *Diplocraterion* (*Di*), *Trichophycus* (*Tr*), and *Palaeophycus* (*Pa*). A remarkable increase in trace-fossil diversity occurred in this environment during the Silurian–Carboniferous with the presence of a number of ichnotaxa, including *Palaeophycus* (*Pa*), *Planolites* (*Pl*), *Asteriacites* (*As*), *Cylindrichnus* (*Cy*), *Lingulichnus*

The second phase (Silurian–Carboniferous) is characterized by the appearance of more varied trace-fossil morphologies and behavioral strategies (Buatois *et al.*, 2005). As a result, a slight increase in ichnodiversity with respect to the previous phase is detected. While Cambrian–Ordovician ichnofaunas are dominated by arthropod trace fossils, those from the Silurian–Carboniferous also include ichnotaxa produced by other benthic organisms, in particular, bivalves, ophiuroids, and polychaetes. The replacement of trilobite-dominated ichnofaunas may have been a consequence of the end-Ordovician mass extinction, although an apparent decline in the abundance of trilobite trace fossils was already apparent by the Late Ordovician (Mángano and Droser, 2004) (see Section 14.1.4). The presence of more varied ichnofaunas may reflect an evolutionary rebound after the Late Ordovician mass extinction. Also, Silurian–Carboniferous benthic faunas experienced a remarkable environmental expansion, as illustrated by trace fossils present in inner- and middle-estuarine deposits as well (Buatois *et al.*, 2002b). The extensive colonization of terrestrial settings by land plants and animals may have promoted environmental expansion and increased complexity of estuarine food webs. Silurian–Carboniferous brackish-water ichnofaunas were essentially restricted to softgrounds, with very limited emplacement in firmgrounds. The intensity of bioturbation remains relatively low.

Our understanding of the third phase (Permian–Triassic) still suffers from a scarcity of studies. Permian brackish-water trace-fossil assemblages are more similar to those from the Mesozoic rather than Paleozoic ones (Buatois *et al.*, 2005, 2007b; Netto *et al.*, 2007). Despite these overall similarities, Permian–Triassic brackish-water deposits remain less bioturbated, and contain lower-diversity trace–fossil suites than those from the fourth phase. Accordingly, Permian-Triassic trace-fossil assemblages seem to represent a transitional phase between Paleozoic and Mesozoic marginal-marine ichnofaunas. Body-fossil data indicate that crustaceans radiated during the late Paleozoic, and that some of them adapted to brackish water (Briggs and Clarkson, 1990). Ichnological studies reveal the presence of numerous burrows that may have been produced by crustaceans, including *Thalassinoides* and *Gyrolithes* (Carmona *et al.*, 2004; Buatois *et al.*, 2007b; Netto *et al.*, 2007). Firmgrounds commonly contained the *Glossifungites* ichnofacies, reflecting adaptations to compacted muds (e.g. Tognoli and Netto, 2003; Buatois *et al.*, 2007b; Netto *et al.*, 2007).

The fourth phase (Jurassic–Paleogene) is marked by a notable increase in ichnodiversity and degree of bioturbation of brackish-water estuarine deposits (Buatois *et al.*, 2005). Although less diverse than their fully marine counterparts, relatively diverse ichnofaunas have been recorded (e.g. Beynon *et al.*, 1988; Beynon and Pemberton, 1992; MacEachern and Pemberton, 1994; MacEachern and Gingras, 2007). Also, Jurassic–Paleogene marginal-marine deposits tend to be more intensely bioturbated than older deposits. While older brackish-water substrates displaying trace fossils were essentially softgrounds and firmgrounds, hardgrounds and xylic substrates also become colonized during the late Mesozoic (e.g. Bromley *et al.*, 1984; Savrda *et al.*, 1993; Gingras *et al.*, 2004).

The fifth phase (Neogene–Recent) is characterized by the appearance of the modern brackish-water benthos. However, differences with respect to Jurassic–Paleogene ichnofaunas are subtle. Brackish-water ichnofaunas may reach moderately high diversities, typically in middle- and outer-estuarine regions. Also, the degree of bioturbation may be rather high in some deposits, such as those of estuarine tidal flats (e.g. Gingras *et al.*, 1999b). All types of substrates were colonized during the Neogene, including cemented surfaces, shells, and clasts. This pattern reflects the radiation of various groups of borers (e.g. sponges, polychaetes, gastropods, and bivalves) into brackish water (Gingras *et al.*, 2001).

Buatois *et al.* (2005) also noticed that although brackish-water ichnofaunas display clear evolutionary trends, some trace-fossil suites and ichnofabrics are remarkably persistent, reflecting the activity of conservative biotas. They proposed, as an example, the common occurrence in brackish-water fine-grained, heterolithic facies of *Teichichnus* forming monospecific suites, or associated with small *Planolites* (Fig. 14.10a–d). This assemblage, commonly associated with synaeresis cracks, occurs in stressed marginal-marine environments from the Cambrian to the Recent.

Caption for Figure 14.9 Continued
(*Li*), *Protovirgularia* (*Pr*), *Chondrites* (*Ch*), *Teichichnus* (*Te*), and *Zoophycos* (*Zo*). Permian–Triassic middle-estuarine ichnofaunas tend to be dominated by *Thalassinoides* (*Th*), *Diplocraterion* (*Di*), *Arenicolites* (*Ar*), *Lingulichnus* (*Li*), *Teichichnus* (*Te*), *Rhizocorallium* (*Rh*), *Planolites* (*Pl*), and *Palaeophycus* (*Pa*). By the Jurassic–Paleogene, crustacean burrows, including *Gyrolithes* (*Gy*), *Thalassinoides* (*Th*) and *Ophiomorpha* (*Op*), become dominant, but many other facies-crossing ichnotaxa are abundant also. Neogene middle-estuarine ichnofaunas are similar to those from the Jurassic–Paleogene, but with the addition of *Psilonichnus* (*Ps*) and *Gastrochaenolites* (*Ga*). Cambrian–Ordovician outer-estuarine deposits tend to display more ichnodiversity than coeval deposits formed further into the estuary. Ichnofaunas are dominated by vertical burrows such as *Skolithos* (*Sk*) and *Diplocraterion* (*Dp*), trilobite trace fossils including *Cruziana* (*Cr*), *Rusophycus* (*Ru*) and *Dimorphichnus* (*Dm*), *Teichichnus* (*Te*), and *Palaeophycus* (*Pa*). During the Silurian–Carboniferous, other ichnotaxa become dominant in outer-estuarine settings, including *Gyrochorte* (*Gc*), *Psammichnites* (*Ps*), *Arenicolites* (*Ar*), and *Cylindrichnus* (*Cy*). Permian–Triassic outer-estuarine deposits contain abundant vertical burrows, but also tend to show crustacean burrow galleries such as *Thalassinoides* (*Th*), together with *Rhizocorallium* (*Rh*), *Lingulichnus* (*Li*), *Trichichnus* (*Tr*), and *Palaeophycus* (*Pa*). Jurassic–Paleogene outer-estuarine ichnofaunas typically display more diversity than those of the Permian–Triassic. Crustacean burrows, including *Thalassinoides* (*Th*) and *Ophiomorpha* (*Op*), are dominant. Polychaete burrows, such as *Rosselia* (*Ro*), *Asterosoma* (*As*), and *Cylindrichnus* (*Cy*) are also common. Grazing trails, such as *Helminthopsis* (*Hl*), are less common. Neogene ichnofaunas are very similar to those of the Jurassic–Paleogene, but with the addition of *Psilonichnus* (*Ps*), *Gastrochaenolites* (*Ga*), and locally *Chondrites* (*Ch*). Modified from Buatois *et al.* (2005).

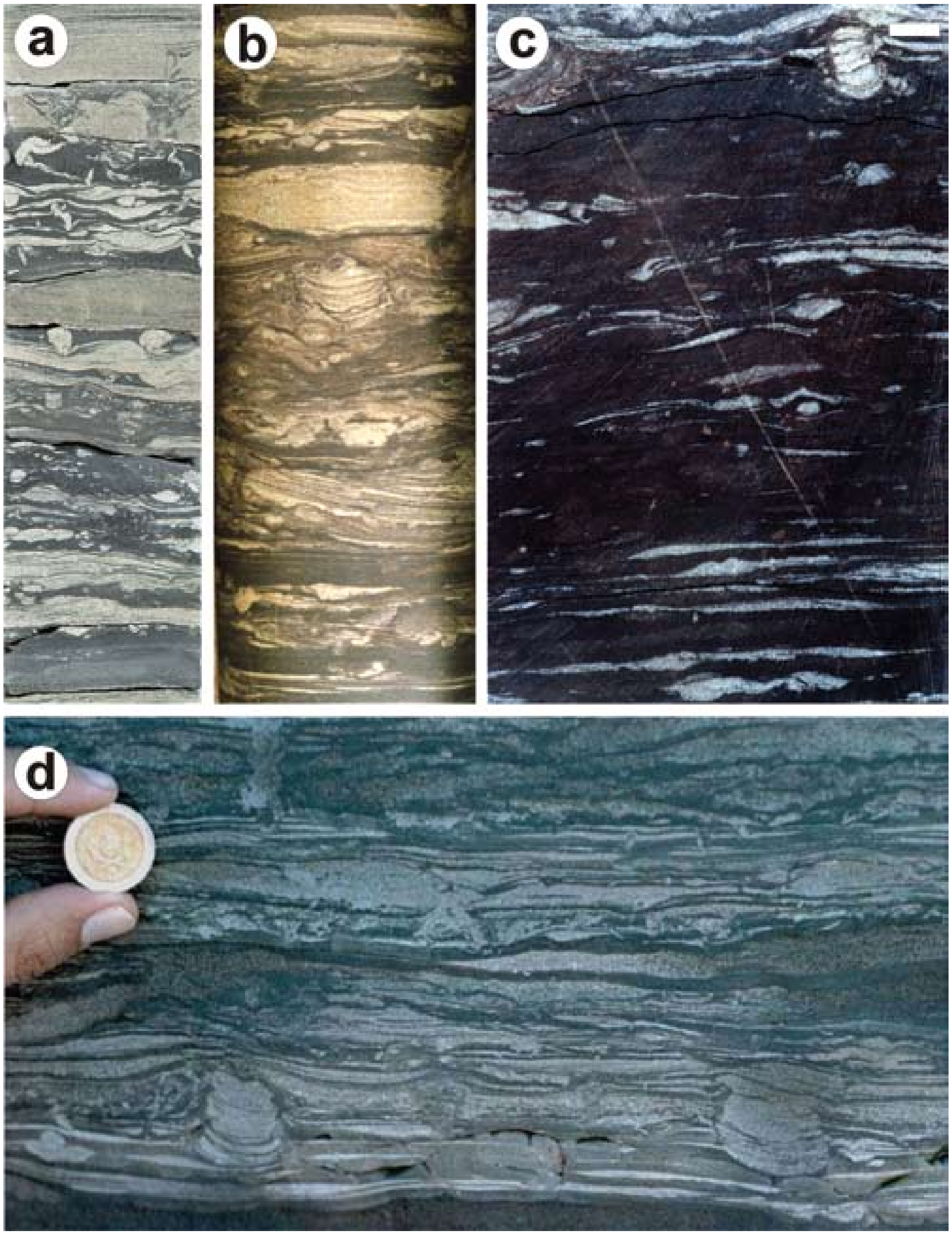


Figure 14.10 The *Teichichnus* ichnofabric as an example of a persistent trace-fossil association in Phanerozoic brackish-water environments. *Teichichnus* may form a monospecific suite or be associated with *Planolites*. Synaeresis cracks are typically present in this heterolithic facies. (a) Middle Cambrian, Earlie Formation, northeast of Edmonton, western Canada. Core width is 9 cm. (b) Lower Permian, Río Bonito Formation, Mina de Iruí, southern Brazil. Core width is 7 cm. See Buatois *et al*. (2007b). (c) Upper Cretaceous, Napo Formation, Shushufindi Field, Oriente Basin, Ecuador. Core width is 10 cm. (d) Lower Miocene Chenque Formation, Caleta Olivia, Patagonia, Argentina. See Carmona *et al*. (2009).

14.2.6 COLONIZATION OF FRESHWATER AND TERRESTRIAL ENVIRONMENTS

Continental ichnofaunas provide a wealth of information on evolutionary paleoecology, providing insights into the process of terrestrialization, evolutionary radiations, environmental faunal expansions, and exploitation of empty or underutilized ecospace (e.g. Miller, 1984; Maples and Archer, 1989; Buatois and Mángano, 1993b; Genise and Bown, 1994b; Buatois *et al*., 1998c; Miller *et al*., 2002; Cohen, 2003; Miller and Labandeira, 2003; Braddy, 2004; Genise, 2004; Mángano and Buatois, 2007) (Fig. 14.11).

Our knowledge of incipient Precambrian and early Paleozoic terrestrial ecosystems is patchy at best. Terrestrial microorganisms have been recorded in Upper Archean rocks (Watanabe *et al*., 2000), probably becoming widespread by the late Mesoproterozoic to the early Neoproterozoic (Horodyski and Knauth, 1994; Prave, 2002). Spore-like microfossils or cryptospores are known since the Middle Cambrian, suggesting the establishment of a nascent semi-aquatic to subaerial flora of bryophyte grade (Strother, 2000; Strother and Beck, 2000). Spores indicative of land vegetation occur in Middle Ordovician rocks (Strother *et al*., 1996), while spores and plant fragments have been documented in Upper Ordovician deposits (Wellman *et al*., 2003). Fluvial style was dominantly sheet-braided with little mud preservation (Davies and Gibling, 2009). The earliest evidence of animal incursions into the land is trackways produced by an amphibious organism in Upper Cambrian to

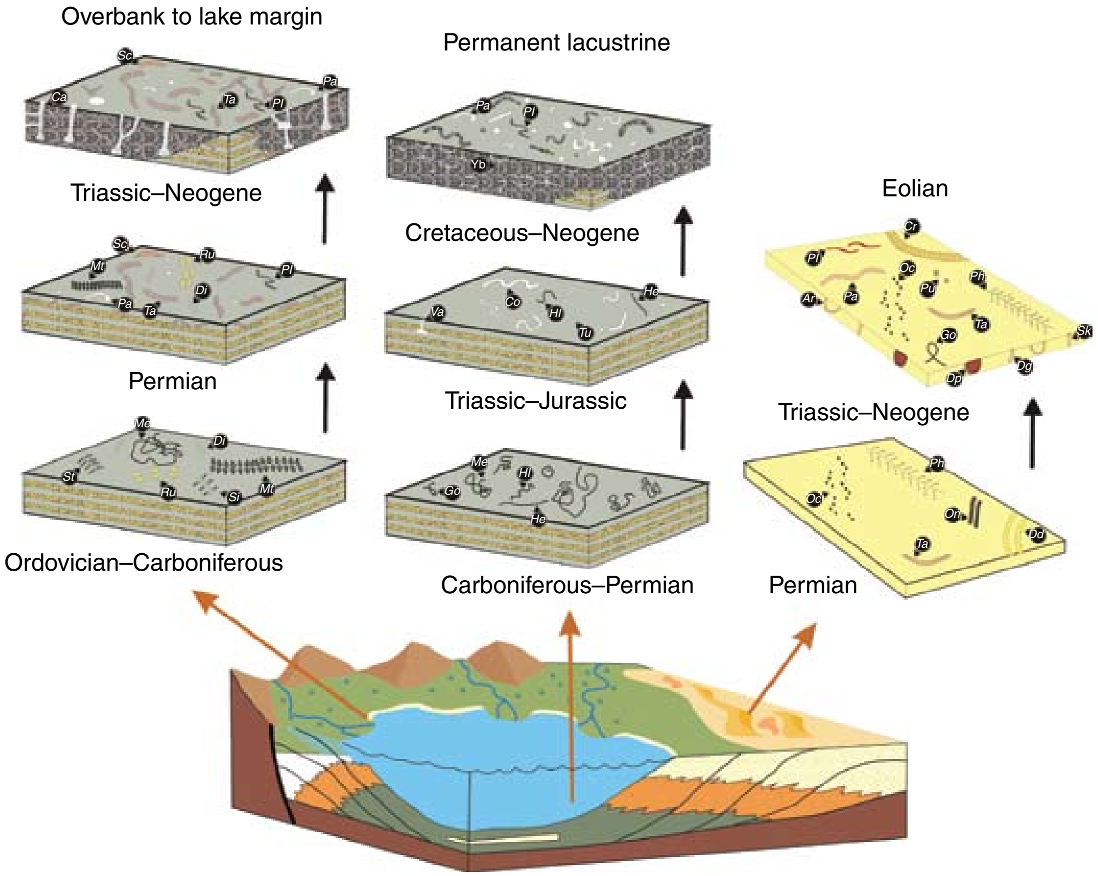


Figure 14.11 Colonization of continental environments. Invertebrate ichnofaunal changes occurred in the different continental environments throughout the Phanerozoic, with the colonization of lacustrine substrates being delayed with respect to that of overbank and lake-margin deposits. Ordovician to Carboniferous overbank to lake-margin deposits are dominated by arthropod trackways, including *Siskemia* (*Si*), *Stiaria* (*St*), *Diplichnites* (*Di*), and *Merostomichnites* (*Mt*), accompanied by bilobate traces such as *Rusophycus* (*Ru*) and grazing trails such as *Mermia* (*Me*). Permian deposits include the striated meniscate trace fossil *Scoyenia* (*Sc*), together with *Taenidium* (*Ta*), *Diplichnites* (*Di*), *Palaeophycus* (*Pa*), *Merostomichnites* (*Mt*), and *Rusophycus* (*Ru*). In contrast, Carboniferous–Permian ichnofaunas in permanent subaqueous portions of lacustrine systems are dominated by grazing trails such as *Mermia* (*Me*), *Helminthopsis* (*Hl*), *Helminthoidichnites* (*He*), and *Gordia* (*Go*). All these horizontal trace fossils are emplaced very close to the sediment–water interface, resulting in almost no disturbance of the primary sedimentary fabric. Overbank to lake-margin deposits display increased degree of bioturbation since the Triassic. Some of the typical elements are the backfilled trace fossils *Scoyenia* (*Sc*) and *Taenidium* (*Ta*), the crayfish burrow *Camborygma* (*Ca*), and simple burrows such as *Planolites* (*Pl*) and *Palaeophycus* (*Pa*). During the Triassic–Jurassic, an increase in depth of bioturbation occurred in permanent subaqueous lacustrine deposits with the appearance of branched burrows such as *Vagorichnus* (*Va*) and *Tuberculichnus* (*Tu*). Grazing trails, such as *Cochlichnus* (*Co*), *Helminthopsis* (*Hl*), and *Helminthoidichnites* (*He*), persisted but occupying a deeper-tier position. After the Cretaceous, mottled texture attributed to *Planolites* (*Pl*) and *Palaeophycus* (*Pa*) became common. Also, a number of biogenic structures attributed to chironomids, including Y-shaped burrows (Yb), are present. Paleozoic and post-Paleozoic eolian ichnofaunas are highly different. Little is known about pre-Permian eolian ichnofaunas, but Permian associations tend to be dominated by arthropod trackways, such as *Octopodichnus* (*Oc*), *Paleohelcura* (*Ph*), *Oniscoidichnus* (*On*), and *Diplopodichnus* (*Dd*); meniscate trace fossils, such as *Taenidium* (*Ta*), are less common. Post-Paleozoic invertebrate eolian ichnofaunas display much more variety of morphological types, including arthropod trackways such as *Octopodichnus* (*Oc*) and *Paleohelcura* (*Ph*), simple burrows such as *Planolites* (*Pl*) and *Palaeophycus* (*Pa*), the bilobate trace fossil *Cruziana* (*Cr*), the meniscate trace *Taenidium* (*Ta*), the grazing trail *Gordia* (*Go*), the small clustered burrow *Pustulichnus* (*Pu*), and various vertical burrows such as *Digitichnus* (*Dg*), *Arenicolites* (*Ar*), and *Diplocraterion* (*Dp*). Modified from Mángano and Buatois (2007).

Lower Ordovician coastal eolian-dune deposits (MacNaughton *et al.*, 2002). Meniscate trace fossils attributed to millipedes in paleosols (Retallack and Feakes, 1987; Retallack, 2001), and arthropod trackways (*Diplichnites* and *Diplopodichnus*) of myriapod-like invertebrates in pond deposits (Johnson *et al.*, 1994) are known from the Late Ordovician. However, marine influence has recently been detected in the deposits hosting the meniscate trace fossils (Davies *et al.*, 2010). Although myriapods are typically considered terrestrial, Early Ordovician to Late Silurian representatives were probably aquatic or amphibious (Almond, 1985).

A significant invasion of continental environments close to the Silurian–Devonian transition is indicated by trace-fossil data (Buatois *et al.*, 1998c). A terrestrial mobile arthropod epifauna representative of the *Diplichnites* ichnoguild was established in backshore, subaerial delta-plain, and floodplain environments

(Bradshaw, 1981; Woolfe, 1990; Trewin and McNamara, 1995; Draganits *et al.*, 2001; Neef, 2004a, b; Davies *et al.*, 2006). By the Devonian, ichnofaunas dominated by arthropod trackways become relatively common in lake-margin environments (Pollard *et al.*, 1982; Pollard and Walker, 1984; Walker, 1985) (Fig. 14.11). It has been suggested that the presence of these ichnofaunas in transitional alluvial-lacustrine deposits, rather than fully subaqueous environments may be a response to the concentration of land-derived plant debris along lake shorelines, particularly near the mouths of distributary channels (Buatois *et al.*, 1998c). Nutrient delivery to lakes may have been quite limited during the early Paleozoic before the onset of abundant upland terrestrial plant cover (Cohen, 2003). Ichnological evidence is consistent with body-fossil data, which indicate that before the Silurian lake inhabitants may have been rare, mostly linked to accidental incursions from marine habitats (Cohen, 2003). Also, by the Late Silurian to Early Devonian, vascular plants became common, an increase in the abundance of underground rooting systems took place, and muddy floodplains were widespread, allowing stabilization of channel banks. As a result, meandering systems became dominant and humic material built up in soils promoting colonization by organisms (Davies and Gibling, 2009).

While these ichnofaunas occur in low-energy, protected areas, vertical burrows seem to be common in relatively high-energy fluvial deposits, reflecting the establishment of a stationary, deep suspension-feeding infauna (*Skolithos* ichnoguild). However, the degree of marine influence in some of these deposits has been controversial (Bradshaw, 1981; Woolfe, 1990). A relatively deep-tier deposit-feeding infauna, represented by large (up to 250 mm wide) meniscate trace fossils (*Beaconites–Taenidium* ichnoguild), becomes widespread in abandoned fluvial-channel and overbank deposits by the Devonian and Carboniferous (e.g. Gevers *et al.*, 1971; Allen and Williams, 1981; Bradshaw, 1981; Gevers and Twomey, 1982; Graham and Pollard, 1982; Bruck *et al.*, 1985; Bamford *et al.*, 1986; Gordon, 1988; Keighley and Pickerill, 1997; Draganits *et al.*, 2001; Morrissey and Braddy, 2004). Ichnodiversity in these fluvial deposits is generally low. Based on the recurrent association of the meniscate trace fossils and large *Diplichnites*, as well as their similar size range, a myriapod (e.g. arthropleurid) producer has been invoked (Morrissey and Braddy, 2004). In particular, a potential producer, the arthropod *Bennettarthra annwnensis*, has been suggested recently (Fayers *et al.*, 2010).

Ordovician–Devonian ichnofaunas were restricted to alluvial and transitional alluvial-lacustrine environments, but Carboniferous trace fossils are also present in fully subaqueous lacustrine settings, signaling a significant environmental expansion of the benthic fauna (Buatois and Mángano, 1993b; Buatois *et al.*, 1998c) (Fig. 14.11). These lacustrine deposits were colonized by a moderately diverse, mobile detritus-feeding epifauna of the *Mermia* ichnoguild. It has been suggested that this expansion was probably linked to the rapid diversification, and increase in abundance of land plants. Vegetation changes may have introduced abundant organic detritus into previously nutrient-poor, lacustrine habitats (Maples and Archer, 1989). An analogous situation was proposed for terrestrial environments based on the migration of plants from geographically marginal areas (upland areas peripheral to major basinal wetlands) to the lowlands during the Carboniferous–Permian transition (DiMichele and Aronson, 1992). This pattern is consistent with environmental trends experienced by aquatic insects, which first originated in running water and later moved into lacustrine habitats (Wooton, 1988; Wiggins and Wichard, 1989). Ichnodiversity diagrams plotted as number of ichnogenera per million years show a rapid diversification during the Silurian–Devonian and then a continuous increase in trace-fossil diversity during the late Paleozoic (Buatois *et al.*, 1998c). However, these authors indicated that when the data are normalized to correct for differences in volume of continental deposits, the major diversification event seems to have occurred during the Carboniferous. This increase in ichnodiversity was accompanied by the diversification of freshwater organisms such as arthropods, annelids, fish, and mollusks (Maples and Archer, 1989). All continental sedimentary environments were colonized by the Carboniferous, and subsequent patterns indicate an increase of ecospace utilization within already colonized depositional settings (Fig. 14.11). For example, during the Permian the presence of striated and meniscate trace fossils of the *Scoyenia* ichnoguild record the establishment of a mobile, intermediate-depth, deposit-feeding infauna that was able to colonize firm, desiccated substrates in floodplain environments.

A decrease in diversity at familial level in lake environments took place during the Early Permian to the Middle Triassic. This was followed by a subsequent increase by the Late Triassic, in an evolutionary event referred to as the “Lacustrine Mesozoic Revolution” by Cohen (2003). In lake-margin and overbank environments, meniscate trace fossils of the *Scoyenia* ichnoguild became more abundant, leading to increased disturbance of the primary fabric since the Triassic (Buatois *et al.*, 1998c). Also in these settings, a stationary deep infauna attributed to freshwater crayfish, the *Camborygma* ichnoguild, was established by the Triassic (Hasiotis and Mitchell, 1993; Hasiotis *et al.*, 1993a) (Fig. 14.11). Parallel to this increase in burrowing extent and depth, a remarkable decrease in the abundance of arthropod trackways is apparent.

Changes also occurred in the permanent subaqueous portion of lacustrine systems with the appearance of penetrative trace fossils consisting of networks of irregularly branched burrows during the Middle to Late Triassic (Voigt and Hoppe, 2010). These burrow systems may reflect the activity of deposit-feeding oligochaetes or insect larvae. This mobile, intermediate-depth, deposit-feeding infauna is also illustrated by the *Vagorichnus* ichnoguild, recorded in Jurassic deep-lake deposits (Buatois *et al.*, 1996b, 1998c). In contrast to Paleozoic permanent subaqueous assemblages typified by surface trails, Mesozoic lacustrine ichnofaunas are dominated by infaunal burrows. Evolutionary innovations resulting from the Mesozoic lacustrine revolution were ultimately conducive to the establishment of modern lacustrine ecosystems and food webs by the Late Cretaceous (Cohen, 2003). High density of infaunal deposit-feeding traces of the *Planolites* ichnoguild has caused major disruption of lacustrine sedimentary fabrics since the Cretaceous (Buatois and Mángano, 1998; Buatois *et al.*, 1998c) (Fig. 14.11).

Interestingly, meniscate trace fossils of the *Beaconites–Taenidium* ichnoguild, which consist of large structures, occupying deeper tiers in the Paleozoic, are commonly smaller and occupied a middle-tier position during the Mesozoic and most of the Cenozoic (Buatois *et al*., 2007a). This pattern is consistent with the idea of Morrissey and Braddy (2004) that a myriapod (e.g. arthropleurid) produced these large meniscate trace fossils in the Silurian–Carboniferous (see also Fayers *et al*., 2010). However, by the Miocene large and deep backfilled burrows reoccupied deep tiers in similar overbank and abandoned-channel deposits (Buatois *et al*., 2007a).

Freshwater ichnofaunas display an overall increase in extent and depth of bioturbation through the Phanerozoic (Miller, 1984; Buatois *et al*., 1998c; Miller *et al*., 2002; Miller and Labandeira, 2003). Comparative analysis of continental ichnofaunas in space and time suggests that increases in bioturbation depth and intensity took place progressively through time, from fluvial and lake-margin settings to permanent subaqueous lacustrine environments (Buatois *et al*., 1998c). This increase in depth and intensity of bioturbation strongly influenced the nature of the stratigraphic record of continental environments, producing increasing disturbance of primary sedimentary fabrics.

Evolutionary aspects also play a major role in paleosol ichnology (Pemberton *et al*., 1992b; Buatois *et al*., 1998c; Genise, 2004). Late Jurassic to Early Cretaceous paleosols tend to be dominated by meniscate trace fossils (e.g. *Taenidium*, *Beaconites*), crayfish burrows (e.g. *Loloichnus baqueroensis*, *Dagnichnus titoi*, *Cellicalichnus meniscatus*) and earthworm boxworks (*Castrichnus*) (Genise *et al*., 2008; Bedatou *et al*., 2008, 2009). In addition, ichnological evidence suggests that fungiculture in social insects may have been attained by the Early Cretaceous (Genise *et al*., 2010b). By the Late Cretaceous, bee nests (*Cellicalichnus chubutensis*) and pupal chambers of coleopterans (*Rebuffoichnus*) and insects of uncertain affinities (*Fictovichnus*, *Pallichnus*) became common (Johnson *et al*., 1996; Genise *et al*., 2002, 2007). The most important families of insect chambered trace fossils (Coprinisphaeridae, Pallichnidae, Krausichnidae, and Celliformidae) are virtually absent in pre-Cenozoic paleosols (Genise and Bown, 1994a, b; Genise *et al*., 2002; Genise, 2004). Claims of Triassic bee cells and termite nests (Hasiotis and Dubiel, 1993, 1995; Hasiotis, 2002) and Jurassic termite nests, bee cells, dung-beetle nests, and ant galleries (Hasiotis, 2002, 2004) have met general rejection (e.g. Grimaldi, 1999; Engel, 2001; Genise, 2000, 2004; Grimaldi and Engel, 2005; Bromley *et al*., 2007). This negative reception has been based on (1) the fact that these ecologically keystone insects have not been found in pre-existing non-angiosperm-dominated ecosystems, and (2) the reported Triassic and Jurassic trace fossils do not show diagnostic features supporting their attribution to these modern groups of insects (e.g. spiral closure cap in bee nests). In fact, recent re-examination of part of this material (the supposed Triassic bee nests) revealed that the observations claimed to identify these structures as produced by bees cannot be replicated (Lucas *et al*., 2010b).

Diversification of modern insects is recorded by the abundance and complexity of structures produced by wasps (e.g. *Chubutolithes*), bees (e.g. *Celliforma*, *Uruguay*, *Ellipsoideichnus*, *Palmiraichnus*, and *Rosellichnus*), dung-beetles (e.g. *Coprinisphaera* and *Fontanai*) ants (e.g. *Attaichnus* and *Parowanichnus*), and termites (e.g. *Termitichnus*, *Vondrichnus*, *Syntermesichnus*, *Coatonichnus*, *Tacuruichnus*, *Fleaglellius*, *Krausichnus* and *Microfavichnus*) in Cenozoic paleosols (Genise and Bown, 1994a, b; Genise, 2004; Duringer *et al*., 2006, 2007). This evolutionary event has been referred to as the "Paleogene Paleosol Revolution" (Buatois and Mángano, 2009b). This pattern reflects the appearance of ecologically keystone insects that coevolved with angiosperms by the mid Early Cretaceous (Thorne *et al*., 2000; Grimaldi and Engel, 2005; Bromley *et al*., 2007). In addition, nests produced by these groups of insects have a greater preservation potential than other continental biogenic structures because they are constructed structures and not merely excavated ones (Genise and Bown, 1994a).

Eolian environments also experienced significant ichnofaunal changes through the Phanerozoic (Fig. 14.11). An increase in diversity of trace fossils occurs in eolian deposits by the Permian–Triassic transition. Post-Paleozoic ichnofaunas display more varied behavioral patterns than their Paleozoic counterparts (Gradzinski and Uchman, 1994; Buatois *et al*., 1998c). Many of the examples of Paleozoic eolian dune ichnofaunas are

Box 14.2 The impact of oribatid mites on plant tissue decomposition in late Paleozoic coal swamps

The field of arthropod–plant interactions has undergone an explosive development during the last 15 years. Trace fossils preserved in plant material provide a wealth of information for understanding food webs in terrestrial to coastal ecosystems. In modern temperate forest ecosystems, oribatid mites are key animals in converting plant litter and wood to organic residues. However, little is known of their fossil history and their body-fossil record commences in the Middle Devonian, but does not reappear until the Early Jurassic. The trace-fossil record, therefore, provides an independent source of data. Analysis of damage produced by oribatid mites in plant tissue preserved in Pennsylvanian coal-ball deposits of eastern North America helps to fill this gap. Examination of these coal balls reveals the presence of a number of trace fossils attributed to mites, including coprolites and tunnels within plant tissues. Virtually all the permineralized tissues from the dominant plant groups, namely lycopsids, calamites, ferns, seed ferns, and cordaites, have been attacked by oribatid mites. This study underscores the role of these arthropods as decomposers in late Paleozoic coal-swamp forests.

Reference: Labandeira *et al*. (1997).

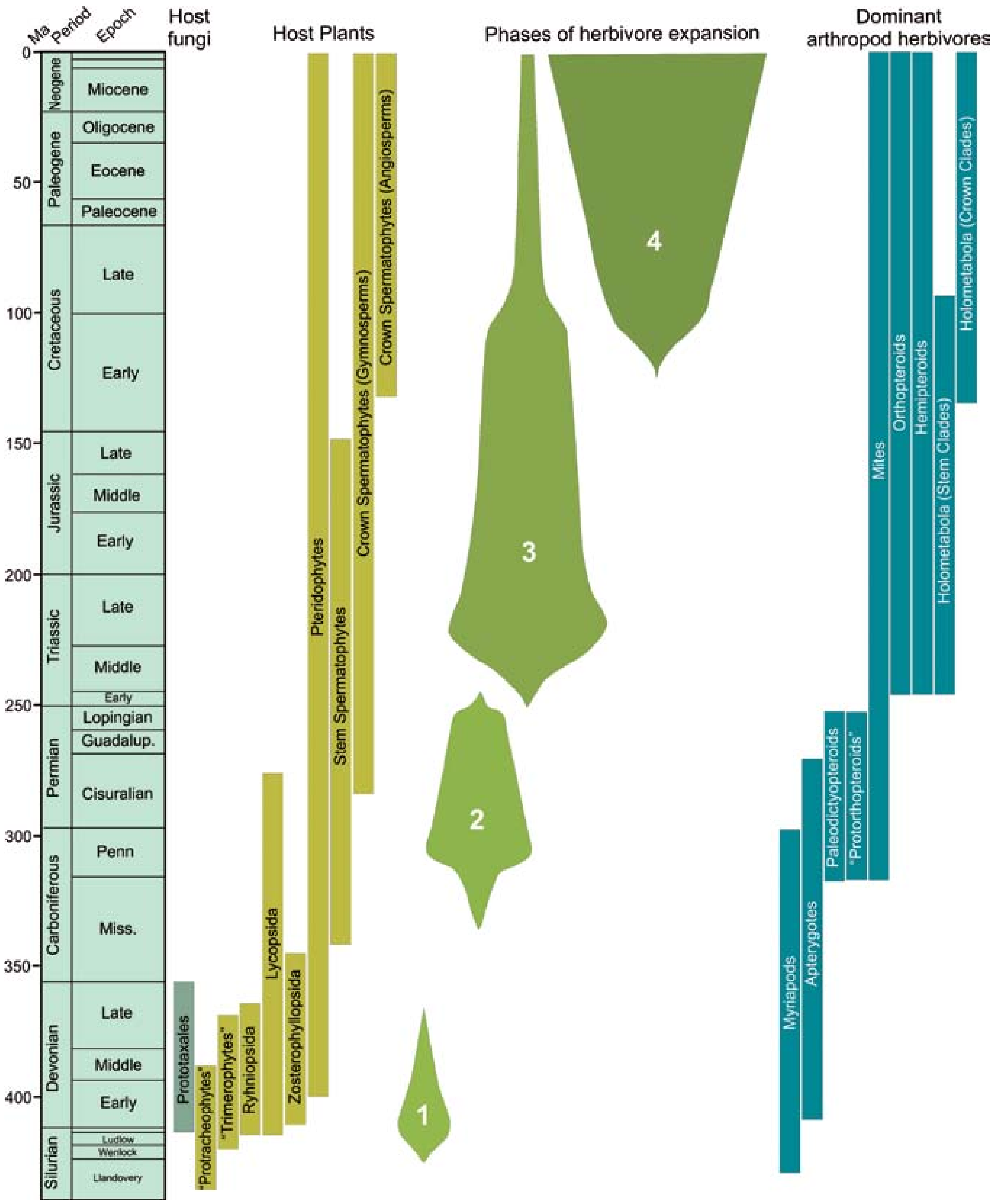


Figure 14.12. Expansion of arthropod herbivory during the Phanerozoic, showing arthropod producers, and host plants and fungi for the four phases of herbivory expansion. Based on Labandeira (2006).

dominated by arthropod and reptile trackways (e.g. Gilmore, 1926, 1927; Brady, 1947; Alf, 1968; Brand and Tang, 1991; Brand, 1992; Lockley, 1992; Loope, 1992; Sadler, 1993; Lockley *et al*., 1994; Braddy, 1995; Kramer *et al*., 1995; Brand and Kramer, 1996; Hunt and Lucas, 2007). Arthropod trackways include *Octopodichnus* (scorpions), *Oniscoidichnus* (isopods), *Diplopodichnus* (millipedes), *Paleohelcura* (scorpions), and *Permichnium* (insects). With respect to reptile trackways, the sinapsid ichnogenera *Laoporus* and *Chelichnus* are common (McKeever, 1991; Lockley *et al*., 1994, 1995; Kramer *et al*., 1995; Morales and Haubold, 1995). In particular, Lockley *et al*. (1995) noted that most of arthropod and vertebrate trackways were produced subaerially on dune faces.

Mesozoic eolian ichnofaunas are more varied rather than being dominated by arthropod trackways. Ichnofaunas from interdunes and dunes contain vertical U-shaped burrows (e.g. *Arenicolites* and *Diplocraterion*), short vertical burrows (*Digitichnus*), meniscate trace fossils (e.g. *Taenidium* and *Entradichnus*), grazing trails (e.g. *Gordia*), bilobate locomotion traces (e.g. *Cruziana*), simple horizontal feeding and dwelling traces (e.g. *Planolites* and *Palaeophycus*) (Ekdale and Picard, 1985; Netto, 1989; Fernandes *et al*., 1990; Gradzinski and Uchman, 1994; Ekdale *et al*., 2007). The typical vertebrate ichnogenus in eolian-dune deposits is the sinapsid trackway *Brasilichnium* (Leonardi, 1981; Lockley *et al*., 1994; Lockley and Meyer, 2000; Hunt and Lucas, 2006c). Cenozoic eolian deposits may contain abundant vertebrate trackways. For example, Fornós *et al*. (2002) documented superbly preserved trackways of the ruminant goat *Myotragus balearicus* in Pleistocene eolianites formed in cliff-front coastal echo dunes.

14.2.7 ARTHROPOD–PLANT INTERACTIONS THROUGH THE PHANEROZOIC

Analysis of arthropod–plant interactions based on the study of traces produced in fossil leaves and other plant remains is revealing an amazing wealth of data which helps to explain the evolution of terrestrial ecosystems through the Phanerozoic (e.g. Labandeira, 1997, 1998, 2000, 2002, 2006, 2007) (Box 14.2). Labandeira (2007) outlined the main advantages of arthropod–plant associational data, namely (1) they are common in deposits that lack insect body fossils; (2) they are more abundant and useful than insect body fossils in the same deposits; (3) they frequently predate the insect body fossil record; (4) they provide behavioral information unavailable from the body-fossil record; and (5) they supply critical information for testing paleobiological and macroevolutionary hypotheses.

Based on this dataset, Labandeira (2006) suggested that the history of arthropod herbivory can be summarized in four main phases of expansion (Fig. 14.12). Each phase is defined by: (1) a temporally constrained and taxonomically distinctive suite of plant–host clades; (2) a coeval assemblage of arthropod herbivore clades in association with plant host clades; and (3) the presence of a representative associational biota early within the development of the phase. An analysis of the evolutionary history of palynivory and nectarivory results in the delineation of similar phases (Labandeira, 2000).

The first phase spans the Late Silurian to Late Devonian, and mostly consists of structures produced by myriapods and, to a lesser extent, apterygote hexapods and possibly true insects. The host plants are basal clades of vascular plants (primitive land plants) and prototaxalean fungus. Arthropod–plant associations include three functional feeding groups, namely external foliage feeding, piercing-and-sucking, and boring. Coprolites containing spores provide the earliest evidence of palynivory (Edwards *et al*., 1995). Evidence for this phase comes essentially from the coastal plains of Euramerica.

The second phase encompasses the mid Carboniferous to end Permian, and includes structures produced by a wider array of makers than in the previous phase, including not only myriapods and apterygote hexapods, but also mites, and paleopterous and neopterous insects (the Paleozoic insect fauna of Labandeira, 2000). The host plants are mostly medulosan and glossopterid pteridosperms, and, to a lesser extent, lyginopterid pteridosperms and cordaites (early seed plants and ferns). With respect to functional feeding groups, three more types are added to those previously present in phase 1, galling, seed predations, and non-feeding oviposition. Considerably more evidence of spore feeding is available from this phase. Information comes from wetlands in fluvial and coastal plains mostly from Euramerica, although information from Gondwana has been added in recent years (e.g. Adami-Rodrigues *et al*., 2004).

The third phase is Middle Triassic to Recent in age, and is represented by structures produced by mites, orthopteroids, hemipteroids, and basal holometabolan clades (earlier phase of the Modern insect fauna of Labandeira 2000). The host plants are pteridophytes and gymnosperms (seed plants). Leaf mining is added to the previous groups and, accordingly, the seven functional feeding groups that characterize modern ecosystems were already present in the early Mesozoic. The dataset for this phase comes from a wide variety of environmental settings in all continents.

The fourth phase spans the mid Early Cretaceous to Recent, and includes structures produced by Modern-aspect orthopteroids and derived hemipteroid and holometabolous insects (later phase of the Modern insect fauna of Labandeira 2000). Angiosperms are the host plants, and the seven functional feeding groups are present. This phase is evidenced by the largest dataset, encompassing a wide array of terrestrial and coastal environments and all continents, although most information comes from North America and western Europe. Most insect mouthpart classes, functional feeding groups, and dietary guilds were established by the end of the Cretaceous (Labandeira, 2002).

15 Ichnology in paleoanthropology and archaeology

> And what had he felt, I asked Mario, when he'd seen it there, the *huella*?
> "One thing is to see artifacts presumably made by somebody and another is to see the *pisada* someone made, what their foot left in the earth. That's what gives you the sense of humanity, right?"
>
> Ariel Dorfman
> *Desert Memories* (2004)

While the previous chapter deals with processes occurring at the scale of deep time, we now move into a more recent past, a time witnessing human activities. For the implications of trace fossils in paleoanthropology, information is based on the study of human fossil footprints (Kim *et al.*, 2008a). Human footprints also play a major role in archaeology, although sources of information are found in many other ichnological datasets, such as bioerosion and bioturbation structures, and other vertebrate tracks as well (Baucon *et al.*, 2008). The aim of this chapter is to review recent research in the area of ichnological applications in paleoanthropology and archaeology. The first half of the chapter will be devoted to review the fossil record of human footprints, from the Pliocene to the Holocene. The second half will explore the uses of ichnology in archaeology.

15.1 APPLICATIONS IN PALEOANTHROPOLOGY

Hominid fossil footprints represent a rich record with examples in all continents with the exception of Antarctica (Kim *et al.*, 2008b) (Fig. 15.1). A recent review indicates the existence of at least 63 reported hominid tracksites (Lockley *et al.*, 2008a). Specifically, the term "hominid ichnology" was introduced by Lockley (1998) for the study of all traces made by hominids. Although, in a broad sense, the field of hominid ichnology includes not only footprints, but also butchering and feeding traces, evidence of stone tool industries, and even any evidence of built structure, it is advisable to restrict the field to avoid full overlap with other disciplines (Kim *et al.*, 2008a). As noted by these authors, fossil footprints are the main field of hominid ichnology and, therefore, we will focus on their implications in paleoanthropology.

15.1.1 THE PLIOCENE RECORD

The only recorded Pliocene hominid footprints are those from Laetoli, Tanzania, which represent the oldest hominid tracks known (Leakey and Hay, 1979; Hay and Leakey, 1982; Suwa, 1984; Leakey and Harris, 1987; Tuttle *et al.*, 1990; Raichlen *et al.*, 2008; Meldrum *et al.*, 2011). The Laetoli site contains three trackways preserved in volcanic ash dated to 3.56 million years ago (Leakey, 1981, 1987). Abundant mammal and avian fossil tracks also occur in the Laetoli area (Musiba *et al.*, 2008). The composition of these vertebrate ichnofaunas suggests a number of microhabitats, such as open grasslands and wooded galleries, in a mosaic landscape.

The original and standard interpretation is that the trackways were produced by *Australopithecus afarensis*, which is essentially consistent with the age of the site and the associated bone record (Suwa, 1984). However, alternative interpretations have been suggested, and some authors have noted the remarkably modern aspect of the tracks, suggesting that they are indistinguishable from those produced by the genus *Homo* (Tuttle, 1987, 1996, 2008; but see Meldrum *et al.*, 2011). Based on these uncertainties, the Laetoli trackways have been classified only at ichnogeneric level as *Hominipes* isp. (Kim *et al.*, 2008b).

15.1.2 THE EARLY PLEISTOCENE RECORD

There is a significant gap between the age of the Laetoli tracksite and the next oldest fossil site (1.5–1.6 million years ago), which is that of the Koobi Fora on the shores of Lake Turkana, Kenya (Behrensmeyer and Laporte, 1981; Lockley *et al.*, 2008a). A hominid trackway consisting of seven tracks occurs in a sandy mudstone layer accumulated in a lake-margin environment. Associated footprints include those of pigmy hippopotamuses and wading birds, which is consistent with the envisaged environmental setting (Behrensmeyer and Laporte, 1981). The hominid trackway is inferred to have been produced by *Homo erectus*. As in the case of the Laetoli trackways, that from Koobi Fora should be classified only at ichnogeneric level as *Hominipes* isp.

15.1.3 THE MIDDLE PLEISTOCENE RECORD

The Middle Pleistocene marks an expansion in the hominid footprint fossil record, with occurrences outside of Africa, specifically in Europe (Italy and France) (Lockley *et al.*, 2008a). Of these two recordings, the best documented is that of the Roccamonfina Volcano site in Italy, dated between 385 000 and 325 000 years old (Mietto *et al.*, 2003; Avanzini

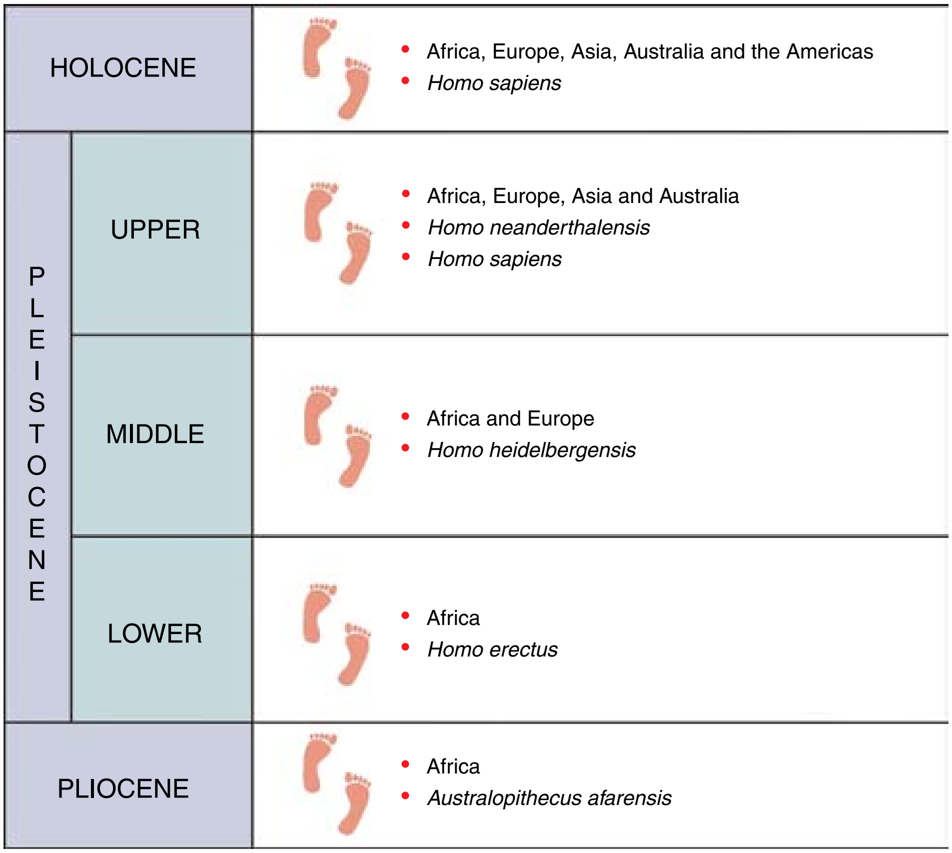


Figure 15.1 Stratigraphic and geographic distribution of human fossil footprints, including the most likely hominid producers. The consistency between the bone and trace-fossil record may be in part an artifact based on the fact that at least some of the footprints are attributed to specific hominids on the basis of age and the bone record itself. The trackway record is not continuous. A large gap exists between the 3.56 million years old Laetoli site (Pliocene) and the 1.5–1.6 million years old Koobi Fora (Early Pleistocene).

et al., 2008). Three trackways have been documented from volcanic ash deposited from pyroclastic flows on a volcano slope. Although fine morphological details are not preserved, the age of the unit is consistent with production by a pre-*Homo sapiens* or pre-*Homo neanderthalensis* species, *H. heidelbergensis* being the most likely candidate.

15.1.4 THE LATE PLEISTOCENE RECORD

Late Pleistocene human trackways are more abundant and widespread and provide definite evidence of the appearance of *H. sapiens* (Lockley *et al.*, 2008a). Early Late Pleistocene hominid tracks of the last interglacial are recorded in two different sites (Nahoon and Langebaan) in South Africa (Roberts, 2008). They are preserved in a coastal-eolian calcarenite, and associated with hyena and bird tracks. As noted by Lockley *et al.* (2008a), these recordings are particularly relevant because they may represent evidence of the presence of *H. sapiens* in Africa close to the Middle to Late Pleistocene transition. The only other Late Pleistocene record in Africa is represented by a single track assigned to *H. sapiens* in Lake Bogoria, Kenya (Scott *et al.*, 2008). The footprint is preserved on a siltstone formed in a lacustrine mud flat and is associated with a wide variety of mammal and bird tracks.

The most extensive Late Pleistocene hominid record occurs in Europe, including tracksites in France, Spain, Italy, Romania, and Greece (Lockley *et al.*, 2008a). European human tracks are almost invariably preserved in caves, such as Lascaux in France (Barriere and Sahly, 1964) or Vârtop in Romania (Onac *et al.*, 2005), reflecting a higher preservation potential. Associated tracks are mostly those of carnivores (Lockley *et al.*, 2008a). The oldest of these are the tracks recorded in Vârtop Cave, which has been attributed to *Homo neanderthalensis* (Onac *et al.*, 2005). Most of the other recordings most likely correspond to *H. sapiens*.

The Late Pleistocene is characterized by the first occurrence of human tracks worldwide, with records extending to Australia (Webb *et al.*, 2005), Tibet (Zhang and Li, 2002), and Korea (Kim *et al.*, 2009). The Tibet finding is particularly significant because no other evidence of humans has been recorded in the area (Zhang and Li, 2002).

15.1.5 THE HOLOCENE RECORD

The Holocene record reveals an expansion into the Americas, with sites recorded in United States (Willey *et al.*, 2009), Mexico (Rodriguez-de la Rosa *et al.*, 2004), Guatemala (Lockley *et al.*, 2008a), El Salvador (Haberland and Grebe, 1957), Honduras (Lockley *et al.*, 2008a), Nicaragua (Lockley *et al.*, 2008b), and Argentina (Bayón and Politis, 1996). In addition, Holocene human footprints have been recorded in Europe, including England (Roberts, 2009), Wales (Lockley *et al.*, 2008a), Spain

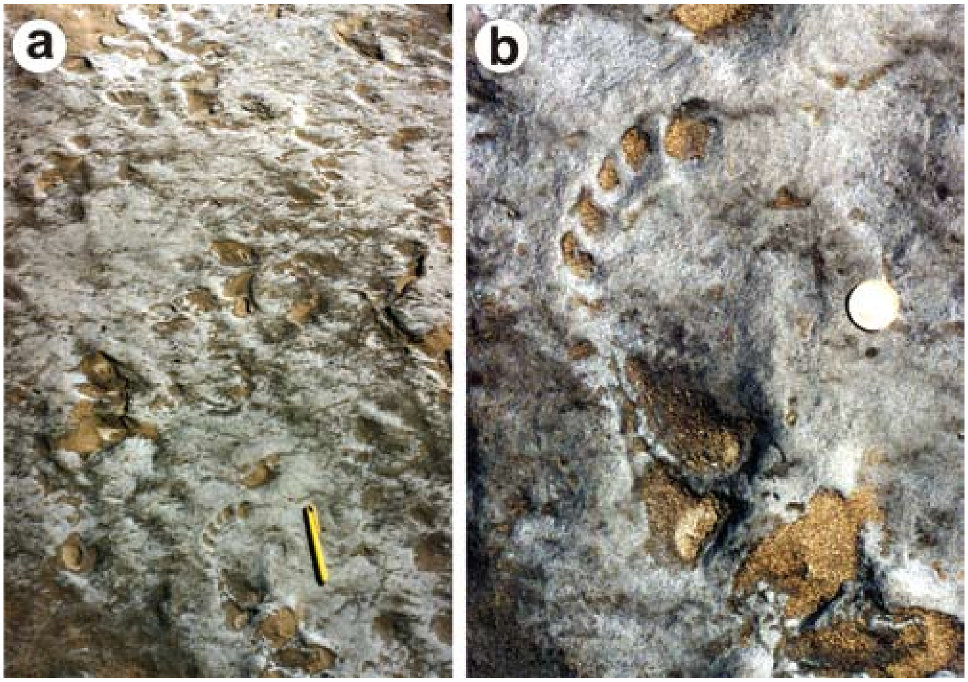


Figure 15.2 Human footprints from the Monte Hermoso site, Buenos Aires Province, Argentina. (a) General view of trackway. Pen is 16 cm. (b) Close up of a track. Coin is 1.5 cm. See Bayón and Politis (1996).

(Lockley *et al.*, 2008a), Italy (Mastrolorenzo *et al.*, 2006), Greece (Bromley *et al.*, 2009b), and Turkey (Westaway *et al.*, 2006). Examples in Africa and Asia are restricted to Mauritania (Mafart, 2006) and Japan (Harada and Noto, 1984), respectively. Additional recordings have been reported from Australia (Lockley *et al.*, 2008a) and New Zealand (Nichol, 1982).

The Acahualinca Footprint Museum site in Nicaragua has been regarded as the most important fossil human tracksite (Lockley *et al.*, 2008b). These authors noted that the site combines accessibility, a large number of well-preserved trackways, and reliable dating. Accordingly, Kim *et al.* (2008b) selected these trackways as the type sample for *Hominipes modernus*, inferred to be produced by *Homo sapiens*. The tracksites in Monte Hermoso and Pehuen-Co, Argentina, are particularly remarkable because they host hundreds of hominid trackways (Fig. 15.2a–b) together with mammal and bird footprints, and invertebrate trace fossils (Bayón and Politis, 1996; Aramayo, 2009; Aramayo and Manera de Bianco, 2009). These sites record the activities of human communities living in the proximity of a coastal lake.

15.2 APPLICATIONS IN ARCHAEOLOGY

The applications of ichnology in archaeology or ichnoarchaeology (Baucon *et al.*, 2008) represent a relatively new field. However, archaeological studies have commonly incorporated trace-fossil information without necessarily referring to the conceptual framework of ichnology (e.g. Pierce, 1992; Milner and Smith, 2005). Only a very few papers have dealt with archaeological aspects from an ichnological perspective (e.g. Mikuláš and Cílek, 1998; West and Hasiotis, 2007; Rodríguez-Tovar *et al.*, 2010b, c). As a result, Baucon *et al.* (2008) noted that a uniform, systematic approach has been lacking. Undoubtedly, ichnoarchaeology is a vibrant new field undergoing expansion particularly in the Mediterranean region (see review by Baucon *et al.*, 2008). In this section, we briefly review some of its most recent developments.

15.2.1 BIOGENIC STRUCTURES IN NATURAL AND ARTIFICIAL SUBSTRATES

Ichnology traditionally deals with biogenic structures produced in natural substrates. In archaeology, trace-fossil information is preserved not only in natural substrates but also in artificial ones. In the case of natural substrates, bioturbation structures may provide information, but their preservation potential is usually low because diagenetic processes have acted for insufficient time (Baucon *et al.*, 2008). Where preserved, footprints may yield valuable insights, as illustrated by human and horse tracks formed in a ceramic manufacturing workshop of the Bronze Age in Qatna, Syria (Baucon *et al.*, 2008). Burrows have received comparatively little attention in archaeological contexts. Burrows may record emplacement contemporaneous with the archaeological site or reveal a later bioturbation event. In the latter case, animals are responsible for significantly mixing sediment at the archaeological sites (Araujo and Marcelino, 2003). Borings are common in archaeological contexts because of their high preservation potential in natural substrates, and have been used to decipher sea-level changes in rocky shorelines, mostly in the Mediterranean region (e.g. Pirazzoli *et al.*, 1982). Work on wood bioerosion essentially reflects the fact that xylophagous insects may significantly damage wood materials, but the potential of wood borings as sources of information remain unexplored in ichnoarchaeology (Baucon *et al.*, 2008).

Artificial substrates commonly help in the preservation of biogenic structures in archaeological sites. Bricks help to preserve tracks because of their geotechnical properties, open-air drying, rapid diagenesis, resistance, and abundance (Baucon *et al.*, 2008). Bird and mammal footprints in bricks of Roman and Medieval sites have been extensively studied (Higgs, 2001). Borings are also preserved in artificial substrates, those in the pillars of the Temple of Serapis, Italy, being the classic example, as illustrated by Lyell (1830).

Also, bones comprise substrates for the preservation of human-produced structures. Of these, human skulls have been modified for various cultural purposes, including surgical or religious ones (e.g. Rytel, 1962; Lillie, 1998). The study of these structures, although technically within the field of ichnoarchaeology, falls close to the boundaries of the discipline (Baucon *et al.*, 2008). Finally, study of trace fossils in archaeological objects (e.g. flint artifacts) offers the opportunity to identify the geological sources of raw material exploited in tool construction (Rodríguez-Tovar *et al.*, 2010b, c) (Box 15.1).

15.2.2 ICHNOLOGICAL HIEROPHANIES

Hierophanies are physical manifestations of the holy or sacred (Eliade, 1959). Baucon *et al.* (2008) noted that some geological features (e.g. sacred rocks) qualify as hierophanies ("geological hierophanies") because ancient cultures have linked them to the divine and the magical. These authors also noted that some biogenic structures in archaeological context may play a similar role, and referred to them as ichnohierophanies or ichnological hierophanies. Baucon *et al.* (2008) proposed a classification of these features in cultural (ichnofossils interpreted

Box 15.1 Identifying the source of archaeological artifacts through ichnological analysis

A recent study has presented a new ichnological technique to identify the source of archaeological tools. This is a non-destructive technique which allows matching the trace fossils present in the tools of an archaeological site with those of outcrops in the same region. This technique has been successfully developed to identify raw materials of flaked artifacts used by Late Neolithic and Copper Age communities of the Iberian Peninsula. This study focuses on blade cores from various archaeological sites in southern Spain. These artifacts contain a distinctive ichnofauna characterized by *Phycosiphon incertum* (Fig. 15.3) and subordinate small specimens of *Chondrites* isp. A survey of outcrops and chert quarries in the region indicates that the same ichnofauna is only present in deep-marine cherts of the Campo de Gibraltar Complex. Accordingly, it has been suggested that these rocks were the most likely source of the artifacts. Flint knappers appear to have preferred cherts from the Campo de Gibraltar over other material located near the settlements.

References: Rodríguez-Tovar *et al.* (2010b, c).

Figure 15.3 Blade core from the Copper Age (*c.* 3000–2500 BP) containing *Phycosiphon incertum.* Los Reconcos, Valle del río Turón, southern Spain. Photograph courtesy of Francisco Rodríguez-Tovar, Antonio Morgado, and José A. Lozano (University of Granada). See Rodríguez-Tovar *et al.* (2010b, c).

Figure 15.4 "Graphoglyptids" from Ancient Greece. National Archaeological Museum, Athens, Greece.

as manifestation of supernatural realities), morphological (inorganic structures interpreted as organic traces of supernatural entities), anthropic (human-generated structures based on ichnological motifs), scientific (trace fossils misinterpreted by archaeologists as cultural artifacts), and composite (superposition of ichnohierophanies of various types).

Mayor and Sarjeant (2001) noted that the fascination of early humans with footprint-shaped marks in rock have led to attribution of these structures to either familiar or fabulous once-living creatures, representing an example of morphological or cultural ichnohierophanies. Envisaged tracemakers range from gods, devils, heroes, and saints to occasionally more accurate interpretations. Early Jurassic dinosaur footprints in the Holy Cross Mountains, Poland, were formerly regarded as imprints produced by the Devil while traveling to participate in occult gatherings (Mayor and Sarjeant, 2001). These authors noted that the Bushmen of Lesotho depicted footprints in cave paintings in an area where dinosaur tracks were abundant. In addition, these paintings also depicted relatively accurate reconstructions of iguanodont-like animal as potential producers. Spiral designs from Ancient Greece may have been inspired by turbidite trace fossils (Fig. 15.4). Ichnology has a long history indeed!

References

Abbassi, N. and Lockley, M. (2004). Eocene bird and mammal tracks from the Karaj Formation, Tarom Mountains, northwestern Iran. *Ichnos*, 11, 349–356.

Aberhan, M., Kiessling, W., and Fürsich, F.T. (2006). Testing the role of biological interactions in the evolution of mid-Mesozoic marine benthic ecosystems. *Paleobiology*, 32, 259–277.

Abrams, P.A. (1987). On classifying interactions between populations. *Oecologia*, 73, 272–281.

Adami-Rodrigues, K., Iannuzzi, R. and Pinto, I.D. (2004). Permian plant-insect interactions from a Gondwana flora of southern Brazil. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, Fossils and Strata, 51, 106–125.

Ahlberg, P.E. (1991). Tetrapod or near tetrapod fossils from the Upper Devonian of Scotland. *Nature*, 354, 298–301.

Ahlbrandt, T.S., Andrews, S. and Gwynne, D.T. (1978). Bioturbation in eolian deposits. *Journal of Sedimentary Petrology*, 48, 839–848.

Aigner, T. (1985) Storm depositional systems. Dynamic stratigraphy in modern and ancient shallow-marine sequences. *Lecture Notes in Earth Sciences*, 3, 174.

Aigner, T. and Reineck, H.E. (1982). Proximality trends in modern storm sands from the Helgoland Bight (North Sea) and their implications for basin analysis. *Senckenbergiana Maritima*, 14, 183–215.

Aitken, A.E. (1990). Fossilization potential of Arctic fjord and continental shelf macrofaunas. In *Glacimarine Environments: Processes and Sediments*, ed. J.A. Dowdeswell and J.E. Scourse, Geological Society Special Publication, 53, 155–176.

Aitken, A.E., Risk, M.J. and Howard, J.D. (1988). Animal–sediment relationships on a subarctic intertidal flat, Pangnirtung Fjord, Baffin Island, Canada. *Journal of Sedimentary Research*, 58, 969–978.

Akpan, E.B. (1986). Depth distribution of endolithic algae from the Firth of Clyde: implications for delineation and subdivision of the photic zone. *Journal of the Marine Biological Association of the United Kingdom*, 66, 269–275.

Akpan, E.B. and Farrow, G.E. (1984). Depth of deposition of early Holocene raised sediments at Irvine deduced from algal borings in mollusc shells. *Scottish Journal of Geology*, 20, 237–247.

Alf, R.M. (1968). A spider trackway from the Coconino Formation, Seligman, Arizona. *Southern California Academy of Sciences, Bulletin*, 67, 125–128.

Allen, G.P. (1991). Sedimentary processes and facies in the Gironde estuary: a model for macrotidal estuarine systems. In *Clastic Tidal Sedimentology*, ed. D.G. Smith, G.E. Reinson, B.A. Zaitlin and R.A. Rahmani, Canadian Society of Petroleum Geologists, Memoir, 16, 219–226.

Allen, G.P. and Posamentier, H.W. (1993). Sequence stratigraphy and facies model of an incised valley fill: The Gironde Estuary, France. *Journal of Sedimentary Petrology*, 63, 378–391.

Allen, J.R.L. and Williams, B.P.J. (1981). *Beaconites antarcticus*: a giant channel–associated trace fossil from the Lower Old Red Sandstone of South Wales and the Welsh Borders. *Geological Journal*, 166, 255–269.

Allison, M.A. and Nittrouer, C.A. (1998) Identifying accretionary mud shorefaces in the geologic record: insights from the modern Amazon dispersal system. In *Mudstones and Shales: Recent Progress in Shale Research*, ed. J. Schieber, W. Zimmerle and P.S. Sethi, Stuttgart: Schweizerbart Publishers, pp. 147–161.

Allison, P.A. and Briggs, D.E.G. (1994). Reply to "Exceptional fossil record. Distribution of soft-tissue preservation through the Phanerozoic". *Geology*, 22, 184.

Almond, J.E. (1985). The Silurian-Devonian fossil record of the Myriapoda. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 309, 227–237.

Almond, J.E., Buatois, L.A., Gresse, P.G. and Germs, G.J.B. (2008). Trends in metazoan body size, burrowing behaviour and ichnodiversity across the Precambrian-Cambrian boundary: ichnoassemblages from the Vanrhynsdorp Group of South Africa. *Conference programme and abstracts, 15th Biennial Meeting of the Palaeontological Society of South Africa, Matjiesfontein*, pp. 15–20.

Alonso, R. (1985). Icnitas de aves como control de niveles boratiferos. *Sociedad Cientifica del Noroeste Argentino*, 1, 37–42.

Alonso-Zarza, A.M. (2003). Palaeoenvironmental significance of palustrine carbonates and calcretes in the geological record. *Earth Science Reviews*, 60, 261–298.

Alonso-Zarza, A.M. and Silva, P.G. (2002). Quaternary laminar calcretes with bees nests; evidence of small scale climatic fluctuations, eastern Canary Islands, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 178, 119–135.

Alonso-Zarza, A.M., Genise, J.F. and Verde, M. (2010). Calizas del Queguay: stratigraphy, sedimentology and trace fossils. *18th International Sedimentological Congress, Abstracts and Program*, p. 106.

Alpert, S.P. (1974). Systematic review of the genus *Skolithos*. *Journal of Paleontology*, 48, 661–669.

Alpert, S.P. (1977). Trace fossils and the basal Cambrian boundary. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 1–8.

Alroy J, Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J. Jr., Sommers, M.G., Wagner, P.J. and Webberal, P.J. (2001). Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences, USA*, 98, 6261–6266.

Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J.W., Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.J., Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J., Bonuso, N., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A., Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nürnberg, S., Powers, C.M., Sessa, J.A., Simpson, C., Tomaovch, A. and Visaggi, C.C. (2008). Phanerozoic trends in the global diversity of marine invertebrates. *Science*, 321, 97–100.

Alvarez, L.W., Alvarez, W., Asaro, F. and Michel, H.V. (1980). Extraterrestrial Cause for the Cretaceous-Tertiary Extinction. *Science*, 208, 1095–1108.

Anderson, A.M. (1976). Fish trails from the early Permian of South Africa. *Palaeontology*, 9, 397–409.

Anderson, B.G. and Droser, M.L. (1998). Ichnofabrics and geometric configurations of *Ophiomorpha* within a sequence stratigraphic framework: an example from the Upper Cretaceous US Western Interior. *Sedimentology*, 45, 379–396.

Anderson, J.G. and Meadows, P.S. (1978). Microenvironments in marine sediments. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, 76, 1–16.

Anderson, K.S., Graham, S.A. and Hubbard, S.M. (2006). Facies, architecture and origin of a reservoir-scale sand-rich succession within submarine canyon fill: Insights from Wagon Caves Rock (Paleocene), Santa Lucia Range, California. *Journal of Sedimentary Research*, 76, 819–838.

Angulo, S. and Buatois, L.A. (2009). Sedimentological and ichnological aspects of a sandy low-energy coast: Upper Devonian–Lower Mississippian Bakken Formation, Williston Basin, southeastern Saskatchewan. In *Summary of Investigations 2009, Volume 1, Saskatchewan Geological Survey*, Saskatchewan Ministry of Energy and Resources, Miscellaneous Report 2009–4.1, Paper A–5, 17.

Angulo, S. and Buatois, L.A. (2010). Sedimentary facies distribution of the Upper Devonian–Lower Mississippian Bakken Formation, Williston Basin, Southeastern Saskatchewan: implications for understanding reservoir geometry, paleogeography and depositional history. In *Summary of Investigations 2010, Saskatchewan Geological Survey*, Saskatchewan Ministry of Energy and Resources, Miscellaneous Report 2010, 1–18.

Ansell, A.D. (1962). Observations on burrowing in the Veneridae (Eulamellibranchia). *Biological Bulletin, Woods Hole*, 123, 521–530.

Ansell, A.D. and Trueman, E.R. (1968). The mechanism of burrowing in the anemone *Peachia hastata* Gosse. *Journal of Experimental Marine Biology and Ecology*, 2, 124–134.

Anthony, E.J. and Orford, J.D. (2002) Between wave- and tide-dominated coasts: the middle ground revisited. *Journal of Coastal Research, Special Issue*, 36, 8–15.

Aquino, R., Buatois, L.A., Somoza, D., Briceño, M. and Moreno, J. (2001). Integration of ichnology, palynology, foraminiferal paleoecology, sedimentology and sequence stratigraphy in reservoir characterization: Oligocene–Lower Miocene, Pirital Field, north of Monagas, Oriental Basin of Venezuela. *VI International Ichnofabric Workshop, Abstracts*, Isla Margarita & Puerto La Cruz, pp. 22–23.

Aramayo, S.A. (2009). A brief sketch of the Monte Hermoso Human Footprint Site, South Coast of Buenos Aires Province, Argentina. *Ichnos*, 16, 49–54.

Aramayo, S.A. and Manera de Bianco, T. (1987a). Hallazgo de una icnofauna continental (Pleistoceno tardío) en la localidad de Pehuen-Co (partido de Coronel Rosales), provincia de Buenos Aires, Argentina. Parte I: Edentata, Litopterna, Proboscidea. *4º Congreso Latinoamericano de Paleontología (Bolivia), Actas*, 1, 516–531.

Aramayo, S.A. and Manera de Bianco, T. (1987b). Hallazgo de una icnofauna continental (Pleistoceno tardío) en la localidad de Pehuen-Co (partido de Coronel Rosales), provincia de Buenos Aires, Argentina. Parte II: Carnivora, Artiodactyla y Aves. *4º Congreso Latinoamericano de Paleontología (Bolivia), Actas*, 1, 532–547.

Aramayo, S.A. and Manera de Bianco, T. (1996). Edad y nuevos hallazgos de icnitas de mamíferos y aves en el yacimiento paleoicnológico de Pehuen-Co (Pleistoceno Tardío), provincia de Buenos Aires, Argentina. *Asociación Paleontológica Argentina, Special Publication*, 4, 47–57.

Aramayo, S.A. and Manera de Bianco, T. (2009). Late Quaternary palaeoichnological sites from the Southern Atlantic Coast of Buenos Aires Province, Argentina: mammal, bird and hominid evidence. *Ichnos*, 16, 25–32.

Araujo M.A.G. and Marcelino J.C. (2003). The role of armadillos in the movement of archaeological materials: an experimental approach. *Geoarchaeology: An International Journal*, 18, 433–460.

Archer, A.W. (1984). Preservational control of trace-fossil assemblages: Middle Mississippian carbonates of South-Central Indiana. *Journal of Paleontology*, 58, 285–279.

Archer, A.W. and Maples, C.G. (1984). Trace-fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwestern Indiana. *Journal of Paleontology*, 58, 448–466.

Archer, A.W., Feldman, H.R., Kvale, E.P. and Lanier, W.P. (1994). Comparison of drier- to wetter-interval estuarine roof facies in the Eastern and Western Interior coal basins, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 106, 171–185.

Arcucci, A.B., Forster, C., Abdala, F., May, C. and Marsicano, C. (1995). "Theropods" tracks from the Los Rastros Formation (Middle Triassic), La Rioja Province, Argentina. *Journal of Vertebrate Paleontology*, 15, supplement 3, 16A.

Astini, R.A., Mángano, M.G. and Thomas, W.A. (2000). El icnogénero *Cruziana* en el Cámbrico Temprano de la Precordillera Argentina: El registro más antiguo de Sudamérica. *Revista de la Asociación Geológica Argentina*, 55, 111–120.

Atkinson, R.J.A. (1974). Spatial distribution of *Nephrops* burrows. *Estuarine and Coastal Marine Science*, 2, 171–176.

Augustinus, P. (1978). *The Changing Shoreline of Surinam (South America)*. Utrecht: Foundation for Scientific Research in Surinam and Netherlands.

Augustinus, P. (1989). Cheniers and chenier plains: a general introduction. *Marine Geology*, 90, 219–229.

Augustinus, P. (2002). Biochemical factors influencing deposition and erosion of fine-grained sediment. In *Muddy Coasts of the World: Processes, Deposits, and Function*, ed. T. Healy, Y. Wang and J.A. Healy, *Proceedings in Marine Science*, 4, 203–228.

Ausich, W.I. and Bottjer, D.J. (1982). Tiering in suspension feeding communities on soft substrate throughout the Phanerozoic. *Science*, 216, 173–174.

Avanzini, M. (2002). Dinosauromorph tracks from the Middle Triassic (Anisian) of the Southern Alps I (Valle di Non, Italy). *Bolletino della Società Paleontologica Italiana*, 41, 37–40.

Avanzini M. and Lockley M. (2002) Middle Triassic archosaur ontogeny and population structure: interpretation based on *Isochirotherium delicatum* fossil footprints (Southern Alps, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 185, 391–402.

Avanzini, M., Ceoloni, P., Conti, M.A., Leonardi, G., Manni, R., Mariotti, N., Mietto, P., Nicosia, U., Santi, G. and Spezzamonte, M. (2001). Tetrapod footprints as key elements of the Permo–Triassic continental biochronology. *Natura Bresciana, Annuario del Museo Civico di Storia Naturale di Brescia, Monografia*, 25, 89–107.

Avanzini, M., Piubelli, D., Mietto, P., Roghi, G., Romano, R. and Masetti, D. (2006). Lower Jurassic (Hettangian-Sinemurian) dinosaur track megasites, southern Alps, northern Italy. In *The Triassic-Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G.

Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 207–216.

Avanzini, M., Mietto, P., Panarello, A., De Angelis, M. and Rolandi, G. (2008). The Devil's Trails: Middle Pleistocene human footprints preserved in a volcanoclastic deposit of Southern Italy. *Ichnos*, 15, 179–189.

Azpeitia-Moros, F. (1933). Datos para el estudio paleontológico de la costa Cantábrica y de algunos otros puntos de España. *Boletín del Instituto Geológico y Minero de España*, 53, 1–65.

Azmi, R.J. (1998). Discovery of lower Cambrian small shelly fossils and brachiopods from the Lower Vindhyan of Son Valley, Central India. *Journal of the Geological Society of India*, 52, 381–389.

Babcock, L.E. (1993). Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology*, 67, 217–229.

Babcock, L.E. and Robinson, R.A. (1989). Preferences of Palaeozoic predators. *Nature*, 337, 695–696.

Bagla, P. (2000). Team rejects claim of early Indian fossils. *Science*, 289, 1273.

Baird, D. (1980). A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*, ed. L.L. Jacobs, Flagstaff, AZ: Museum of Northern Arizona Press, pp. 219–230.

Bajard, J. (1966). Figures et structures sédimentaires dans la zone intertidale de la partie orientale de la Baie du Mont-Saint-Michel. *Revue de Géographie physique et de Géologie Dynamique*, 8, 39–111.

Bak, K. (1995). Trace fossils and ichnofabrics in the Upper Cretaceous red deep-water marly deposits of the Pieniny Klippen Belt, Polish Carpathians. *Annales Societatis Geologorum Poloniae*, 64, 81–97.

Baker, M.E. and B.V. Barnes. (1998). Landscape ecosystem diversity of river floodplains in northwestern Lower Michigan, USA. *Canadian Journal of Forestry Research*, 28, 1405–1418.

Baldwin, C.T. (1975). The stratigraphy of the Cabos series in the section between Cadavedo and Luarca, Province of Oviedo, NW Spain. *Breviora Geologica Asturica*, 19, 4–9.

Baldwin, C.T. (1977). The stratigraphy and facies associations of trace fossils in some Cambrian and Ordovician rocks of north western Spain. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 9–40.

Baldwin, C.T., Strother, P.K., Beck, J.H. and Rose, E. (2004). Palaeoecology of the Bright Angel Shale in the eastern Grand Canyon, Arizona, USA, incorporating sedimentological, ichnological and palynological data. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society of London Special Publication*, 228, 213–236.

Balistieri, P.R.M.N., Netto, R.G. and Lavina, E.L.C. (2002). Ichnofauna from the Upper Carboniferous–Lower Permian rhythmites from Mafra, Santa Catarina State, Brazil: Ichnotaxonomy. *Revista Brasileira de Paleontologia*, 4, 13–26.

Balistieri, P.R.M.N., Netto, R.G. and Lavina, E.L.C. (2003). Icnofauna de ritmitos do topo da Formação Mafra (Permo-Carbonífero da bacia do Paraná) em Rio Negro, Estado do Paraná (PR), Brasil. In *Icnología: Hacia una convergencia entre geología y biología*, ed. L.A Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 131–139.

Bambach, R.K. (1983). Ecospace utilization and guilds in marine communities through the Phanerozoic. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenus Press, pp. 719–746.

Bambach, R.K. (1993). Seafood through time; changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology*, 19, 372–397.

Bambach, R.K., A.H. Knoll and J.J. Sepkoski Jr. (2002). Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proceedings of the National Academy of Sciences, USA*, 99, 6854–6859.

Bambach, R.K., Bush, A.M. and Erwin, D.H. (2007). Autecology and the filling of ecospace: Key metazoan radiations. *Palaeontology*, 50, 1–22.

Bamford, M.L.F., Bruck, P.M., Cooper, M.A., Forbes, W.H. and MacCarthy, I.A.J. (1986). *Beaconites*–type burrows from the Old Red Sandstone of Hook Head, Co. Wexford, Ireland. *Proceedings Geological Association*, 97, 59–71.

Banks, N.L. (1970). Trace fossils from the late Precambrian and Lower Cambrian of Finmark, Norway. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 19–34.

Barnes, R.S.K. and Hughes, R.N. (1999). *An Introduction to Marine Ecology.* 3rd edn. Oxford, UK: Blackwell Science.

Barnes, R.S.K., Calow, P. and Olive, P.J.W. (1993). *The Invertebrates: A New Synthesis*. Oxford, UK: Blackwell Science.

Barras, C.G. and Twitchett, R.J. (2007). Response of the marine infauna to Triassic-Jurassic environmental change: ichnological data from southern England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 244, 223–241.

Barriere, C. and Sahly, A. (1964). Les empreintes humaines de Lascaux. In *Miscelanea en homenaje a Abate H. Breuil*. Barcelona: Instituto de Prehistoria y Arqueología, pp. 173–180.

Barthel, K.W., Swinburne, N.H.M. and Conway Morris, S. (1990). *Solnhofen: A Study in Mesozoic Palaeontology*. Cambridge, UK: Cambridge University Press.

Basan, P.B. and Frey, R.W. (1977). Actual-palaeontology and neoichnology of salt marshes near Sapelo Island, Georgia. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 41–69.

Bates, C.C. (1953). A rational theory of delta formation as exemplified by the present-day Mississippi Delta. *Journal of Sedimentary Petrology*, 23, 132–133.

Batra, S.W.T. (1984). Solitary bees. *Scientific American*, 250, 120–127.

Baucon, A. (2008). Neoichnology of a microbial mat in a temperate, siliciclastic environment: Spiaggia al Bosco (Grado, Northern Adriatic, Italy). In *Italian Ichnology*, ed. M. Avanzini and F. Petti, *Studi Trentini di Scienze Naturali Acta Geologica*, 83, 183–203.

Baucon A., Privitera S., Morandi Bonacossi D., Canci A., Neto de Carvalho C., Kyriazi E., Laborel-Deguen F., Morhange C. and Marriner N. (2008). Principles of ichnoarchaeology: new frontiers for studying past times. In *Italian Ichnology*, ed. M. Avanzini and F. Petti, *Studi Trentini di Scienze Naturali Acta Geologica*, 83, 43–72.

Bayón, C. and Politis, G. (1996). Estado actual de las investigaciones en el sitio Monte Hermoso 1 (Prov. de Buenos Aires). *Arqueología*, 6, 83–116.

Beall, A. (1968). Sedimentary processes operative along the western Louisiana shoreline. *Journal of Sedimentary Petrology*, 38, 869–877.

Beatty, T.W., Zonnenveld, J.-P. Henderson, C.M. (2008). Anomalously diverse Early Triassic ichnofossil assemblages in Northwest Pangea: a case for a shallow-marine habitable zone. *Geology*, 36, 771–774.

Bechtel, D.J., Yuill, C.N., Ranger, M.J. and Pemberton, S.G. (1994). Ichnology of inclined heterolithic stratification of the Fort McMurray Formation, northwestern Alberta. In *Mannville Core Conference*, ed. S.G. Pemberton, D.P. James and D.M. Wightman, Canadian Society of Petroleum Geologists, Exploration Update, pp. 351–368.

Bedatou, E., Melchor, R.N., Bellosi, E.S. and Genise, J.F. (2008). Crayfish burrows from Late Jurassic–Late Cretaceous continental deposits of Patagonia: Argentina: their palaeoecological, palaeoclimatic and palaeobiogeographical significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257, 169–184.

Bedatou, E., Melchor, R.N. and Genise, J.F. (2009). Complex palaeosol ichnofabrics from Late Jurassic–Early Cretaceous volcaniclastic successions of Central Patagonia, Argentina. *Sedimentary Geology*, 218, 74–102.

Behrends, G. and Michaelis, H. (1977). Zur Deutung der Lebensspuren des Polychaeten *Scolelepis squamata*. *Senckenbergiana Maritima*, 9, 47–57.

Behrensmeyer, A.K. and Laporte, L.F. (1981). Footprints of a Pleistocene hominid in northern Kenya. *Nature*, 289, 167–169.

Bell, C.M. (2004). Asteroid and ophiuroid trace fossils from the Lower Cretaceous of Chile. *Palaeontology*, 47, 51–66.

Bellwood, D.R. and Wainwright, P.C. (2006). The history and biogeography of fishes on coral reefs. In *Coral reef fishes: Dynamics and Diversity in a Complex Ecosystem*, ed. P.F. Sale, Burlington, VT: Academic Press, pp. 5–32.

Bengtsön, S. and Yue, Z. (1992). Predatorial borings in Late Precambrian mineralized exoskeletons. *Science*, 257, 367–369.

Bengtsön, S., Rasmussen, R. and Krape, B. (2007). The Paleoproterozoic megascopic Stirling biota. *Paleobiology*, 33, 351–381.

Benner, J.S., Ekdale, A.A. and Gibert, J.M. de (2004). Macroborings *Gastrochaenolites* in Lower Ordovician hardgrounds of Utah: sedimentologic, paleoecologic, and evolutionary implications. *Palaios*, 19, 543–550.

Benner, J.S., Ridge, J.C. and Knecht, R.J. (2009). Timing of post-glacial reinhabitation and ecological development of two New England, USA, drainages based on trace fossil evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 212–231.

Benton, M.J. (1982). Trace fossils from Lower Palaeozoic ocean-floor sediments of the Southern Uplands of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 73, 67–87.

Benton, M.J. (2003). *When Life Nearly Died: The Greatest Mass Extinction of All Time*. London: Thames and Hudson.

Benton, M.J. and Trewin, N.J. (1980). *Dictyodora* from Silurian of Peeblesshire, Scotland. *Palaeontology*, 23, 501–513.

Berger, W.H., Ekdale, A.A. and Bryant, P.P. (1979). Selective preservation of burrows in deep-sea carbonates. *Marine Geology*, 32, 205–230.

Bergström, J. (1973). Organization, life and systematics of trilobites. *Fossils and Strata*, 2, 1–69.

Bergström, J. (1976). Lower Palaeozoic trace fosils from eastern Newfoundland. *Canadian Journal of Earth Sciences*, 13, 1613–1633.

Bergström, J. (1990). Precambrian trace fossils and the rise of bilaterian animals. *Ichnos*, 1, 3–13.

Berkenbusch, K. and Rowden, A.A. (2003). Ecosystem engineering: moving away from "just-so" stories. *New Zealand Journal of Ecology*, 27, 67–73.

Bertling, M. (1997). Bioerosion of Late Jurassic reef corals: Implications for reef evolution. *8th International Coral Reef Symposium, Proceedings*, 2, 1663–1668.

Bertling, M. (1999). Taphonomy of trace fossils at omission surfaces (Middle Triassic, East Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 149, 27–40.

Bertling, M. and Hermanns, K. (1996). Autochtone Muschelbohrungen im Neogen des Rheinischen Braunkohlenreviers und ihre sedimentologische Bedeutung. *Zentralblatt für Geologie und Paläontologie Teil I*, 1/2, 33–44.

Bertling, M., Braddy, S.J. and Bromley, R.G. (2006). Names for trace fossils: a uniform approach. *Lethaia*, 39, 265–286.

Bertness, M.D. (1999). *The Ecology of Atlantic Shorelines*. Sunderland, MA: Sinauer Associates.

Beukema, J.J. (1976). Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Nethearlands Journal of Sea Research*, 10, 236–261.

Beynon, B.M. and Pemberton, S.G. (1992). Ichnological signature of a brackish water deposit: an example from the Lower Cretaceous Grand Rapids Formation, Cold Lake oil sands area, Alberta. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, Society for Sedimentary Geology Core Workshop, 17, 191–221.

Beynon, B.M., Pemberton, S.G., Bell, D.A. and Logan, C.A. (1988). Environmental implications of ichnofossils from the Lower Cretaceous Grand Rapids Formation, Cold Lake Oil Sands Deposit. In *Sequences, Stratigraphy, Sedimentology: Surface and Subsurface*, ed. D.P. James and D.A. Leckie, *Canadian Society of Petroleum Geologists Memoir*, 15, 275–290.

Bhattacharya, J.P. (2006). Deltas. In *Facies Models Revisited*, ed. H. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 237–292.

Bhattacharya, J.P. and Giosan, L. (2003). Wave-influenced deltas, geomorphological implications for facies reconstruction. *Sedimentology*, 50, 187–210.

Bhattacharya, J.P. and MacEachern, J.A. (2009). Hyperpycnal rivers and prodeltaic shelves in the Cretaceous seaway of North America. *Journal of Sedimentary Research*, 79, 184–209.

Bhattacharya, J.P. MacEachern, J.A., Garrison J.R. Jr., Ryer, T.A. and Pemberton, S.G. (2007). *Integrated sedimentology and ichnology of fluvial-dominated and wave-influenced deltas in the Cretaceous seaway: Ferron Sandstone and Panther Tongue, Utah*. Society for Sedimentary Geology Research Conference, Ichnological Applications to Sedimentological and Sequence Stratigraphic Problems, Field Trip Guidebook, Price.

Billett, D.S.M., Lampitt, R.S., Rice, A.L. and Mantoura, R.F.C. (1983). Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature*, 302, 520–522.

Bishop, G.A. (1975). Traces of predation. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 261–281.

Blair, T.C. and McPherson, J.G. (1994). Alluvial Fan Processes and Forms. In *Geomorphology of Desert Environments*, ed. A.D. Abrahams and A.J. Parsons, London: Chapman & Hall, pp. 354–402.

Bockelie, J.F. (1991). Ichnofabric mapping and interpretation of Jurassic reservoir rocks of the Norwegian North Sea. *Palaios*, 6, 206–215.

Bockelie, J.F. (1994). Plant roots in core. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 177–199.

Bockelie, J.F., Eldoy, A., Gran, K. and Porturas, F. (1998). Ichnofabric analysis using borehole and core images: examples of the Norwegian sector of the North Sea. *American Association of Petroleum Geologists, Annual Meeting* (Salt Lake City), *Expanded Abstracts*, A77.

Bohacs, K.M, Carroll, A.R., Neal, J.E. and Mankiewicz, P.J. (2000). Lake-Basin type, source potential, and hydrocarbon character: an integrated sequence-stratigraphic-geochemical framework. In *Lake Basins through Space and Time*, ed. E. Gierlowski-Kordesch and K. Kelts, *American Association of Petroleum Geologists Studies in Geology*, 46, 3–34.

Bohacs, K.M, Hasiotis, S.T. and Demko, T.M. (2007). Continental ichnofossils of the Green River and Wasatch Formation, Eocene, Wyoming: a preliminary survey, proposed relation to lake-basin type, and application to integrated paleo-environmental interpretation. *Mountain Geologist*, 11, 79–108.

Bosence, D. and Wilson, J. (2003). Sequence stratigraphy of carbonate depositonal systems. In *Sedimentary Record of Sea-Level Change*, ed. A.L. Coe, Ambridge, UK: Cambridge University Press and Open University, pp. 234–255.

Bottjer, D.J. (1985). Trace fossils and paleoenvironments of two Arkansas Upper Cretaceous discontinuity surfaces. *Journal of Paleontology*, 59, 282–298.

Bottjer, D.J. and Clapham, M.E. (2006). Evolutionary paleoecology of Ediacaran Benthic marine animals. In *Neoproterozoic Geobiology and Paleobiology*, ed. S. Xiao and A.J. Kaufman, Dordrecht: Springer, pp. 91–114.

Bottjer, D.J. and Droser, M.L. (1991). Ichnofabric and basin analysis. *Palaios*, 6, 199–205.

Bottjer, D.J., Droser, M.L. and Jablonski, D. (1988). Palaeoenvironmental trends in the history of trace fossils. *Nature*, 333, 252–255.

Bottjer, D.J., Hagadorn, J.W. and Dornbos, S.Q. (2000). The Cambrian substrate revolution. *GSA Today*, 10, 1–8.

Bouma, A.H. (2000a). Coarse-grained and fine-grained turbidite systems as end member models: applicability and dangers. *Marine and Petroleum Geology*, 17, 137–143.

Bouma, A.H. (2000b). Fine-grained, mud-rich turbidite systems: model and comparison with coarse-grained, sand-rich systems. In *Fine-Grained Turdidite Systems*, ed. A.H. Bouma and C.G. Stone, *AAPG Memoir 72/SEPM Special Publication*, 68, 9–20.

Bouma, A.H. (2004). Key controls on characteristics of turbidite systems. In *Confined Turbidite Systems*, ed. S.A. Lomas and P. Joseph, *Geological Society Special Publication*, 222, 9–22.

Bown, T.M. 1982. Ichnofossils and rhizoliths of the nearshore fluvial Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 40, 255–309.

Bown, T.M. and Laza, J.H. (1990). A Miocene termite nest from southern Argentina and its paleoclimatological implications. *Ichnos*, 1, 73–79.

Bown, T.M. and Ratcliffe, B.C. (1988). The origin of *Chubutholites* Ihering, ichnofossils from the Eocene and Oligocene of Chubut Province, Argentina. *Journal of Paleontology*, 62, 163–167.

Boyd, R., Dalrymple, R. and Zaitlin, B.A. (1992). Classification of clastic coastal depositional environments. *Sedimentary Geology*, 80, 139–150.

Boyd, R., Dalrymple, R.W. and Zaitlin, B.A. (2006). Estuarine and incised-valley facies models. In *Facies Models revisited*, ed. H.W. Posamentier and R. Walker, *Society for Sedimentary Geology Special Publication*, 84, 175–240.

Bracken, B. and Picard, M.D. (1984). Trace fossils from Cretaceous/Tertiary North Horn Formation in central Utah. *Journal of Paleontology*, 58, 477–487.

Braddy, S.J. (1995). The Ichnotaxonomy of the invertebrate trackways of the Coconino Sandstone (Lower Permian), Northern Arizona. In *Early Permian footprints and facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 219–224.

Braddy, S.J. (2004). Ichnological evidence for the arthropod invasion of land. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 136–140.

Braddy, S.J. and Almond, J.E. (1999). Eurypterid trackways from the Table Mountain Group (Ordovician) of South Africa. *Journal of African Earth Sciences*, 29, 165–177.

Braddy, S.J. and Briggs, D.E.G. (2002). New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. *Journal of Paleontology*, 76, 546–557.

Bradshaw, M.A. (1981). Palaeoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (Lower Beacon Supergroup), Antarctica. *New Zealand Journal of Geology and Geophysics*, 24, 615–652.

Bradshaw, M. and Harmsen, F. (2007). The paleoenvironmental significance of trace fossils in Devonian sediments (Taylor Group), Darwin Mountains to the Dry Valleys, southern Victoria Land. *US Geological Survey and The National Academies; USGS OF-2007–1047*, 15–19.

Brady, L.F. (1947). Invertebrate tracks from the Coconino Sandstone of northern Arizona. *Journal of Paleontology*, 21, 466–472.

Braithwaite, C.J.R. and Talbot, M.R. (1972). Crustacean burrows in the Seychelles, Indian Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 11, 265–285.

Brand, L.R. (1992). Reply to "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin". *Geology*, 20, 668–670.

Brand, L.R. and Kramer, J. (1996). Underprints of vertebrate and invertebrate trackways in the Permian Coconino Sandstone in Arizona. *Ichnos*, 4, 225–230.

Brand, L.R. and Tang, T. (1991). Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin. *Geology*, 19, 1201–1204.

Brandt, D.S., Meyer, D.L. and Lask, P.B. (1995). *Isotelus* (Trilobita) "hunting burrow" from Upper Ordovician strata, Ohio. *Journal of Paleontology*, 69, 1079–1083.

Brandt, D.S., Seitz, M., McCoy, V., Csonka, J., Barringer, J., Holmquist, E., Kraig, S., Morgan, R., Myers, J. and Paquette, L. (2010). A new ichnospecies of *Arthrophycus* from the Late Carboniferous (Pennsylvanian) of Michigan, USA. *Ichnos*, 17, 12–19.

Brasier, M.D., Cowe, J.W. and Taylor, M.E. (1994). Decision on the Precambrian–Cambrian boundary. *Episodes*, 17, 3–8.

Brenchley, P.J. and Harper, D.A.T. (1998). *Palaeoecology: Ecosystems, Environments and Evolution*. London: Chapman & Hall.

Brenchley, P.J., Pickerill, R.K. and Stromberg, S.G. (1993). The role of wave reworking on the architecture of storm sandstone facies, Bell Island Group (Lower Ordovician), eastern Newfoundland. *Sedimentology*, 40, 359–38.

Brenchley, P.J., Marshall, J.D. and Underwood, C.J. (2001). Do all mass extinctions represent an ecological crisis? Evidence from the Late Ordovician. *Geological Journal*, 36, 329–340.

Brett, C.E. (1990). Obrution Deposits. In *Palaeobiology: A Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 239–243.

Bridges, P.H. and Leeder, M.R. (1976). Sedimentary model for intertidal mudflat channels, with examples from the Solway Firth, Scotland. *Sedimentology*, 23, 533–552.

Briggs, D.E.G. and Clarkson, E.N.K. (1990). The late Palaeozoic radiation of malacostracan crustaceans. In *Major Evolutionary Radiations*, ed. P.D. Taylor and G.P. Larwood, *Systematics Association Special Volume*, 42, 165–186.

Briggs, D.E.G. and Fortey, R.A. (1989). The Early radiation and relationships of the major arthropod groups. *Science*, 246, 241–243.

Briggs, D.E.G., Fortey, R.A. and Wills, M.A. (1992). Morphologic disparity in the Cambrian. *Science*, 256, 1670–1673.

Bromham, L. (2006). Molecular dates for the Cambrian Explosion: is the light at the end of the tunnel an oncoming train? *Palaeontologia Electronica*, 9, 1–3.

Bromley, R.G. (1967). Some observations on burrows of thalassinidean Crustacea in chalk hardgrounds. *Quarterly Journal Geological Society of London*, 123, 157–182.

Bromley, R.G. (1970). Borings as trace fossils and *Entobia cretacea* Portlock, as an example. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 49–90.

Bromley, R.G. (1975). Trace fossils at omission surfaces. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 399–428.

Bromley, R.G. (1978). Bioerosion of Bermuda reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 169–197.

Bromley, R.G. (1979). Chalk and Bryozoan limestone: facies, sediments and depositional environments. In *Cretaceous–Tertiary Boundary Events Symposium, I: The Maastrichtian and Danian of Denmark*, ed. T. Birkelund and R.G. Bromley, Copenhagen: University of Copenhagen, pp. 16–32.

Bromley, R.G. (1981). Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispánica*, 16, 55–64.

Bromley, R.G. (1990). *Trace Fossils. Biology and Taphonomy*. London: Unwin Hyman.

Bromley, R.G. (1991). *Zoophycos*: Strip mine, refuse dump, cache or sewage farm? *Lethaia*, 24, 460–462.

Bromley, R.G. (1992). Bioerosion: eating rocks for fun and profit. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 121–129.

Bromley, R.G. (1993). Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis. Bulletin of the Geological Society of Denmark*, 40, 167–173.

Bromley, R.G. (1994). The palaeoecology of bioerosion. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 134–154.

Bromley, R.G. (1996). *Trace fossils. Biology, Taphonomy and Applications*. London: Chapman & Hall.

Bromley, R.G. (2001). Tetrapod tracks deeply set in unsuitable substrates; recent musk oxen in fluid earth (East Greenland) and Pleistocene caprines in aeolian sand (Mallorca). *Bulletin of the Geological Society of Denmark*, 48, 209–215.

Bromley, R.G. (2004). A stratigraphy of marine bioerosion. In *The application of Ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 455–479.

Bromley, R.G. (2005). Preliminary study of bioerosion in the deep-water coral *Lophelia*, Pleistocene, Rhodes, Greece. In *Cold-water Corals and Ecosystems*, ed. A. Freiwald, and J.M. Roberts, Berlin: Springer-Verlag, pp. 895–914.

Bromley, R.G. and Allouc, J. (1992). Trace fossils in bathyal hardgrounds, Mediterranean Sea. *Ichnos*, 2, 43–54.

Bromley, R.G. and Asgaard, U. (1972a). The burrows and microcoprolites of *Glyphea rosenkrantzi*, a Lower Jurassic palinuran crustacean from Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse Rapport*, 49, 15–21.

Bromley, R.G. and Asgaard, U. (1972b). Freshwater *Cruziana* from the Upper Triassic of Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse Rapport*, 49, 15–21.

Bromley, R.G. and Asgaard, U. (1975). Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bulletin of the Geological Society of Denmark*, 24, 261–281.

Bromley, R.G. and Asgaard, U. (1979). Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 28, 39–80.

Bromley, R.G. and Asgaard, U. (1991). Ichnofacies: a mixture of taphofacies and biofacies. *Lethaia*, 24, 153–163.

Bromley, R.G. and Asgaard, U. (1993a). Two bioerosion ichnofacies produced by early and late burial associated with sea-level change. *Geologische Rundschau*, 82, 276–280.

Bromley, R.G. and Asgaard, U. (1993b). Endolithic community replacement on a Pliocene rocky coast. *Ichnos*, 2, 93–116.

Bromley, R.G. and D'Alessandro, A. (1983). Bioerosion in the Pleistocene of Southern Italy: Ichnogenera *Caulostrepsis* and *Maeandropolydora*. *Rivista Italiana di Paleontologia e Stratigrafia*, 89, 283–309.

Bromley, R.G. and D'Alessandro, A. (1990). Comparative analysis of bioerosion in deep and shallow water, Pliocene to recent, Mediterranean Sea. *Ichnos*, 1, 43–49.

Bromley, R.G. and Ekdale, A.A. (1984a). Trace fossil preservation in flint in the European chalk. *Journal of Paleontology*, 58, 298–311.

Bromley, R.G. and Ekdale, A.A. (1984b). *Chondrites*: a trace fossil indicator of anoxia in sediments. *Science*, 224, 872–874.

Bromley, R.G. and Ekdale, A.A. (1986). Composite ichnofabrics and tiering of burrows. *Geological Magazine*, 123, 59–65.

Bromley, R.G. and Frey, R.W. (1974). Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. *Bulletin of the Geological Society of Denmark*, 23, 311–335.

Bromley, R.G. and Fürsich, F.T. (1980). Comments on the proposed amendments to the international Code of zoological nomenclature regarding ichnotaxa. Z.N.(S.) 1973. *Bulletin of Zoological Nomenclature*, 37, 6–10.

Bromley, R.G. and Hanken, N.M. (1991). The growth vector in trace fossils: examples from the Lower Cambrian of Norway. *Ichnos*, 1, 261–276.

Bromley, R.G. and Hanken, N.M. (2003). Structure and function of large, lobed *Zoophycos*, Pliocene of Rhodes, Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 79–100.

Bromley, R.G., Pemberton, S.G. and Rahmani, R.A. (1984). A Cretaceous woodground: the *Teredolites* ichnofacies. *Journal of Paleontology*, 58, 488–498.

Bromley, R.G., Jensen, M. and Asgaard, U. (1995). Spatangoid echinoids: deep-tier trace fossils and chemosymbiosis. *Neues Jahrbuch fr Geologie und Palontologie, Abhandlungen*, 195, 25–35.

Bromley, R.G., Ekdale A.A. and Asgaard, U. (1999). *Zoophycos* in the Upper Cretaceous chalk of Denmark and Sweden. *Greifswalder Geowissenschaftliche Beiträge*, 6, 133–142.

Bromley, R.G., Uchman, A. Gregory, M.R. and Martin, A.J. (2003). *Hillichnus lobosensis* igen. et isp. nov., a complex trace fossil produced by tellinacean bivalves, Paleocene, Monterey, California, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 157–186.

Bromley, R.G., Buatois, L.A., Genise, J.F., Labandeira, C.C., Mángano, M.G., Melchor, R.N., Schlirf, M. and Uchman, A. (2007). Comments on the paper "Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis. *Sedimentary Geology*, 200, 141–150.

Bromley R.G., Kedzierski, M., Kolodziej, B. and Uchman, A. (2009a). Large chambered sponge borings on a Late Cretaceous abrasion platform at Cracow, Poland. *Cretaceous Research*, 30, 149–160.

Bromley, R.G., Uchman, A., Milàn, J., and Hansen, K.S. (2009b). Rheotactic *Macaronichnus*, and human and cattle trackways in Holocene beachrock, Greece: Reconstruction of paleo- shoreline orientation. *Ichnos*, 16, 103–117.

Brown, A.C. and McLachlan, A. (1990). *Ecology of Sandy Shores*, Amsterdam: Elsevier.

Brown, D.E., Lowe, C.H. and Pase, C.P. (1979). A digitized classification system for the biotic communities of North America, with community (Series) and association examples for the Southwest. *Journal of the Arizona-Nevada Academy of Science*, 14, 1–16.

Bruck, P.M., Forbes, W.H., Nance, D. and Pickerill, R.K. (1985). *Beaconites antarcticus* in the (?Middle) Late Devonian McAras Brook Formation, Cape George, Nova Scotia. *Maritime Sediments and Atlantic Geology*, 21, 87–96.

Buatois, L.A. (1995). A new ichnospecies of *Fuersichnus* from the Cretaceous of Antarctica and its paleoecologic and stratigraphic implications. *Ichnos*, 3, 259–263.

Buatois, L.A. and Encinas, A. (2006). La icnofacies de *Glossifungites* en el contacto entre las formaciones Navidad (Miembro Rapel) y La cueva, Plioceno de la Cordillera de la Costa, Chile: su significado estratigráfico-secuencial. *Ameghiniana*, 43, 3–9.

Buatois, L.A. and Encinas, A. (2011). Ichnology, sequence stratigraphy and depositional evolution of an Upper Cretaceous rocky shoreline in central Chile: bioerosion structures in a transgressed metamorphic basement. *Cretaceous Research*, 32, 203–212.

Buatois, L.A. and López Angriman, A.O. (1992a). Trazas fósiles y sistemas deposicionales, Grupo Gustav, Cretácico de la isla James Ross, Antártida. In *Geología de la isla James Ross*, ed. C.A. Rinaldi, Buenos Aires: Publicación del Instituto Antártico Argentino, pp. 239–262.

Buatois, L.A. and López Angriman, A.O. (1992b). The ichnology of a submarine braided channel complex: The Whisky Bay Formation, Cretaceous, James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 94, 119–140.

Buatois, L.A. and Mángano, M.G. (1992). La oxigenación como factor de control en la distribución de asociaciones de trazas fósiles, Formacion Kotick Point, Cretácico de Antártida. *Ameghiniana*, 29, 69–84.

Buatois, L.A. and Mángano, M.G. (1993a). Trace fossils from a Carboniferous turbiditic lake: Implications for the recognition of additional nonmarine ichnofacies. *Ichnos*, 2, 237–258.

Buatois, L.A. and Mángano, M.G. (1993b). Ecospace utilization, paleoenvironmental trends and the evolution of early nonmarine biotas. *Geology*, 21, 595–598.

Buatois, L.A. and Mángano, M.G. (1995a). Postglacial lacustrine event sedimentation in an ancient high mountain setting: the Carboniferous Lake Malanzán from western Argentina. *Journal of Paleolimnology*, 12, 1–22.

Buatois, L.A. and Mángano, M.G. (1995b). The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. *Ichnos*, 4, 151–161.

Buatois, L.A. and Mángano, M.G. (1995c). Sedimentary dynamics and evolutionary history of a Late Carboniferous Gondwanic lake at Northwestern Argentina. *Sedimentology*, 42, 415–436.

Buatois, L.A. and Mángano, M.G. (1996). Icnología de ambientes continentales: Problemas y perspectivas. *Asociación Paleontológica Argentina, Publicación Especial*, 4, 5–30.

Buatois, L.A. and Mángano, M.G. (1998). Trace fossil analysis of lacustrine facies and basins. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 140, 367–382.

Buatois, L.A. and Mángano, M.G. (2000). Icnología: Aplicaciones de la icnología en prospección de hidrocarburos y caracterización de reservorios en la geología sedimentaria y la industria petrolera. *Boletín de Informaciones Petroleras*, 62, 64–85.

Buatois, L.A. and Mángano, M.G. (2002). Trace fossils from Carboniferous floodplain deposits in western Argentina: implications for ichnofacies models of continental environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183, 71–86.

Buatois, L.A. and Mángano, M.G. (2003a). Early colonization of the deep sea: Ichnologic evidence of deep-marine benthic ecology from the Early Cambrian of northwest Argentina. *Palaios*, 18, 572–581.

Buatois, L.A. and Mángano, M.G. (2003b). Caracterización icnológica y paleoambiental de la localidad tipo de *Orchesteropus atavus*, Huerta de Huachi, provincia de San Juán, Argentina: Implicancias en el debate sobre los ambientes de sedimentación en el Carbonífero de Precordillera. *Ameghiniana*, 40, 53–70.

Buatois, L.A. and Mángano, M.G. (2003c). Sedimentary facies and depositional evolution of the Upper Cambrian to Lower Ordovician Santa Rosita Formation in northwest Argentina. *Journal of South American Earth Sciences*, 16, 343–363.

Buatois, L.A. and Mángano, M.G. (2004a). Animal–substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 311–333.

Buatois, L.A. and Mángano, M.G. (2004b). Terminal Proterozoic–Early Cambrian ecosystems: ichnology of the Puncoviscana Formation, Northwest Argentina. In *Trace* Fossils in Evolutionary Palaeoecology, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils & Strata*, 51, 1–16.

Buatois, L.A. and Mángano, M.G. (2007). Invertebrate Ichnology of Continental Freshwater Environments. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 285–323.

Buatois, L.A. and Mángano, M.G. (2008a). Trazas fósiles de invertebrados. In *Invertebrados Fósiles*, ed. H. Camacho, Buenos Aires: Vázquez Manzzini Editores, pp. 751–785.

Buatois, L.A. and Mángano, M.G. (2008b). Continental ichnology and the marine–nonmarine transition. Ichnia 2008, 2nd International Congress on Ichnology, Craków, Poland, p. 22.

Buatois, L.A. and Mángano, M.G. (2009a). Applications of ichnology in lacustrine sequence stratigraphy: potential and limitations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 127–142.

Buatois, L.A. and Mángano, M.G. (2009b). The invertebrate trace fossil record of Mesozoic continental ecosystems. 10th International Symposium on Mesozoic Terrestrial Ecosystems, Abstract Volume, p. 41–42.

Buatois, L.A. and Mángano, M.G. (2010). The trace fossils record of organism-matground interactions in space and time. *Society for Sedimentary Geology Field Conference Abstracts, Microbial Mats in Siliciclastic Deposits (Archean to Today), Denver*, 14.

Buatois, L.A., Martinioni, D. and Lirio, J.M. (1993). Trazas fósiles en una plataforma dominada por tormentas, Formación Rabot (Cretácico superior – Punta Rabot, Isla James Ross, Antártida). *Segundas Reuniones de Comunicaciones Antárticas*, 163–166.

Buatois, L.A., Mángano, M.G. and Aceñolaza, F.G. (1996a). Icnofaunas paleozoicas en sustratos firmes no marinos: Evidencias del Pérmico de la cuenca Paganzo. *Ameghiniana*, 33, 265–270.

Buatois, L.A., Mángano, M.G., Wu X. and Zhang G. (1996b). Trace fossils from Jurassic lacustrine turbidites of the Anyao Formation (Central China) and their environmental and evolutionary significance. *Ichnos*, 4, 287–303.

Buatois, L.A., Jalfin, G. and Aceñolaza, F.G. (1997a). Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina: Ichnologic signatures of substrate consolidation and colonization sequences. *Journal of Paleontology*, 71, 324–336.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1997b). The paradox of nonmarine ichnofaunas in tidal rhythmites: Integrating sedimentologic and ichnologic data from the Late Carboniferous of eastern Kansas, USA. *Palaios*, 12, 467–481.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1998a). Ichnology of an Upper Carboniferous fluvio–estuarine paleovalley: the Tonganoxie Sandstone, Buildex Quarry, eastern Kansas. *Journal of Paleontology*, 71, 152–180.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1998b). Taxonomic reassessment of the ichnogenus *Beaconichnus* and additional examples from the Carboniferous of Kansas, USA. *Ichnos*, 5, 287–302.

Buatois, L.A., Mángano, M.G., Genise, J.F. and Taylor, T.N. (1998c). The ichnologic record of the invertebrate invasion of nonmarine ecosystems: evolutionary trends in ecospace utilization, environmental expansion, and behavioral complexity. *Palaios*, 13, 217–240.

Buatois, L.A., Mángano, M.G., Maples, C.G. and Lanier, W.P. (1998d). Allostratigraphic and sedimentologic applications of trace fossils to the study of incised estuarine valleys: An example from the Virgilian Tonganoxie sandstone of eastern Kansas. *Current Research in Earth Sciences*, 241, 1–27.

Buatois, L.A., Mángano, M.G. and Carr, T.R. (1999). Sedimentology and ichnology of Paleozoic estuarine and shoreface reservoirs, Morrow Sandstone, Lower Pennsylvanian of Southwest Kansas, USA. *Current Research in Earth Sciences*, 241, 1–27.

Buatois, L.A., Mángano, M.G., Fregenal-Martinez, M.A. and Gibert, J.M. de (2000). Short-term colonization trace-fossil assemblages in a carbonate lacustrine konservat–lagerstätte (Las Hoyas fossil site, Lower Cretaceous, Cuenca, central Spain). Facies, 43, 145–156.

Buatois, L.A., Mángano, M.G. and Sylvester, Z. (2001). A diverse deep marine ichnofauna from the Eocene Tarcau Sandstone of the Eastern Carpathians, Romania. *Ichnos*, 8, 23–62.

Buatois, L.A., Mángano, M.G. and Aceñolaza, F.G. (2002a). *Trazas fósiles: Señales de comportamiento en el registro estratigráfico*. Trelew, Argentina: Museo Paleontológico Egidio Feruglio.

Buatois, L.A., Mángano, M.G., Alissa, A. and Carr, T.R. (2002b). Sequence stratigraphic and sedimentologic significance of biogenic structures from a late Paleozoic marginal to open-marine reservior, Morrow Sandstone, subsurface of southwest Kansas, USA. *Sedimentary Geology*, 152, 99–132.

Buatois, L.A., Bromley, R.G., Mángano, M.G., Bellosi, E. and Carmona, N.B. (2003). Ichnology of shallow marine deposits in the Miocene Chenque Formation of Patagonia: Complex ecologic structure and niche partitioning in Neogene ecosystems. *In Icnología: Hacia una convergencia entre geología y biología*, ed. L.A. Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 85–95.

Buatois, L.A., Gingras, M.K., MacEachern, J., Mángano, M.G., Zonneveld, J.-P, Pemberton, S.G., Netto, R.G. and Martin, A.J. (2005). Colonization of brackish-water systems through time: Evidence from the trace-fossil record. *Palaios*, 20, 321–347.

Buatois, L.A., Netto, R.G., Mángano, M.G., Balistieri, P. (2006a). Extreme freshwater release during the late Paleozoic Gondwana deglaciation and its impact on coastal ecosystems. *Geology*, 34, 1021–1024.

Buatois, L.A., Zeballo, F.J., Albanesi, G.L., Ortega, G., Vaccari, N.E. and Mángano, M.G. (2006b). Depositional environments and stratigraphy of the upper Cambrian-Lower Ordovician Santa Rosita Formation at the Alfarcito area, Cordillera Oriental, Argentina: Integration of Bioestratigraphy data within a sequence stratigraphic framework. *Latin American Journal of Sedimentology and Basin Analysis*, 13, 1–29.

Buatois, L.A., Uba, C.E., Mángano, M.G. and Hulka, C. (2007a). Deep bioturbation in continental environments: Evidence from Miocene fluvial deposits of Bolivia. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 123–136.

Buatois, L.A., Netto, R.G. and Mángano, M.G. (2007b). Ichnology of Permian marginal-marine to shallow-marine coal-bearing successions: Rio Bonito and Palermo Formations, Parana basin, Brazil. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 167–177.

Buatois, L.A., Almond, J., Gresse, P. and Germs, G. (2007c). The Elusive Proterozoic-Cambrian boundary: Ichnologic data from Vanrynsdorp Group of South Africa. In *IX International Ichnofabric Workshop*, *Abstracts with Program*, ed. J.P. Zonneveld and M.K. Gingras, Calgary, 8–9.

Buatois, L.A., Santiago, N., Parra, K. and Steel, R. (2008). Animal–substrate interactions in an Early Miocene wave-dominated tropical delta: delineating environmental stresses and depositional dynamics (Tácata field, eastern Venezuela). *Journal of Sedimentary Research*, 78, 458–479.

Buatois, L.A., Macsotay, O. and Quiroz, L. (2009a). The trace fossil *Sinusichnus* in Antarctica and Venezuela: expanding the dataset of crustacean burrows. *Lethaia*, 42, 511–518.

Buatois, L.A., Mángano, M.G., Brussa, E., Benedetto, J.L. and Pompei, J. (2009b). The changing face of the deep: Colonization of the Early Ordovician deep-sea floor, Puna, northwest Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 280, 291–299.

Buatois, L.A., Netto, R. and Mángano, M.G (2010a). Ichnology of late Paleozoic post-glacial transgressive deposits in Gondwana: reconstructing salinity conditions in coastal ecosystems affected by strong meltwater discharge. In *Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana*, ed. O. Lopez Gamundi and L.A. Buatois, *Geological Society of America Special Paper*, 468, 149–173.

Buatois, L.A., Mángano, M.G. and Pattison, S. (2010b). Trace fossils from a prodeltaic channel and lobe complex, Aberdeen and Kenilworth members, Upper Cretaceous, Book Cliffs, Utah: Ichnologic signatures of turbidites and hyperpycnites in deltaic systems. *18th International Sedimentological Congress, Sedimentology at the Foot of the Andes, Abstracts*.

Buatois, L.A. Saccavino, L.L. and Zavala, C. (2011). Ichnologic signatures of hyperpycnal-flow deposits in Cretaceous river-dominated deltas, Austral Basin, southern Argentina. In *Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology*, 61, in press.

Buck, S.G. and Goldring, R. (2003). Conical sedimentary structures, trace fossils or not? Observations experiments and review. *Journal of Sedimentary Research*, 73, 338–353.

Buckman, J.O. (1994). *Archaeonassa* Fenton and Fenton 1937 reviewed. *Ichnos*, 3, 185–192.

Buckman, J.O. (1996). *Heimdallia* from the Lower Carboniferous of Ireland: *H. mullaghmori* a new ichnospecies, and re-evaluation of the three-dimensional format of the ichnogenus. *Ichnos*, 5, 43–51.

Budd, G.E. (2003). The Cambrian fossil record and the origin of phyla. *Integrative and Comparative Biology*, 43,157–165.

Budd, G.E. and Jensen, S. (2000). A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Review* 75, 253–295.

Budd, G.E. and Jensen, S. (2004). The limitations of the fossil record and the dating of the origin of the Bilateria. In *Telling the Evolutionary Time: Molecular Clocks and the Fossils Record*, ed. P.C.I. Donoghue and M.P. Smith, London: Taylor and Francis, pp. 166–189.

Bujok, A., Sadlok, G. and Pieńkowski, G. (2008). Stop 4, Baranóv, Lower Triassic, Upper Spathian. In *Second International Congress on ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Moiuntains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 54–59.

Bull, W.B. (1977). The alluvial-fan environment. *Progress in Physical Geography*, 1, 222–270.

Burzin, M.B., Debrenne, F. and Zhuravlev, A.Y. (2000). Evolution of shallow-water level-bottom communities. In *The Ecology of the Cambrian Radiation*, ed. A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, pp. 217–237.

Buscombe, D. and Masselink, G. (2006). Concepts in gravel beach dynamics. *Earth Science Reviews*, 79, 33–52.

Bush, A.M., Bambach, R.K. and Daley, G.M. (2007). Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology*, 33, 76–97.

Butterfield, N.J. (2001). Ecology and evolution of Cambrian plankton. In *The Ecology of the Cambrian Radiation*, A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, pp. 217–237.

Byers, C.W. (1977). Biofacies patterns in euxinic basins: A general model. In *Deep-Water Carbonate Environments*, ed. H.E. Cook and P. Enos, *Society for Sedimentary Geology Special Publication*, 25, 5–17.

Cadée, G.C. (1998). Influence of benthic fauna and microflora. In *Intertidal Deposits: River Mouths, Tidal Flats, and Lagoons*, ed. D. Eisma, Boca Raton: CRC Press, pp. 383–402.

Cadée, G.C. and Goldring, R. (2007). The Wadden Sea, cradle of invertebrate ichnology. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 3–13.

Calafat, F., Fornós, J.J., Marzo, M., Ramos-Guerrero, E. and Rodríguez-Perea, A. (1986). Icnología de vertebrados de la facies Buntsandstein de Mallorca. *Acta Geológica Hispánica*, 21, 515–520.

Campbell, K.A., Nesbitt, E.A. and Bourgeois, J. (2006). Signatures of storms, oceanic floods and forearc tectonism in marine shelf strata of the Quinault Formation (Pliocene), Washington, USA. *Sedimentology*, 53, 945–969.

Cañas, F. (1995). Early Ordovician carbonate platform facies of the Argentine Precordillera: Restricted shelf to open platform evolution. In *Ordovician Odyssey*, ed. J.D. Cooper, M.L. Droser and S.C. Finney, *Society for Sedimentary Geology Pacific Section*, 77, 221–224.

Carew, J.L. and Mylroie, J.E. (2001). Quaternary carbonate eolianites of the Bahamas: useful analogs for the interpretation of ancient rocks? In *Modern and Ancient Carbonate Eolianites: Sedimentology, Sequence Stratigraphy, and Diagenesis*, ed. F.E. Abegg, D.B. Loope and P.M. Harris, *Society for Sedimentary Geology Special Publications*, 71, 33–45.

Carmona, N.B. and Buatois, L.A. (2003). Estructuras de crustáceos en el Mioceno de la Cuenca del Golfo San Jorge: Implicancias Paleobiológicas y Evolutivas. In *Icnología: Hacia una convergencia entre geología y biología,* ed. L.A. Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 97–108.

Carmona, N.B. and Ponce, J.J. (2011). Ichnology and Sedimentology of the foreland Austral Basin (Tierra del Fuego, Argentina): Trace-fossil distribution and paleoecological implications. In *Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology*, 61, in press.

Carmona, N.B., Buatois, L.A. and Mángano, M.G. (2004). The trace fossil record of burrowing decapods crustaceans: evaluating evolutionary radiations and behavioural convergence. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 141–153.

Carmona, N.B., Ponce, J.J., Mángano, M.G. and Buatois, L.A. (2006). Variabilidad de la icnofacies de *Glossifungites* en el contacto entre las Formaciones Sarmiento (Eoceno medio-Mioceno temprano) y Chenque (Mioceno temprano) en el Golfo San Jorge, Chubut, Argentina. *Ameghiniana*, 43, 413–425.

Carmona, N.B., Mángano, M.G., Buatois, L.A. and Ponce, J.J. (2007). Bivalve trace fossils in an early Miocene discontinuity surface in Patagonia, Argentina: Burrowing behavior and implications for ichnotaxonomy at the firmground–hardground divide. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255, 329–341.

Carmona, N.B., Buatois, L.A., Mángano, M.G., and Bromley, R.G. (2008). Ichnology of the Lower Miocene Chenque Formation, Patagonia, Argentina: Animal–substrate interactions and the Modern Evolutionary Fauna. *Ameghiniana*, 45, 93–122.

Carmona, N.B., Buatois, L.A., Ponce, J.J. and Mángano, M.G. (2009). Ichnology and sedimentology of a tide-influenced delta, Lower Miocene Chenque Formation, Patagonia, Argentina: Trace-fossil distribution and response to environmental stresses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273, 75–86.

Carmona, N.B., Mángano, M.G., Buatois, L.A. and Ponce, J.J. (2010). Taphonomy and paleoecology of the bivalve trace fossil *Protovirgularia* in deltaic heterolithic facies of the Miocene Chenque Formation, Patagonia, Argentina. *Journal of Paleontology*, 84, 730–738.

Carney, R.S. (1981). Bioturbation and Biodeposition. In *Principles of Benthic Marine Paleoecology*, ed. A.J. Boucot, New York: Academic Press, pp. 357–399.

Caron, J.B., Gaines, R.R., Mángano, M.G., Streng, M. and Daley, A.C. (2010). A new Burgess Shale-type assemblage from the thin Stephen Formation of the Southern Canadian Rockies. *Geology*, 38, 811–814.

Carrano, M.T. and Wilson, J.A. (2001). Taxon distributions and the tetrapod track record. *Paleobiology*, 27, 564–582.

Carvalho, I.S. (1996). As pegadas de dinossauros da Bacia de Uiraúna-Brejo das Freiras (Cretáceo Inferior, Estado da Paraíba). *4º Simposio sobre o Cretáceo do Brasil (Aguas de São Pedro), Boletim*, 115–121.

Carvalho, I.S., Viana, M.S.S. and Lima Filho, M.F. (1995). Os icnofósseis de Dinossauros da Bacia do Araripe (Cretáceo Inferior, Ceará-Brasil). *Anais da Academia brasileira de Ciencias*, 67, 433–442.

Cattaneo, A. and Steel, R.J. (2003). Transgressive deposits: a review of their variability. *Earth Science Reviews*, 1277, 1–43.

Catuneanu, O. (2006). *Principles of Sequence Stratigraphy*. Amsterdam: Elsevier.

Caumette, P. (1986). Phototrophic sulfur bacteria and sulfatereducing bacteria causing red waters in a shallow brackish coastal lagoon (Prévost Lagoon, France). *FEMS Microbiology Letters*, 38, 113–124.

Chamberlain, C.K. (1971). Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. *Journal of Paleontology*, 45, 212–246.

Chamberlain, C. K. (1975). Recent lebensspuren in nonmarine aquatic environments. In *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 431–458.

Chamberlain, C.K. (1978). Recognition of trace fossils in cores. In *Trace Fossil Concepts*, ed. P.B. Basan, *Society for Sedimentary Geology Short Course Notes*, 5, 119–166.

Chiappe, L.M., Jackson, F., Coria, R.A. and Dingus, L. (2005). Nesting Titanosaurs from Auca Mahuevo and Adjacent Sites: Understanding Sauropod Reproductive Behaviour and Embryonic Development. In *The Sauropods: Evolution and Paleobiology*, ed. K.A. Curry Rogers and J.A. Wilson, Berkley, CA: University of California Press, pp. 285–302.

Chiappe, L.M., Schmitt, J.G., Jackson, F.D., Garrido, A., Dingus, L. and Grellet-Tinner, G. (2004). Nest Structure for Sauropods: Sedimentary criteria for recognizing dinosaur nesting traces. *Palaios*, 19, 89–95.

Clack, J.A. (2002). *Gaining Ground: The Origin and Evolution of Tetrapods*. Bloomington, IN: Indiana University Press.

Clack, J.A. (2005). Making headway and finding a foothold: tetrapods come ashore. In *Evolving Form and Function: Fossils and Development*, ed. D.E.G. Briggs, *Peabody Museum of Natural History Special Publications*, 223–244.

Clapham, M.E., Narbonne, G.M. and Gehling, J.G. (2003). Paleoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology*, 29, 527–544.

Clarkson, E.N.K. (1992). *Invertebrate Palaeontology and Evolution*. London: Chapman & Hall.

Clemmensen, L.B., Kent, D.V. and Jenkins, F.A. Jr. (1998). A Late Triassic lake system in East Greenland: facies, depositional cycles and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 140, 135–159.

Clemmey, H. (1976). World's oldest animal traces. *Nature*, 261, 576–578.

Clifton, H.E. (2006). A Reexamination of Facies Models for Clastic Shorelines. In: *Facies Models Revisited*, ed. H.W. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 293–337.

Clifton, H.E. and Thompson, J.K. (1978). *Macaronichnus segregatis*: A feeding structure of shallow marine polychaetes. *Journal of Sedimentary Petrology*, 48, 1293–1302.

Clifton, H.E., Hunter, R.E. and Phillips, R.L. (1971). Depositional structures and processes in the non-bar high energy nearshore. *Journal of Sedimentary Petrology*, 41, 651–670.

Cloud, P., Gustafson, L.B. and Watson, J.A. (1980). The works of living social insects as pseudofossils and the age of the oldest known Metazoa. *Science*, 210, 1013–1015.

Cloudsey-Thompson, J.L. (1991). *Ecophysiology of Desert Arthropods and Reptiles*. New York: Springer-Verlag.

Cohen, A.S. (1982). Paleoenvironments of root casts from the Koobi For a Formation, Kenya. *Journal of Sedimentary Petrology*, 52, 401–414.

Cohen, A.S. (2003). *Paleolimnology: The History and Evolution of Lake Systems*. New York: Oxford University Press.

Cohen, A.S., Lockley, M., Halfpenny, J. and Michel, E. (1991). Modern vertebrate track taphonomy at Lake Manyara, Tanzania. *Palaios*, 6, 371–389.

Cohen, A.S., Halfpenny, J., Lockley, M. and Michel, E. (1993). Modern vertebrate tracks from Lake Manyara, Tanzania and their paleobiological implications. *Paleobiology*, 19, 433–458.

Coleman, F.C. and Williams, S.L. (2002). Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution*, 17, 40–44.

Conway Morris, S. (1989). The persistence of Burgess Shale-type faunas: implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 80, 271–283.

Conway Morris, S. (2000). The Cambrian "explosion": Slow-fuse or megatonnage? *Proceedings of the National Academy of Sciences, USA*, 97, 4426–4429.

Conway Morris, S. (2002). Ancient animals or something else entirely? *Science*, 298, 57–58.

Conway Morris, S. and Bengtson, S. (1994). Cambrian predators: possible evidence from boreholes. *Journal of Paleontology*, 68, 1–23.

Conybeare, D.M., Cannon, S., Karaouz, S. and Uygur, E. (2004). Reservoir modelling of the Hamitabat Field, Thrace Basin, Turkey: an example of a sand-rich turbidite system. In *Confined Turbidite Systems*, ed. S.A. Lomas and P. Joseph, *Geological Society Special Publication*, 222, 307–320.

Cook, A.G. and Bann, K. (2000). Trace fossils from the upper Carboniferous Jericho Formation, Central Queensland. *Memoirs of the Queensland Museum*, 45, 235–251.

Corbeanu, R.M., Wizevich, M.C., Bhattacharya, J.P., Zeng, X. and McMechan, G.A. (2004). Three-dimensional architecture of ancient lower delta-plain point bars using ground-penetrating radar, Cretaceous Ferron Sandstone, Utah. In *Regional to Wellbore Analog for Fluvial-Deltaic Reservoir Modeling: The Ferron Sandstone of Utah*, ed. J.T.C. Chidsey, R.D. Adams and T.H. Morris, *American Association of Petroleum Geologists Studies in Geology*, 50, 285–309.

Corner, G.D. and Fjalstad, A. (1993). Spreite trace fossils (*Teichichnus*) in a raised Holocene fjord-delta, Breidvikeidet, Norway. *Ichnos*, 2, 155–164.

Cornish, F. G. (1986). The trace-fossil *Diplocraterion*: evidence of animal–sediment interactions in Cambrian tidal deposits. *Palaios*, 1, 478–491.

Cosarinsky, M.I. (2003). Micromorphology of the nest of *Cornitermes cumulans* Kollar (Isoptera, Termitidae). In *Icnología: Hacia una convergencia entre geología y biología*, ed. L.A. Buatois and M.G. Mángano, *Publicación Especial Asociación Paleontológica Argentina*, 9, 53–64.

Cotton, W.D., Hunt, A.P. and Cotton, J.E. (1995). Paleozoic vertebrate tracksites in eastern North America. *New Mexico Museum of Natural History and Science Bulletin*, 6, 189–211.

Crame, J.A. (1990). Trophic structure. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Boston, MA, and Oxford, UK: Blackwell, pp. 385–390.

Crawford, C.S. (1988). Surface-active arthropods in a desert landscape: Influences of microclimate, vegetation, and soil texture on assemblage structure. *Pedobiologia*, 32, 373–385.

Crimes, T.P. (1969). Trace fossils from the Cambro–Ordovician rocks of North Wales and their stratigraphic significance. *Geological Journal*, 6, 333–337.

Crimes, T.P. (1970a). Trilobite tracks and other trace fosils from the Upper Cambrian of North Wales. *Geological Journal*, 7, 47–68.

Crimes, T.P. (1970b). The significance of trace fossils in sedimentology, stratigraphy and palaeoecology, with examples from Lower Palaeozoic strata. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 101–126.

Crimes, T.P. (1974). Colonisation of the early ocean floor. *Nature*, 248, 328–330.

Crimes, T.P. (1975). The stratigraphical significance of trace fossils. In *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 109–130.

Crimes, T.P. (1977). Trace fossils of an Eocene deep-sea sand fan. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 71–90.

Crimes, T.P. (1987). Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geological Magazine*, 124, 97–119.

Crimes, T.P. (1992). The record of trace fossils across the Proterozoic-Cambrian boundary. In *Origin and Early Evolution of the Metazoa*, ed. J.H. Lipps and P.W. Signor, New York: Plenum Press, pp. 177–199.

Crimes, T.P. (1994). The period of early evolutionary failure and the dawn of evolutionary success. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 105–133.

Crimes, T.P. (2001). Evolution of the deep-water benthic community. In *The Ecology of the Cambrian Radiation*, ed. A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, 275–290.

Crimes, T.P. and Anderson, M.M. (1985). Trace fossils from Late Precambrian–Early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications. *Journal of Paleontology*, 59, 310–343.

Crimes, T.P. and Crossley, J.D. (1991). A diverse ichnofauna from Silurian flysch of the Aberystwyth Grits Formation, Wales. *Geological Journal*, 26, 27–64.

Crimes, T.P. and Fedonkin, M.A. (1994). Evolution and dispersal of deepsea traces. *Palaios*, 9, 74–83.

Crimes, T.P. and Fedonkin, M.A. (1996). Biotic changes in platform communities across the Precambrian-Phanerozoic boundary. *Revista italiana di Paleontologia e Stratigrafia*, 102, 317–332.

Crimes, T.P. and Germs, G.J.B. (1982). Trace fossils from the Nama Group (Precambrian-Cambrian) of southwest Africa (Namibia). *Journal of Paleontology*, 56, 890–907.

Crimes, T.P. and Jiang, Z. (1986). Trace fossils from the Precambrian-Cambrian boundary candidate at Meishucun, Jinning, Yunnan, China. *Geological Magazine*, 36, 633–642.

Crimes, T.P. and McCall, G.J.H. (1995). A diverse ichnofauna from Eocene-Miocene rocks of the Makran Range (S.E. Iran). *Ichnos*, 3, 231–258.

Crimes, T.P. and McIlroy, D. (1999). An Ediacaran biota from lower Cambrian strata on the Digermul Peninsula, Arctic Norway. *Geological Magazine*, 36, 633–642.

Crimes, T.P. and Marcos, A. (1976). Trilobite traces and the age of the lowest part of the Ordovician reference section for NW Spain. *Geological Magazine*, 113, 349–356.

Crimes, T.P., Legg, I., Marcos, A. and Arboleya, M. (1977). Late Precambrian–low Lower Cambrian trace fossils from Spain. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 91–138.

Crimes, T.P., Goldring, R., Homewood, P., Van Stuijvenberg, J. and Winkler, W. (1981). Trace fossil assemblages of deep-sea fan deposits, Gurnigel and Schlieren flysch (Cretaceous–Eocene), Switzerland. *Eclogae Geologicae Helvetiae*, 74, 953–995.

Crimes, T.P., García Hidalgo J.F. and Poiré D.G. (1992). Trace fossils from Arenig flysch sediments of Eire and their bearing on the early colonisation of the deep seas. *Ichnos*, 2, 61–77.

Croghan, P.C. (1983). Osmotic regulation and the evolution of brackish- and fresh-water faunas. *Journal of the Geological Society, London*, 140, 39–46.

Cunningham, K.J., Sukop, M.C., Huang, H., Alvarez, P.F., Curran, H.A., Renken, R.A. and Dixon, J.F. (2009). Prominence of ichnologically influenced macroporosity in the karst Biscayne aquifer: Stratiform 'super-K' zones. *Geological Society of America, Bulletin*, 121, 164–180.

Curran, H.A. (1984). Ichnology of Pleistocene carbonates on San Salvador, Bahamas. *Journal of Paleontology*, 58, 312–321.

Curran, H.A. (1992). Trace fossils in Quaternary, Bahamian-Style Carbonate Environments: the Modern to Fossil transition. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 105–120.

Curran, H.A. (1994). The palaeobiology of ichnocoenoses in Quaternary, Bahamian-Style carbonate environments: The Modern to Fossil transition. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 83–104.

Curran, H.A. (2007). Ichnofacies, ichnocoenoses and ichnofabrics of Quaternary shallow-marine to dunal tropical carbonates: a model and implications. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 232–247.

Curran, H.A. and Harris, L.A. (1996). Bioturbation of carbonate lagoonal sediments by callianassid shrimp: Examples from the Bahamas. *Geological Society of America, Abstracts with Programs*, 28, A-274.

Curran, H.A. and Martin, A.J. (2003). Complex decapod burrows and ecological relationships in Modern and Pleistocene intertidal carbonate environments, San Salvador Island, Bahamas. *Palaeogeography, Palaeoclimatology, Paleoecology*, 192, 229–245.

Curran, H.A. and White, B. (1991). Trace fossils of shallow subtidal to dunal ichnofacies in Bahamian Quaternary carbonates. *Palaios*, 6, 498–510.

Curran, H.A. and White, B. (1997). A *Conichnus conicus*-generated ichnofabric in the late Pleistocene limestones at Clifton Pier, New Providence Island, Bahamas. In *Guide to Bahamian Ichnology: Pleistocene, Holocene and Modern Environments*, ed. H.A. Curran, San Salvador: Bahamian Field Station, pp. 55–61.

Curran, H.A. and White, B. (2001). Ichnology of Holocene carbonate eolianites of the Bahamas. In *Modern and Ancient Carbonate Eolianites: Sedimentology, Sequence Stratigraphy and Diagenesis*, ed. F.E. Abegg, P.M. Harris and D.B. Loope, *Society for Sedimentary Geology Special Publication*, 71, 47–56.

Currie, P.J., Badamgarav, D. and Koppelhu, E.B. (2003). The first Late Cretaceous footprints from the Nemegt locality in the Gobi of Mongolia. *Ichnos*, 10, 1–12.

Cushing, C.E. and Allan, D. (2001). *Streams: Their Ecology and Life.* San Diego, CA: Academic Press.

D'Alessandro, A. (1980). Prime osservazioni sulla ichnofauna Miocenica della formazione di Gorgoglione' (Castelmezzano, Potenza). *Rivista Italiana di Paleontologia*, 86, 357–398.

D'Alessandro, A. and Bromley, R.G. (1987). Meniscate trace fossils and the *Muensteria–Taenidium* problem. *Palaeontology*, 30, 743–763.

D`Alessandro, A., Ekdale, A.A. and Sonnino, M. (1986). Sedimentologic significance of turbidite ichnofacies in the Saraceno Formation (Eocene), Southern Italy. *Journal of Sedimentary Petrology*, 56, 294–206.

D'Alessandro, A., Ekdale, A.A. and Picard, M.D. (1987). Trace fossils in fluvial deposits of the Duchesne River Formation (Eocene), Uinta Basin, Utah. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 61, 285–301.

Dale, J.E., Aitken, A.E., Gilbert, R. and Risk, M.J. (1989). Macrofauna of Canadian arctic fjords. *Marine Geology*, 85, 331–358.

Daley, B. (1968). Sedimentary structures from a non-marine horizon in the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire, England. *Journal of Paleontology*, 38, 114–127.

Dalrymple, R.W. (1992). Tidal depositional systems. In *Facies Models and Sea Level Changes*, ed. R.G. Walker and N.P. James, St. John's, Canada: Geological Association of Canada, 195–218.

Dalrymple, R.W. (2006). Incised-valleys in time and space: An introduction to the volume and an examination of the controls on valley formation and filling. In *Incised Valleys in Time and Space* ed. R.W. Dalrymple, D.A. Leckie and R.W. Tillman, *Society for Sedimentary Geology Special Publications*, 85, 5–12.

Dalrymple, R.W. and Choi, K. (2007). Morphologic facies trends through the fluvial-marine transition in tide-dominated depositional systems: A schematic framework for environmental and sequence-stratigraphic interpretation. *Earth Science Reviews*, 81, 135–174.

Dalrymple, R.W. and Rhodes, R.N. (1995). Estuarine dunes and bars. *Geomorphology and Sedimentology of Estuaries, Developments in Sedimentology*, 53, 359–406.

Dalrymple, R.W., Knight, R.J., Zaitlin, B.A. and Middleton, G.V. (1990). Dynamics and facies model of a macrotidal sand-bar complex, Cobequid Bay-Salmon River estuary, (Bay of Fundy). *Sedimentology*, 37, 577–612.

Dalrymple, R.W., Zaitlin, B.A. and Boyd, R. (1992). Estuarine facies models: conceptual basis and stratigraphic implications. *Journal of Sedimentary Petrology*, 62, 1130–1146.

Dalrymple, R.W., Baker, E.K., Harris, P.T. and Hughes, M.G. (2003). Sedimentology and stratigraphy of a tide-dominated foreland-basin delta (Fly River, Papua New Guinea). In *Tropical Deltas of Southeast Asia: Sedimentology, Stratigraphy and Petroleum Geology*, ed. F.H. Sidi, D. Nummedal, P. Imbert, H. Darman and H.W. Posamentier, *Society for Sedimentary Geology Special Publication*, 76, 147–173.

Dam, G. (1990). Paleoenvironmental significance of trace fossils from the shallow marine Lower Jurassic Neill Klinter Formation, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 79, 221–248.

Dam, G. and Stemmerik, L. (1994). East Greenland lacustrine complexes. In *Global Geological Record of Lake Basins 1*, ed. E. Gierlowski-Kordesch and K. Kelts, Cambridge, UK: Cambridge University Press, 19–27.

Damiani, R., Modesto, S., Yates, A. and Neveling, J. (2003). Earliest evidence of cynodont burrowing, *Proceedings of the Royal Society B: Biological Sciences*, 270, 1747–1751.

Darwin, C. (1881). *The Formation of Vegetable Mould, Through the Action of Worms*. London: John Murray.

Dashtgard, S.E. and Gingras, M.K. (2005). Facies architecture and ichnology of recent salt-marsh deposits: Waterside Marsh, New Brunswick, Canada. *Journal of Sedimentary Research*, 75, 596–607.

Dashtgard, S.E., Gingras, M.K. and MacEachern, J.A. (2009). Tidally modulated shorefaces. *Journal of Sedimentary Research*, 79, 793–807.

Dashtgard, S.E., MacEachern, J.A., Frey, S.E. and Gingras, M.K. (2011). Tidal effects on the shoreface: Towards a conceptual framework. *Sedimentary Geology*, in press.

Davies, N.S. and Gibling, M.R. (2009). Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. *Earth Science Reviews*, 98, 171–200.

Davies, N.S., Sansom, I.J. and Turner, P. (2006). Trace fossils and paleoenvironments of a Late Silurian marginal-marine/alluvial system: the Ringerike Group (Lower Old Red Sandstone), Oslo region, Norway. *Palaios*, 21, 46–62.

Davies, N.S., Rygel, M.C. and Gibling, M.R. (2010). Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): Implications for the history of life on land. *Palaios*, 25, 527–539.

Davis, R.B., Minter, N. and Braddy, S. (2007). The neoichnology of terrestrial arthropods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255, 284–307.

Debriette, P. and Gand, G. (1990). Stratigraphic and paleoenvironmental results from new paleontological observations made in the Permian of the western part of the Lodève basin (South Massif Central). *Géologie de la France*, 19–32.

de Boer, P.L. (1998). Intertidal sediments: composition and structure. In *Intertidal Deposits: River Mouths, Tidal Flats and Coastal Lagoons*, ed. D. Eisma, *Marine Science Series*, 912–921.

de Mowbray, T. (1983). The genesis of lateral accretion deposits in recent intertidal mudflat channels, Solway Firth, Scotland. *Sedimentology*, 30, 425–435.

Delgado, M., Kabbabe, T., Sampson, E. and Chacartegui, F. (2001). Ichnofossils as a tool for environmental interpretation, Pauji and Misoa formations, Barúa and Motatán fields, Zulia and Trujillo states, Venezuela. *VI International Ichnofabric Workshop Abstarcts, Isla Margarita & Puerto La Cruz*, 27.

Demathieu, G. (1977). La palichnologie de vertebras. Developpement recent et role dans la stratigraphie du Trias. *Bulletin du Bureau Recherches Geologiques et Minires*, 3, 269–278.

Demathieu, G. (1984). Une ichnofaune du Trias moyen du basin de Lodve (Hrault, France). *Annales de Palontologie*, 70, 247–273.

Demathieu, G. (1989). Appearance of the first dinosaur tracks in the French Middle Triassic and their probable significance. In *Dinosaur tracks and traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 201–207.

Demathieu, G. (1994). Synthèse géologique du Sud-Est de la France: Donées bistratigraphiques. *Mémoire du Bureau de Recherches Géologiques et Minières*, 125, 63–64.

Demathieu, G. and Demathieu, P. (2004). *Chirotheria* and other ichnotaxa of the European Triassic. *Ichnos*, 11, 79–88.

Demathieu, G., Gand, G. and Toutin-Morin, N. (1992). La palichnofaune des basins permiens provencaux. *Geobios*, 25, 19–54.

Demircan, H. and Toker, V. (2003). Trace fossils in the western fan of the Cingoz Formation in the northern Adana Basin (Southern Turkey). *Mineral Research and Exploration Bulletin*, 127, 15–32.

Desjardins, P.R., Mángano, M.G., Buatois, L.A. and Pratt, B.R. (2010a). *Skolithos* pipe rock and associated ichnofabrics from the southern Rocky Mountains, Canada: colonization trends and environmental controls in an early Cambrian sand-sheet complex. *Lethaia*, 214, 507–528.

Desjardins, P.R., Buatois, L.A., Mángano, M.G. and Limarino, C.O. (2010b). Ichnology of the latest Carboniferous – earliest Permian transgression in the Paganzo Basin of western Argentina: The changing ecology of sea-level rise during postglacial times in Gondwana. In *Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana*, ed. O. Lopez Gamundi, and L.A. Buatois, *Geological Society of America Special Paper*, 468, 175–192.

Dewitt, T.H., D'Andrea, A.F., Brown, C.A., Griffin, B.D. and Eldridge, P.M. (2004). Impact of burrowing shrimp populations on nitrogen cycling and water quality in western North American temperate estuaries. In *Proceedings of the Symposium on "Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments- from Individual Behaviour to their Role as Ecosystem Engineers*, ed. A. Tamaki, Nagasaki University, Nagasaki, pp. 107–118.

DiMichele, W.A. and Aronson, R.B. (1992). The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore–offshore hypothesis. *Evolution*, 46, 807–824.

Domènech, R., Gibert, J.M. de and Martinell, J. (2001). Ichnological features of a marine transgression: Middle Miocene rocky shores of Tarragona, Spain. *Geobios*, 34, 99–107.

Donovan, S.K. (1994) (ed.). *The Palaeobiology of Trace Fossils*. Chichester, UK: John Wiley & Sons.

Dornbos, S.Q., Bottjer, D.J. and Chen, J.Y. (2004). Evidence for seafloor microbial mats and associated metazoan lifestyles in Lower Cambrian phosphorites of Southwest China. *Lethaia*, 37, 127–137.

Dornbos, S.Q., Bottjer, D.J. and Chen, J.Y. (2005). Paleoecology of benthic metazoans in the Early Cambrian Maotianshan Shale biota and the Middle Cambrian Burgess Shale biota: Evidence for the Cambrian substrate revolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 220, 47–67.

Dornbos, S.Q., Bottjer, D.J. Chen, J.-Y., Gao, F., Oliveri, P. and Li, C.-W. (2006). Environmental controls on the taphonomy of phosphatized animals and animal embryos from the Neoproterozoic Doushantuo Formation, Southwest China. *Palaios*, 21, 3–14.

Dornbos, S.Q., Plotnick, R.E. and Chen, J.Y. (2009). Movement paleoecology of the early Cambrian Chengjiang biota. *Geological Society of America Annual Meeting, Abstracts with Programs*, 41, 163.

Downing, K.P. and Walker, R.G. (1988). Viking Formation, Joffre Field, Alberta: shoreface origin of long, narrow sand body encased in marine mudstones. *American Association of Petroleum Geologists, Bulletin*, 72, 1212–1228.

Draganits, E., Braddy, S.J. and Briggs, D.E.G. (2001). A Gondwanan coastal arthropod ichnofauna from the Muth Formation (Lower Devonian, Northern India): Paleoenvironment and tracemaker behavior. *Palaios*, 16, 126–147.

Draper, J.J. (1980). *Rusophycus* (Early Ordovician ichnofossil) from the Mithaka Formation, Georgina Basin. *Journal of Australian Geology and Geophysics*, 5, 57–61.

Driese, S.G. and Foreman, J.L. (1991). Traces and related chemical changes in a Late Ordovician paleosol *Glossifungites* ichnofacies, southern Appalachians, USA. *Ichnos*, 1, 207–219.

Droser, M.L. (1991). Ichnofabric of the Paleozoic *Skolithos* ichnofacies and the nature and distribution of the *Skolithos* piperock. *Palaios*, 6, 316–325.

Droser, M.L. and Bottjer, D.J. (1986). A semiquantitative field classification of ichnofabric. *Journal of Sedimentary Petrology*, 56, 558–559.

Droser, M.L. and Bottjer, D.J. (1989). Ichnofabric of sandstones deposited in high-energy nearshore environments: Measurement and utilization. *Palaios*, 4, 598–604.

Droser, M.L. and Bottjer, D.J. (1993). Trends and patterns of Phanerozoic ichnofabrics. *Annual Reviews of Earth and Planetary Sciences*, 21, 205–225.

Droser, M.L. and Finnegan, S. (2003). The Ordovician radiation: A follow-up to the Cambrian explosion. *Integrative and Comparative Biology*, 43, 178–184.

Droser, M.L. and Li, X. (2001). The Cambrian radiation and the diversification of sedimentary fabrics. In *The Ecology of the Cambrian Radiation*, ed. A.Y. Zhuravlev and R. Riding, New York: Columbia University Press, pp. 137–164.

Droser, M.L., Bottjer, D.J. and Sheehan, P.M. (1997). Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life. *Geology*, 25, 167–170.

Droser, M.L., Jensen, S., Gehling, J.G., Myrow, P.M. and Narbonne, G.M. (2002). Lowermost Cambrian ichnofabrics from the Chapel Island Formation, Newfoundland: Implications for Cambrian substrates. *Palaios*, 17, 3–15.

Droser, M.L., Jensen, S. and Gehling, J.G. (2004). Development of early Palaeozoic ichnofabrics: evidence from shallow marine siliciclastics. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, *ed.* D. McIlroy, *Geological Society Special Publication*, 228, 383–396.

Droser, M.L., Gehling, J.G. and Jensen, S. (2005). Ediacaran Trace Fossils: True and False. In *Evolving Form and Function: Fossils and Development*, ed. D.E.G. Briggs, *A Special Publication of the Peabody Museum of Natural History, Yale University*, pp. 125–138.

Droser, M.L., Gehling, J.G. and Jensen, S. (2006). Assemblage palaeoecology of the Ediacara biota: The unabridged edition? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232, 131–147.

Durand, J. (1985). Le grès armoricain. Sédimentologie: Traces fossiles. Milieux de dépôt. *Memoires et Documents du Centre Armoricain d'estude Structurale des Socles*, 3–6, 1–119.

Duringer, P., Schuster, M., Genise, J.F., Andossa, L., Machaye, H.T., Vignaud, P. and Brunet, M. (2006). The first fossil fungus gardens of Isoptera: Oldest evidence of symbiotic termite fungiculture (Miocene, Chad basin). *Naturwissenschaften*, 93, 610–615.

Duringer, P., Schuster, M., Genise, J.F., Mackaye, H.T., Vignaud, P. and Brunet, M. (2007). New termite trace fossils: Galleries, nests and fungus combs from the Chad basin of Africa (upper Miocene-Lower Pliocene). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 251, 323–353.

Dworschak, P. and Ott, J.A. (1993). Decapod burrows in mangrove-channel and back-reef environments at the Atlantic Barrier Reef, Belize. *Ichnos*, 2, 277–290.

Dzik, J. (2005). Behavioral and anatomical unity of the earliest burrowing animals and the cause of the "Cambrian explosion". *Paleobiology*, 31, 503–521.

Eagar, R.M.C., Baines, J.G., Collinson, J.D., Hardy, P.G., Okolo, S.A. and Pollard, J.E. (1985). Trace fossil assemblages and their occurrence in Silesian (Mid-Carboniferous) deltaic sediments of the Central Pennine Basin, England. In *Biogenic Structures: Their Use in Interpreting Depositional Environments*, ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 99–149.

Eberth, D.A., Berman, D.S., Sumida, S.S. and Hopf, H. (2000). Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, central Germany): the Upland Holy Grail. *Palaios*, 15, 293–313.

Edwards, D., Selden, P.A., Richardson, J.B. and Axe, L. (1995). Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature*, 377, 329–331.

Edwards, D., Yi, W., Bassett, M.G. and Sen, L.C. (2007). The Earliest vascular plants or a later rooting system? *Pinnatiramosus qianensis* from the marine Lower Silurian Xiushan Formation, Guizhou province, China. *Palaios*, 22, 155–165.

Edwards, J.M. and Frey, R.W. (1977). Substrate Characteristics within a Holocene Salt Marsh, Sapelo Island, Georgia. *Senckenbergiana maritima*, 9, 215–259.

Egenhoff, S.O., Weber, B., Lehnret, O. and Maletz, J. (2007). Biostratigraphic precision of the *Cruziana rugosa* group: a study from the Ordovician succession of southern and central Bolivia. *Geological Magazine*, 144, 289–303.

Eisma, D.E. (1998). *Intertidal Deposits: River Mouths, Tidal Flats, and Coastal Lagoons*. Boca Raton, FL: CRC Press.

Ekdale, A.A. (1977). Abyssal trace fossils in worldwide Deep Sea Drilling Project cores. In, *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 163–182.

Ekdale, A.A. (1978). Trace fossils in Leg 42A cores. *Initial Reports Deep Sea Drilling Project*, 42, 821–827.

Ekdale, A.A. (1979). Trace-fossil evidence for deep-water sedimentation in Cretaceous arc-trench gap, South-central Alaska. *American Association of Petroleum Geologists, Bulletin*, 63, 443.

Ekdale, A.A. (1980). Graphoglyptid burrows in modern deep-sea sediment. *Science*, 207, 304–306.

Ekdale, A.A. (1985). Paleoecology of the marine endobenthos. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 50, 63–81.

Ekdale, A.A. (1988). Pitfalls of paleobathymetric interpretations based on trace fossil assemblages. *Palaios*, 3, 464–472.

Ekdale, A.A. (1992). Muckraking and mudslinging: the joys of deposit feeding. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 145–171.

Ekdale, A.A. and Berger, W.H. (1978). Deep-sea ichnofacies: modern organism traces on and in pelagic carbonates of the western equatorial Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 263–278.

Ekdale, A.A. and Bromley, R.G. (1984a). Comparative ichnology of shelf-sea and deep-sea chalk. *Journal of Paleontology*, 58, 323–332.

Ekdale, A.A. and Bromley, R.G. (1984b). Sedimentology and ichnology of the Cretaceous–Tertiary boundary in Denmark; implications for the causes of the terminal Cretaceous extinction. *Journal of Sedimentary Research*, 54, 681–703.

Ekdale, A.A. and Bromley, R.G. (1991). Analysis of composite ichnofabrics: an example in uppermost Cretaceous chalk of Denmark. *Palaios*, 6, 232–249.

Ekdale, A.A. and Bromley, R.G. (2001a). A day and a night in the life of a cleft-foot clam: *Protovirgularia–Lockeia–Lophoctenium. Lethaia*, 34, 119–124.

Ekdale, A.A. and Bromley, R.G. (2001b). Bioerosional innovation in the Early Ordovician of Sweden: A revolutionary adaptation for living in carbonate hardgrounds. *Lethaia*, 34, 1–12.

Ekdale, A.A. and Gibert, J.M. de. (2010). Paleoethologic significance of bioglyphs: fingerprints of the subterraneans. *Palaios*, 25(8), 540–545.

Ekdale, A.A. and Lewis, D.W. (1991a). The New Zealand *Zoophycos* revisited: morphology, ethology, and paleoecology. *Ichnos*, 1, 183–194.

Ekdale, A.A. and Lewis, D.W. (1991b). Trace fossils and paleoenvironmental control of ichnofacies in a late Quaternary gravel and loess fan delta complex, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 81, 253–279.

Ekdale, A.A. and Lewis, D.W. (1993). Sabellariid reefs in Ruby Bay, New Zealand: A modern analogue of *Skolithos* "piperock" that is not produced by burrowing activity. *Palaios*, 8, 614–620.

Ekdale, A.A. and Mason, T.R. (1988). Characteristic trace-fossil associations in oxygen-poor sedimentary environments. *Geology*, 16, 720–723.

Ekdale, A.A. and Picard, M.D. (1985). Trace fossils in a Jurassic eolianite, Entrada Sandstone, Utah, USA. *Society for Sedimentary Geology, Special Publication*, 35, 3–12.

Ekdale, A.A. and Stinnesbeck, W. (1998). Trace fossils in Cretaceous-Tertiary (KT) boundary beds in northeastern Mexico: implications for sedimentation during the KT boundary event. *Palaios*, 13, 593–602.

Ekdale, A.A. and Warme, J.E. (1975). Trace fossil facies in the Jurassic High Atlas Trough, Morocco. *American Association of Petroleum Geologists, Annual Meeting Abstracts*, 21.

Ekdale, A.A., Bromley, R.G. and Pemberton, S.G. (1984). *Ichnology, Trace Fossils in Sedimentology and Stratigraphy*. *Society for Sedimentary Geology Short Course Notes*, 15.

Ekdale, A.A., Brown, F.H. and Feibel, C.S. (1989). Non-marine macroborings in early Pleistocene algal biolithites (Stromatolites) of the Turkana Basin, northern Kenya. *Palaios*, 4, 389–396.

Ekdale, A.A., Benner, J.S., Bromley, R.G. and Gibert, J.M. de (2002). Bioerosion of Lower Ordovician hardgrounds in southern Scandinavia and western North America. *Acta Geologica Hispanica*, 37, 9–13.

Ekdale, A.A., Bromley, R.G., and Loope, D.B. (2007). Ichnofacies of an Ancient Erg: A Climatically Influenced Trace Fossil Association in the Jurassic Navajo Sandstone, Southern Utah, USA. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 562–564.

Eldredge, N. (1970). Observations on burrowing behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites. *American Museum of Natural History, New York, American Museum Novitates*, 2436, 17.

El Khayal, A.A. and Romano, M. (1988). A revision of the upper part of the Saq Formation and Hanadir Shale (lower Ordovician) of Saudi Arabia. *Geological Magazine*, 125, 161–174.

Eliade, M. (1959). *The Sacred and the Profane: The Nature of Religion*. San Diego, CA: Harvest Books.

Elliott, D.K. and Nations, J. D. (1998). Bee burrows in the Late Cretaceous (Late Cenomanian) Dakota Formation, Northeastern Arizona. *Ichnos*, 5, 243–253.

Emig, C.C., Gall, J.-C., Pajaud, D. and Plaziat, J.-C. (1978). Réfexions critiques sur l'écologie et la systématique des lingules actuelles et fossiles. *Géobios*, 11, 573–609.

Encinas, A., Buatois, L.A. and Finger, K.L. (2008). Paleoecological and paleoenvironmental implications of a high-density *Chondrites* association in slope deposits of the Neogene Santo Domingo Formation, Valdivia, south-central Chile. *Ameghiniana*, 45, 225–231.

Engel, M.S. (2001). A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 1–192.

English, A.M. and Babcock, L.E. (2007). Feeding behaviour of two Ordovician trilobites inferred from trace fossils and non-biomineralised anatomy, Ohio and Kentucky, USA. *Memoirs of the Association of Australasian Palaeontologists*, 34, 537–544.

Ernst, G. and Gierlowski-Kordesch, E. (1989). Epeiric sea deposits and graphoglyptid burrows in upper Cretaceous of Tanzania. *International Geological Congress Abstracts*, 28, 1460.

Erwin, D.H. (2001). Metazoan origins and early evolution. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Publishing Company, pp. 25–31.

Erwin, D.H. (2006). *Extinction*. Princeton, NJ: Princeton University Press.

Erwin, D.H. (2007). Disparity: morphological pattern and developmental context. *Paleontology*, 50, 57–73.

Ettema, C.H. and Wardle, D.A. (2002). Spatial soil ecology. *Trends in Ecology and Evolution*, 17, 177–183.

Ewing, M. and Davis, R.A. (1967). Lebensspuren photographed on the ocean floor. In *Deep Sea Photography*, ed. J.B. Hersey, Baltimore, MD: The John Hopkins University Press, pp. 259–294.

Eyles, N., Vossler, S.M. and Lagoe, M.B. (1992). Ichnology of a glacially-influenced continental shelf and slope; the late Cenozoic Gulf of Alaska (Yakataga Formation). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 94, 193–221.

Falcon-Lang, H.J., Benton, M.J. and Stimson, M. (2007). Ecology of earliest reptiles inferred from basal Pennsylvanian trackways. *Journal of the Geological Society*, 164, 1113–1118.

Falkingham, P.L., Margetts, L., Smith, I.M. and Manning, P.L. (2009). Reinterpretation of palmate and semi-palmate (webbed) fossil tracks: Insights from finite element modeling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 271, 69–76.

Farlow, J.O. (1992). Sauropod Tracks and Trackmakers: Integrating the Ichnological and Skeletal Records. Logrono, Spain. *Zubia, Instituto de Estudios Riojanos*, 10, 89–138.

Farlow, J.O. and Galton, P.M. (2003). Dinosaur trackways of Dinosaur State Park, Rocky Hill, Connecticut. In *The Great Rift Valleys of Pangea in Eastern North America*, Vol. 2, ed. P.M. Letourneau and P.E. Olsen, New York: Columbia University Press, pp. 248–263.

Farrow, G.E. (1971). Back-reef and lagoonal environments of Aldabra Atoll distinguished by their crustacean burrows. *Zoological Society of London, Symposia*, 28, 455–500.

Farrow. G.E., Syvitski, J.P.M. and Tunnicliffe, V. (1983). Suspended particulate loading on the macrobenthos in a highly turbid fjord: Knight Inlet, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 273–288.

Fauchald, K. and Jumars, P. (1979). The diet of worms: a study of polychaetes feeding guilds. *Oceanography and Marine Biology: An Annual Review*, 17, 193–284.

Faugères, J.-C. and Stow, D.A.V. (2008) contourite drifts: Nature, Evolution and Controls. In *Contourites*, ed. M. Rebesco and A. Carmerlenghi, Developments in Sedimentology, Elsevier, 60, 259–288.

Fayers, S.R., Trewin, N.H. and Morrissey, L. (2010). A large arthropod from the Lower Old Red Sandstone (Early Devonian) of Tredomen Quarry, South Wales. *Palaeontology*, 53, 627–643.

Feder, H.M. and Keiser, G.E. (1980). Intertidal biology. In *Port Valdez, Alaska: Environmental studies 1976–1979*, ed. J.M. Colonell, *Institute of Marine Science, University of Alaska, Occasional Publication*, 5, 143–233.

Feder, H.M. and Matheke, G.E.M. (1980). Subtidal benthos. In: *Port Valdez, Alaska: Environmental Studies 1976–1979*, ed. J.M. Colonell and H. Stockholm, Fairbanks, Alaska: Institute of Marine Science, University of Alaska, pp. 235–318.

Fedonkin, M.A. (1985). Paleoichnology of Vendian Metazoa. In *The Vendian System 1: Historic-Geological and Palaeontological Basis*, ed. B.S. Sokolov and A.B. Ivanovskiy, Moscow: Nauka, pp. 112–116.

Fedonkin, M.A. (2003). Origin of the Metazoa in the light of Proterozoic fossil records. *Paleontological Research*, 7, 9–41.

Fedonkin, M.A. and Waggoner, B.M. (1997). The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature*, 388, 868–871.

Fedonkin, M.A., Simonetta, A. and Ivantsov, A.Y. (2007). New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): Palaeoecological and evolutionary implications. *Geological Society of London Special Publication*, 286, 157–179.

Fell, H.B. (1966). The ecology of ophiuroids. In *Physiology of Echinodermata*, ed. R.A. Boolootian, New York: Interscience, pp. 129–143.

Ferguson, R.L., Thayer, G.W. and Rice, T.R. (1981). Marine primary producers. In *Functional Adaptations of Marine Organisms*, ed. F.J. Vernberg and W.B. Vernberg, New York: Academic Press, pp. 9–69.

Fernandes, A.C.S., Carvalho, I.S. and Netto, R.G. (1990). Icnofósseis de invertebrados da Formacao Botucatu, Sao Paulo (Brasil). *Anais da Academia brasileira de Ciencias*, 62, 45–49.

Fey, M. (2010). *Soils of South Africa*. Singapore: Cambridge University Press.

Fillion, D. and Pickerill, R.K. (1990). Ichnology of the Lower Ordovician Bell Island and Wabana Groups of eastern Newfoundland. *Palaeontographica Canadiana*, 7, 1–119.

Fillion, D., Pickerill, R.K. and Harland, T.L. (1990). Influence de la diagènese sur la production, la préservation et l'échantillonnage des ichnofossiles au sein des séries carbonatées: L'exemple du bassin intracratonique ordovicien du lac-St-Jean et de Chicoutimi (Québec). *Geobios*, 23, 485–511.

Fitzgerald, P.G. and Barret, P.J. (1986). *Skolithos* in a Permian braided river deposit, southern Victoria Land, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52, 237–247.

Flint, S.S. and Hodgson, D.M. (2005). Submarine slope systems: processes and products. *Geological Society of London, Special Publication*, 244, 1–6.

Föllmi, K.B. and Grimm, K.A. (1990). Doomed pioneers: gravity-flow deposition and bioturbation in marine oxygen-deficient environments. *Geology*, 18, 1069–1072.

Foote, M. (1993). Contributions of individual taxa to overall morphological disparity. *Paleobiology*, 19, 403–419.

Foote, M. (1997). The evolution of morphological diversity. *Annual Review of Ecology and Systematics*, 28, 129–152.

Fordyce, R.W. (1980). Trace fossils from Ohika Formation (Pororari Group, Lower Cretaceous), lower Buller Gorge, Buller, New Zealand. *New Zealand Journal of Geology and Geophysics*, 23, 121–124.

Fornós, J.J., Bromley, R.G., Clemmensen, L.B. and Rodriguez-Perea, A. (2002). Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic islands, western Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 180, 277–313.

Forster C.A., Arcucci A.B., Marsicano C.A., Abdala, F. and May C.L. (1995). New vertebrate material from the Los Rastros Formation (Middle Triassic), La Rioja Province, northwestern Argentina. *Journal of Vertebrate Paleontolology*, 15, 29A.

Fortes, M.D. (2002). Natural biological processes and controls. In *Muddy Coasts of the World: Processes, Deposits and Function*, ed. T. Healy, Y. Wang and J.-A. Healy, *Proceedings in Marine Science*, 4, 229–244.

Fortey, R.A. and Owens, R.M. (1999). Feeding habits in trilobites. *Palaeontology*, 42, 429–465.

Fortey, R.A. and Seilacher, A. (1997). The trace fossil *Cruziana semiplicata* and the trilobite that made it. *Lethaia*, 30, 105–112.

Fortey, R.A., Briggs, D.E.G. and Wills, M.A. (1996). The Cambrian evolutionary 'explosion': Decoupling cladogenesis from morphological disparity. *Biological Journal of the Linnean Society*, 57, 13–33.

Foster, J. and Lockley, M.G. (2006). Preservation and abundance patterns in the ichnological record of the Morrison Formation (Upper Jurassic, North America). In *Paleontology and Geology of the Upper Jurassic Morrison Formation*, ed. J.R. Foster and S.G. Lucas, *New Mexico Museum of Natural History and Science Bulletin*, 36, 203–216.

Fraaye, R.H.B. and Werver, O.P. (1990). Trace fossils and their environmental significance in Dinantian carbonates of Belgium. *Palaöntologische Zeitschrift*, 64, 367–377.

Fraiser, M.L. and D.J. Bottjer. (2009). Opportunistic behaviour of invertebrate marine tracemakers during the Early Triassic aftermath of the end-Permian mass extinction. *Australian Journal of Earth Sciences*, 56, 841–857.

Francois, F., Poggiale, J-C., Durbec, J-P. and Stora, G. (1997). A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheoretica*, 45, 295–319.

Frey, R.W. (1970). Trace fossils of Fort Hays Limestone Member of Niobrara Chalk (Upper Cretaceous), west-central Kansas. *University of Kansas Paleontological Contributions*, 53, 1–41.

Frey, R.W. (1971). Ichnology: the study of fossil and recent lebenspurren, In *Trace Fossils, A Field Guide to Selected Localities in Pennsylvanian, Permian, Cretaceous and Tertiary Rocks of Texas,* *and Related Papers*, ed. B.F. Perkins, *Louisiana State University School of Geoscience, Miscellaneous Publication*, 71, 91–125.

Frey, R.W. (1972). Paleoecology and depositional environment of Fort Hays Limestone Member, Niobrara Chalk (Upper Cretaceous), west-central Kansas. *University of Kansas Paleontological Contributions*, 58, 1–72.

Frey, R.W. (1973). Concepts in the study of biogenic sedimentary structures. *Journal of Sedimentary Petrology*, 43, 6–19.

Frey, R.W. (1975). The realm of ichnology, its strengths and limitations. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 13–38.

Frey, R.W. (1990). Trace fossils and hummocky cross-stratification, Upper Cretaceous of Utah. *Palaios*, 5, 203–218.

Frey, R. W and Bromley, R.G. (1985). Ichnology of American chalks: the Selma Group (Upper Cretaceous), western Alabama. *Canadian Journal of Earth Sciences*, 22, 801–828.

Frey, R.W. and Cowles, J. (1969). New observations on *Tisoa*, a trace fossil from the Lincoln Creek Formation (Mid-Tertiary) of Washington. *The Compass*, 47, 10–22.

Frey, R.W. and Goldring, R. (1992). Marine event beds and recolonization surfaces as revealed by trace fossil analysis. *Geological Magazine*, 129, 325–335.

Frey, R.W. and Pemberton, S.G. (1984). Trace fossils *Facies Models*. In *Facies Models*, ed. R.G. Walker, *Geoscience Canada Reprint Series*, 189–207.

Frey, R.W. and Pemberton, S.G. (1985). Biogenic structures in outcrops and cores; I, Approaches to ichnology. *Bulletin of Canadian Petroleum Geology*, 33, 72–115.

Frey, R.W. and Pemberton, S.G. (1986). Vertebrate Lebensspuren in Intertidal and Supratidal Environments, Holocene Barrier Islands, Georgia. *Senckenbergiana Maritima*, 18, 45–95.

Frey, R.W. and Pemberton, S.G. (1987). The *Psilonichnus* ichnocoenose, and its relationship to adjacent marine and nonmarine ichnocoenoses along the Georgia coast. *Bulletin of Canadian Petroleum Geology*, 35, 333– 357.

Frey, R.W. and Pemberton, S.G. (1991). Or is it bioturbate texture? *Ichnos*, 1, 327–329.

Frey, R.W. and Seilacher, A. (1980). Uniformity in marine invertebrate ichnology. *Lethaia*, 13, 183–207.

Frey, R.W. and Wheatcroft, R.A. (1989). Organism–substrate relations and their impact on sedimentary petrology. *Journal of Geological Education*, 37, 261–279.

Frey, R.W., Curran, H.A. and Pemberton, S.G. (1984a). Tracemaking activities of crabs and their environmental significance; the ichnogenus *Psilonichnus*. *Journal of Paleontology*, 58, 333–350.

Frey, R.W., Pemberton, S.G. and Fagerstrom, J.A. (1984b). Morphological, ethological and environmental significance of the ichnogenera *Scoyenia* and *Ancorichnus*. *Journal of Paleontology*, 58, 511–528.

Frey, R.W., Hong, J.S., Howard, J.D., Park, B.K. and Han, S.J. (1987a). Zonation of benthos on a macrotidal flat, Inchon, Korea. *Senckenbergiana Maritima*, 19, 295–329.

Frey, R.W., Howard, J.D. and Hong, J.S. (1987b). Prevalent Lebensspuren on a modern macrotidal flat, Inchon, Korea: ethological and environmental significance. *Palaios*, 2, 571–593.

Frey, R.W., Pemberton, S.G. and Saunders, T.D.A. (1990). Ichnofacies and bathymetry: A passive relationship. *Journal of Paleontology*, 64, 155–158.

Fu, S. (1991). Funktion, Verhalten und Einteilung fucoider und lophocteniider Lebensspuren. *Courier Forschung-Institut Senckenberg*, 135, 1–79.

Fu, S. and Werner, F. (1994). Distribution and composition of biogenic structures on the Iceland–Faeroe Ridge: relation to different environments. *Palaios*, 9, 92–101.

Fu, S. and Werner, F. (1995). Is *Zoophycos* a feeding trace? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 195, 37–47.

Fuchs, T. (1895). Studien über Fucoiden und Hyeroglyphen. *Akademie der Wissenschaften zu Wien, mathematisch-naturwissenschaftliche Klasse, Denkschriften*, 62, 369–448.

Fuchs, T. (1909). Über einiger neure Arbeiten zur Aufklärung der Natur der Alectoruriden. *Mitteilungen der Geologischen Gesellschaft in Wien*, 2, 335–350.

Fuglewicz, R., Ptaszyliski, T. and Rdzanek, K. (1990). Lower Triassic footprints from the Swigtokrzyskie (Holy Cross) Mountains, Poland. *Acta Palaeontologica Polonica*, 35, 109–164.

Furnes, H., Banerjee, N.R., Muehlenbachs, K., Staudigel, H. and de Wit, M. (2004). Early life recorded in Archean pillow lavas. *Science*, 304, 578–581.

Fürsich, F.T. (1972). *Thalassinoides* and the origin of nodular limestone in the Corallian beds (Upper Jurassic) of southern England. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 3, 136–156.

Fürsich, F.T. (1973). A revision of the trace fossils *Spongeliomorpha, Ophiomorpha* and *Thalassinoides*. *Neues Jahrbuch für Geologie, und Paläontologie, Monatshefte*, 1973, 719–735.

Fürsich, F.T. (1974). Ichnogenus *Rhizocorallium*. *Palaontologische Zeitschrift*, 48, 16–28.

Fürsich, F.T. (1981). Invertebrate trace fossils from the Upper Jurassic of Portugal. *Comunicações Servicio Geologico de Portugal*, 67, 153–168.

Fürsich, F.T. 1998. Environmental distribution of trace fossils in the Jurassic of Kachch (western India). *Facies*, 39, 46–53.

Fürsich, F.T. and Mayr, H. (1981). Non–marine *Rhizocorallium* (trace fossil) from the Upper Freshwater Molasse (Upper Miocene) of southern Germany. *Neues Jahrbuch für Geologie und Palaontologie, Monashefte*, 321–333.

Fürsich, F.T., Taheri, J. and Wilmsen, M. (2007). New occurrences of the trace fossil *Paleodictyon* in shallow marine environments: Examples from the Triassic-Jurassic of Iran. *Palaios*, 22, 424–432.

Gage, J.D. and Tyler, P.A. (1991). *Deep-sea Biology*. Cambridge, UK: Cambridge University Press.

Gaigalas A. and Uchman, A. (2004). Trace fossils form the Upper Pleistocene varved clays S of Kaunas, Lithuania. *Geologija*, 45, 16–26.

Gaillard, C. (1988). Bioturbation récente au large de la Nouvelle-Calédonie. Premiers résultats de la campagne Biocal. *Oceanologica Acta*, 11, 389–399.

Gaillard, C. (1991). Recent organism traces and ichnofacies on the deep-sea floor off New Caledonia, southwestern Pacific. *Palaios*, 6, 302–315.

Gaillard, C. and Olivero, D. (1993). Interprétation paléoécologique nouvelle de *Zoophycos* Massalongo, 1855. *Comptes Rendus de l'Académie des Sciences de Paris*, 316, 823–830.

Gaillard, P. B, Gall, J. C, Gruet, Y., Barale, G., Bourseau, J. P, Buffetaut, E. and Wenz, S. (1994). Ichnofabric from the Upper Jurassic Lithographic Limestone of Cerin, Southeast France. *Palaeontology*, 37, 285–304.

Galloway, W.E. (1975). Process framework for describing the morphologic and stratigraphic evolution of deltaic depositional systems. In *Deltas, Models for Exploration*, ed. M.L. Broussard, Houston, TX: Houston Geological Society, pp. 87–89.

Gámez Vintaned, J.A., Liñan, E., Mayoral, E., Dies, M.E., Gozalo, R. and Muñiz, F. (2006). Trace and soft body fossils from the Pedroche Formation (Ovetian, Lower Cambrian of the Sierra de Córdoba, S Spain) and their relation to the Pedroche event. *Geobios*, 39, 443–468.

Gand, G. (1975). Sur quelques empreintes de pas de vertbrs rcoltes dans le Stphanien moyen de Montceau-les-Mines (Sane-et-Loire-France). *Bulletin de la Socit d'Historie Naturelle d'Autun*, 74, 9–31.

Gand, G., Kerp, H., Parsons, C. and Martínez García, E. (1997). Palaeoenvironmental and stratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Peña Sagra, Cantabrian Mountains, Spain). *Geobios*, 30, 295–318.

Gandini, R., Netto, R.G. and Souza, P.A. (2007). Paleoicnologia e a Palinologia dos ritmitos do Grupo Itararé na pedreira de Águas Claras (Santa Catarina, Brasil). *Gaea*, 3, 47–59.

Gangloff, R.A., May, K.C. and Storer, J.E. (2004). An early Late Cretaceous dinosaur tracksite in central Yukon Territory, Canada. *Ichnos*, 11, 299–309.

García-Ramos, J.C. and Valenzuela, M. (1979). Estudio e interpretación de la icnofauna (vertebrados e invertebrados) en el Jurásico de la costa asturiana. *Cuadernos Geológicos*, 10, 13–22.

Garrison, J.R. Jr. and van den Bergh, T.C.V. (2004). The high-resolution depositional sequence stratigraphy of the Upper Ferron Sandstone, Last Chance Delta: An application of coal zone stratigraphy. In *Regional to Wellbore Analog for Fluvial–Deltaic Reservoir Modeling: The Ferron Sandstone of Utah*, ed. T.C. Chidsey Jr., R.D. Adams and T.H. Morris, *American Association of Petroleum Geologists Studies in Geology*, 50, 125–192.

Gehling, J.G. (1999). Microbial mats in terminal Proterozoic siliciclastic Ediacaran masks. *Palaios*, 14, 40–57.

Gehling, J. (2002). *Terminal Proterozoic–Cambrian of the Flinders Ranges, South Australia. 1st International Palaeontological Congress, Field Trip Pre-3 Guide Book*.

Gehling, J.G., Droser, M., Jensen, S. and Runnegar, B. (1998). Similar cycles – different strokes: Closing a taphonomic window across the Precambrian-Cambrian boundary. *Inaugural Sprigg Symposium: The Ediacaran Revolution, Abstracts & Programme*, 20–21.

Gehling, J.G., Narbonne, G.M. and Anderson, M. (2000). The first named Ediacaran body fossil, *Aspidella terranovica*. *Palaeontology*, 43, 427–456.

Gehling, J.G., Jensen, S., Droser, M.L., Myrow, P.M. and Narbonne, G.M. (2001). Burrowing below the basal Cambrian GSSP, Fortune Head, Newfoundland. *Geological Magazine*, 138, 213–218.

Gehling, J.G., Droser, M., Jensen, S. and Runnegar, B. (2005). Ediacara organisms: relating form to function. In *Evolving Form and Function: Fossils and Development. A Special Publication of the Peabody Museum of Natural History*, ed. D.E.G. Briggs, New Haven, CT: Yale University Press, pp. 43–66.

Genise, J.F. (1995). Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos*, 3, 287–299.

Genise, J.F. (1997). A fossil termite nest from the Marplatan stage (Late Pliocene) of Argentina: paleoclimatic indicator. *Palaeogeography, Paleoclimatology, Palaeoecology*, 136, 139–144.

Genise, J.F. (1999). Insect paleoichnology. *Revista de la Sociedad Entomologica Argentina*, 58, 104–116.

Genise, J.F. (2000). The ichnofamily Celliformidae for *Celliforma* and allied ichnogenera. *Ichnos*, 7, 267–284.

Genise, J.F. (2004). Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, ants and termites. In *The application of ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 419–453.

Genise, J.F. and Bown, T.M. (1990). The constructor of the ichnofossil *Chubutolithes*. *Journal of Paleontology*, 64, 482–483.

Genise, J.F. and Bown, T.M. (1994a). New Miocene scarabeid and hymenopterous nests and Early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos*, 3, 107–117.

Genise, J.F. and Bown, T. M. (1994b). New trace fossils of termites (Insecta: Isoptera) from the Late Eocene–Early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. *Ichnos*, 3, 155–183.

Genise, J.F. and Cladera, G. (2004). *Chubutolithes gaimanensis* and other wasp trace fossils: breaking through the taphonomic barrier. *Journal of the Kansas Entomological Society*, 77, 626–638.

Genise, J.F. and Edwards, N. (2003). Ichnotaxonomy, Origin, and palaeoenvironment of Quaternary insect cells from Fuerteventura, Canary Islands, Spain. *Journal of the Kansas Entomological Society*, 76, 320–327.

Genise, J.F. and Hazeldine, P.L. (1995). A new insect trace fossil in Jurassic wood from Patagonia, Argentina. *Ichnos*, 4, 1–5.

Genise, J.F. and Hazeldine, P.L. (1998). 3D-reconstruction of insect trace fossils: *Ellipsoideichnus meyeri* Roselli. *Ichnos*, 5, 167–175.

Genise, J.F. and Laza, J.H. (1998). *Monesichnus ameghinoi* Roselli: A complex insect trace fossil produced by two distinct trace makers. *Ichnos*, 5, 213–223.

Genise, J.F. and Verde, M. (2000). *Corimbatichnus fernandezi*: A cluster of fossil bee cells from the Late Cretaceous-Early Tertiary of Uruguay. *Ichnos*, 7, 115–125.

Genise, J.F., Mángano, M.G., Buatois, L.A., Laza, J. and Verde, M. (2000). Insect trace fossil associations in paleosols: The *Coprinisphaera* ichnofacies. *Palaios*, 15, 33–48.

Genise, J.F., Sciutto, J.C., Laza, J.H., Gonzalez, M.G. and Bellosi, E.S. (2002). Fossil bee nests, coleopteran pupal chambers and tuffaceous Paleosol from the Late Cretaceous Laguna Palacios Formation, central Patagonia (Argentina). *Paleogeography, Paleoclimatology, Paleoecology*, 177, 215–235.

Genise, J.F., Mángano, M.G. and Buatois, L.A. (2004a). Ichnology moving out of the water: a model for terrestrial ichnofacies. In *First International Congress on Ichnology, Trelew, Argentina*, ed. L.A. Buatois and M.G. Mángano, *Museo Paleontologico Egidio Feruglio, Abstract Book*, 38.

Genise, J.F., Bellosi, E.S. and Gonzalez, M.G. (2004b). An approach to the description and interpretation of ichnofabrics in palaeosols. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 355–382.

Genise, J.F., Melchor, R.N., Bellosi, E.S., Gonzalez, M.G. and Krause, M. (2007). New insect pupation chambers (Pupichnia) from the Upper Cretaceous of Patagonia, Argentina. *Cretaceous Research*, 28, 545–559.

Genise, J.F., Bedatou, E. and Melchor, R.N. (2008). Terrestrial crustacean breeding trace fossils from the Cretaceous of Patagonia (Argentina): palaeobiological and evolutionary significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 264, 128–139.

Genise J.F., Melchor R.N., Archangelsky M., Bala L.O., Straneck R. and de Valais S. (2009). Application of neoichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: the Late Triassic–Early Jurassic? Santo Domingo Formation, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 143–161.

Genise, J.F., Melchor R.N., Bellosi, E.S. and Verde. (2010a). Invertebrate and Vertebrate Trace Fossils from Continental Carbonates. In *Carbonates in Continental Settings: Facies, Environments, and Processes*, ed. A.M. Alonso-Zarza and L. Tanner, *Developments in Sedimentology*, 61, 319–369.

Genise, J.F., Alonso-Zarza, A.M., Krause, J.M., Sánchez, M.V., Sarzetti, L., Farina, J.F., González, M.G., Cosarinsky, M. and Bellosi, E.S. (2010b). Rhizolith balls from the Lower Cretaceous of Patagonia: Just roots or the oldest evidence of insect agriculture? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 287, 128–142.

Gérard, J. and Bromley, R. (2008) *Ichnofabrics in Clastic Sediments. Applications to Sedimentological Core Studies. A Practical Guide*. Madrid: J. Gérard.

Gerdes, G., Krumbein, W.E. and Reineck, H.E. (1985). The depositional record of sandy, versicolored tidal flats (Mellum Island, southern North Sea). *Journal of Sedimentary Petrology*, 55, 265–278.

Gerdes, G., Krumbein, W.E., and Reineck, H.E. (1994). Microbial mats as architects of sedimentary surface structures. In *Biostabilization of Sediments*, ed. W.E. Krumbein, D.M. Peterson and L.J. Stal, Oldenburg, Germany: BIS, pp. 165–182.

Gerdes, G., Klenke, T. and Noffke, N. (2000). Microbial signatures in peritidal siliciclastic sediments: A catalogue. *Sedimentology*, 47, 279–308.

Getty, P.R. (2005). Excavated and *in situ* dinosaur footprints from the Murray Quarry (Early Jurassic East Berlin Formation), Holyoke, Massachusetts, USA. *Ichnos*, 12, 163–178.

Getty, P.R. and Hagadorn, J.W. (2008). Reinterpretation of *Climactichnites* Logan 1860 to include subsurface burrows, and erection of *Musculopodus* for resting traces of the trailmaker. *Journal of Paleontology*, 82, 1161–1172.

Getty, P.R. and Hagadorn, J.W. (2009). Palaeobiology of the *Climactichnites* tracemaker. *Palaeontology*, 52, 753–778.

Gevers, T.W. and Twomey, A. (1982). Trace fossils and their environment in Devonian (Silurian?) Lower Beacon strata in the Asgaard Range, Victoria Land, Antarctica. In *Antarctic Geoscience*, ed. C. Craddock, J.K. Loveless, T.L. Vierima and K.A. Crawford, Madison, WI: University of Wisconsin Press, pp. 639–647.

Gevers, T.W., Frakes, L.A., Edwards, L.N. and Marzolff, J.E. (1971). Trace fossils in the Lower Beacon sediments (Devonian), Darwin Mountains, southern Victoria Land, Antarctica. *Journal of Paleontology*, 45, 81–94.

Geyer, G. and Uchman, A. (1995). Ichnofossil assemblages from the Nama Group (Neoproterozoic–Lower Cambrian) in Namibia and the Proterozoic–Cambrian boundary problem revisited. *Beringeria Special Issue*, 2, 175–202.

Ghare, M.A. and Badve, R.M. (1984). Observations on ichnoactivity from the intertidal environment, West Coast of Raigad District, Maharashtra. *Biovigyanam*, 10, 173–178.

Ghibaudo, G., Grandesso, P., Massari, F. and Uchman, A. (1996). Use of trace fossils in delineating sequence stratigraphic surfaces (Tertiary Venetian Basin, northeastern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 120, 261–279.

Gibbard, P.L. (1977). Fossil tracks from varved sediments near Lammi, south Finland. *Bulletin Geological Society of Finland*, 49, 53–57.

Gibbard, P.L. and Dreimanis, A. (1978). Trace fossils from late Pleistocene glacial lake sediments in southwestern Ontario, Canada. *Canadian Journal of Earth Sciences*, 15, 1967–1976.

Gibbard, P.L. and Stuart, A.J. (1974). Trace fossils from proglacial lake sediments. *Boreas*, 3, 69–74.

Gibert, J.M. de (1996). A new decapod burrow system from the NW Mediterranean Pliocene. *Revista Española de Paleontología*, 11, 251–254.

Gibert, J.M. de, and Ekdale, A.A. (1999). Trace fossil assemblages reflecting stressed environments in the Middle Jurassic Carmel Seaway of central Utah. *Journal of Paleontology*, 73, 711–720.

Gibert, J.M. de and Martinell, J. (1992). Principales estructuras biogénicas en el Plioceno marino de la Cuenca del Baix Llobregat (Catalunya). *Geogaceta*, 12, 104–106.

Gibert, J.M. de and Martinell, J. (1993). Controles paleoambientales sobre la distribución de las paleoicnocenosis en el estuario plioceno del Baix Llobregat (Barcelona, Catalunya). *Revista Española de Paleontología*, 8, 140–146.

Gibert, J.M. de and Martinell, J. (1996). Trace fossil assemblages and their palaeoenvironmental significance in the Pliocene marine deposits of the Baix Ebre (Catalonia, NE Spain). *Géologie Méditerranéenne*, 23, 211–225.

Gibert, J.M. de and Sáez A. (2009). Paleohydrological significance of trace fossil distribution in Oligocene fluvial-fan-to-lacustrine systems of the Ebro Basin, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 162–175.

Gibert, J.M. de, Martinell, J. and Domenech, R. (1996). El Mioceno marino entre las playas de L'Arrabassada y El Miracle (Tarragona): aspectos paleontológicos e implicaciones sedimentológicas. *Acta Geologica Hispanica*, 29, 133–148.

Gibert, J.M. de, Martinell, J. and Domènech, R. (1998). *Entobia* ichnofacies in fossil rocky shores, Lower Pliocene, Northwestern Mediterranean. *Palaios*, 13, 476–487.

Gibert, J.M. de, Buatois, L.A., Fregenal-Martinez, M.A., Mángano, M.G., Ortega, F., Poyato-Ariza, F.J. and Wenz, S. (1999). The fish trace fossil *Undichna* from the Cretaceous of Spain: Taphonomic and palaeoenvironmental implications for the ichnogenus. *Palaeontology*, 42, 409–427.

Gibert, J.M. de, Fregenal-Martínez, M.A., Buatois, L.A and Mángano, M.G. (2000). Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. *Paleogeography, Paleoclimatology, Palaeoecology*, 156, 89–101.

Gibert, J.M. de, Arbués, P., Puig, M., and Marzo, M. (2001a). Ichnological signatures of turbidite channels from the Eocene Ainsa slope complex (Spanish Pyrenees). *American Association of Petroleum Geologists Annual Meeting 2001: An Energy Odyssey, Expanded Abstracts*, 71.

Gibert, J.M. de, Arbués, P., Puig, M., and Marzo, M. (2001b). Implicaciones sedimentológicas de *Diplocraterion* en canales turbidíticos de talud (Eoceno, Ainsa, NE de España). *IV Reunión de icnología y segunda reunion de icnología del Mercosur, Tucuman, Resumenes*, 48.

Gibert, J.M. de, Domènech, R. and Martinell, J. (2004). An ethological framework for animal bioerosion trace fossils upon mineral substrates with a proposal for a new class, Fixichnia. *Lethaia*, 37, 429–437.

Gibert, J.M. de, Domènech, R. and Martinell, J. (2007). Bioerosion in shell beds from the Pliocene Roussillon Basin, France: implications for the (macro) bioerosion ichnofacies model. *Acta Palaeontologica Polonica*, 52, 783–798.

Gierliński, G., Pieńkowski, G. and Niedźwiecki, G. (2004). Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. *Ichnos*, 11, 195–213.

Gierlowski-Kordesch, E. (1991). Ichnology of an ephemeral lacustrine/alluvial plain system: Jurassic East Berlin formation, Hartford Basin, USA. *Ichnos*, 1, 221–232.

Gierlowski-Kordesch, E. and Ernst, F. (1987). A flysch trace fossil assemblage from the Upper Cretaceous shelf of Tanzania. In *Current Research in African Earth Sciences*, ed. G. Mathies and H. Schandelmeir, *14th Coloquium on African Geology (Berlin), Extended Abstracts*, 217–221.

Gierlowski-Kordesch, E. and Park, L.E. (2004). Comparing species diversity in the modern and fossil record of lakes. *The Journal of Geology*, 112, 703–717.

Gili, J.M. and Coma, R. (1998). Benthic suspension Feeders: Their paramount role in littoral marine; food webs. *Trends in Ecology and Evolution*, 13, 316–321.

Giller, P.S. and Malmquist, B. (1998). *The Biology of Streams and Rivers.* Oxford, UK: Oxford University Press.

Gilmore, C.W. (1926). Fossil footprints from the Grand Canyon. *Smithsonian Miscellanea Collection*, 77, 1–41.

Gilmore, C.W. (1927). Fossil footprints from the Grand Canyon. *Smithsonian Miscellanea Collection*, 80, 1–78.

Ginsburg, R.N. (1953). Intertidal erosion on the Florida Keys. *Bulletin of Marine Science*, *Gulf Caribbean*, 3, 1–14.

Gingras, M.K. (2008). Revisiting Willapa Bay: facies templates for estuary deposits modelled from Pleistocene outcrops. *Back to Exploration, CSPG CSEG CWLS Convention*, 562–563.

Gingras, M.K. and Pemberton, S.G. (2000). A field method for determining the firmness of colonized sediment subtrates. *Journal of Sedimentary Research*, 70, 1341–1344.

Gingras, M.K., MacEachern, J.A. and Pemberton, S.G. (1998). A comparative analysis of the ichnology of wave- and river-dominated allomembers of the Upper Cretaceous Dunvegan Formation. *Bulletin of Canadian Petroleum Geology*, 46, 51–73.

Gingras, M.K., Pemberton, S.G., Mendoza, C.A. and Henk, F. (1999). Assessing the anisotropic permeability of *Glossifungites surfaces. Petroleum Geoscience*, 5, 349–357.

Gingras, M.K., Pemberton, S.G., Saunders, T.D.A. and Clifton, H.E. (1999). The ichnology of Modern and Pleistocene brackish-water deposits at Willapa Bay, Washington: Variability in estuarine settings. *Palaios*, 14, 352–374.

Gingras, M.K., Pemberton, S.G. and Saunders, T.D.A. (2000). Firmness Profiles associated with tidal creek deposits: the temporal significance of *Glossifungites* assemblages. *Journal of Sedimentary Research*, 70, 1017–1025.

Gingras, M.K., Pemberton, S.G., Saunders, T.D.A. (2001). Bathymetry, sediment texture, and substrate cohesiveness; their impact on *Glossifungites* Ichnofacies at Willapa Bay, Washington. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 169, 1–21.

Gingras, M.K., MacMillan, B., Balcom, B.J. and Saunders, T. (2002). Using magnetic resonance imaging and petrographic techniques to understand the textural attributes and porosity distribution in *Macaronichnus*-burrowed sandstone. *Journal of Sedimentary Research*, 72, 552–558.

Gingras, M.K., MacEachern, J.A., and Pickerill, R.K. (2004). Modern Perspectives on the *Teredolites* Ichnofacies: Observations from Willapa bay, Washington. *Palaios*, 19, 79–88.

Gingras, M.K., Dashtgard, S.E. and Pemberton, S.G. (2006). Latitudinal (climatic) controls on neoichnological assemblages of modern marginal-marine depositional environments. *American Association of Petroleum Geologists 2006 Annual Convention (Houston)*, Abstract, 38.

Gingras, M.K., Lalonde, S.V., Amskold, L. and Konhauser, K.O. (2007). Wintering chironomids mine oxygen. *Palaios*, 22, 433–438.

Gingras, M.K., Dashtgard, S.E., MacEachern, J.A. and Pemberton, S.G. (2008a). Biology of shallow marine ichnology: a modern perspective. *Aquatic Biology*, 2, 255–268.

Gingras, M.K., Pemberton, S.G., Dashtgard, S. and Dafoe, L. (2008b). How fast do marine invertebrates burrow? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 280–286.

Giosan, L. and Bhattacharya, J.P. (2005) (eds.). *River Deltas: Concepts, Models and Examples*. *Society for Sedimentary Geology Special Publication*, 83.

Giosan, L., Vespremeanu, E., Donnelly, J.P., Bhattacharya, J.P. and Buonaiuto, F. (2005). Morphodynamics and evolution of Danube delta. In *River Deltas: Concepts, Models and Examples*, ed. L. Giosan and J.P. Bhattacharya, *Society for Sedimentary Geology Special Publication*, 83, 391–410.

Glaessner, M.F. (1984). *The Dawn of Animal Life. A Biohistorical Study*. Cambridge, UK: Cambridge University Press.

Glaub, I. (1994). Mikrobohrspuren in ausgewählten Ablagerungsräumen des europäischen Jura und der Unterkreide. *Courier Forschungsinstitut Senckenberg*, 174, 1–324.

Glaub, I. (2004). Recent and sub-recent microborings from the upwelling area off Mauritania (West Africa) and their implications for palaeoecology. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 63–76.

Glaub, I. and Vogel, K. (2004). The stratigraphic record of microborings. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 126–135.

Glaub, I., Vogel, K. and Gektidis, M. (2001). The role of modern and fossil cyanobacterial borings in bioerosion and bathymetry. *Ichnos*, 8, 185–196.

Glaub, I., Gektidis, M., and Vogel, K. (2002). Microborings from different North Atlantic shelf areas- variability of the euphotic zone extension and implications for paleodepth reconstructions. *Courier Forschungsinstitut Senckenberg*, 237, 25–37.

Glaub, I., Golubic, S., Gektidis, M., Radtke, G. and Vogel, K. (2007). Microborings and microbial endoliths: Geological implications. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 368–381.

Głuszek, A. (1995). Invertebrate trace fossils in the continental deposits of an Upper Carboniferous coal-bearing succession, Upper Silesia, Poland. *Studia Geologica Polonica*, 108, 171–202.

Groenewald, G.H., Welman, J. and MacEachern, J.A. (2001). Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios*, 16, 148–160.

Gobetz, K.E., Lucas, S.G. and Lerner, A.J. (2006). Lungfish burrows of varying morphology from the Upper Triassic Redonda Formation, Chinle Group, eastern New Mexico. In *The Triassic–Jurassic Terrestrial Transition*, ed. J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 140–147.

Goldring, R. (1962). The trace fossils of the Baggy Beds (Upper Devonian) of North Devon, England. *Paläontologische Zeitschrift*, 36, 232–251.

Goldring, R. (1964). Trace fossils and the sedimentary surface in shallow water marine sediments. *Developments in Sedimentology*, 1, 136–143.

Goldring, R. (1991). *Fossils in the Field. Information Potential and Analysis*. Singapore: Longman Scientific & Technical.

Goldring, R. (1993). Ichnofacies and facies interpretation. *Palaios*, 8, 403–405.

Goldring, R. (1995). Organisms and the substrate: Response and effect. In *Marine Palaeoenvironmental Analysis from Fossils*, ed. D.W.J. Bosence and P.A. Allison, *Geological Society Special Publication*, 83, 151–180.

Goldring, R. (1996). The sedimentological significance of concentrically laminated burrows from Lower Cretaceous Ca-bentonites, Oxfordshire. *Journal of the Geological Society, London*, 153, 255–263.

Goldring, R. and Kaźmierczak, J. (1974). Ecological succession in intraformational hardground formation. *Palaeontology*, 17, 949–962.

Goldring, R. and Seilacher, A. (1971). Limulid undertracks and their sedimentological implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 137, 422–442.

Goldring, R., Pollard, J.E. and Taylor, A.M. (1991). *Anconichnus horizontalis*: a pervasive ichnofabric-forming trace fossil in post-Paleozoic offshore siliciclastic facies. *Palaios*, 6, 250–263.

Goldring, R., Pollard, J.E. and Taylor, A.M. (1997). Naming trace fossils. *Geological Magazine*, 134, 265–268.

Goldring, R., Cadée, G.C., D'Alessandro, A., Gibert, J.M. de, Jenkins, R. and Pollard, J.E. (2004). Climatic Control of Trace Fossil Distribution in the Marine Realm. In *The application of Ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 77–92.

Gordon, E.A. (1988). Body and trace fossils from the Middle–Upper Devonian Catskill magnafacies, southeastern New York, USA. In *The Devonian of the World*, ed. N.J. McMillan, A.F. Embry and D.J. Glass, *Canadian Society of Petroleum Geologists Memoir*, 14, 139–155.

Gore, P.J.W. (1989). Toward a model for open– and closed–basin deposition in ancient lacustrine sequences: the Newark Supergroup (Triassic–Jurassic), eastern North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 70, 29–51.

Gould, S.J. (1987). *Time's Arrow, Time's Cycle*. Cambridge, MA: Harvard University Press.

Gould, S.J. (1989). *Wonderful life: The Burgess Shale and the Nature of History*. New York: Norton.

Gould, S.J. (1991). The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology*, 17, 411–423.

Gowland, A.S. (1996). Facies characteristics and depositional models of highly bioturbated shallow marine siliciclastic strata: an example from the Fulmar Formation (Late Jurasic), UK Central Graben. In *Geology of the Humber Group: Central Graben and Moray Firth, UKCS*, ed. A. Hurst, *Geological Society Special Publication*, 114, 185–214.

Gradzinski, R. and Uchman, A. (1994). Trace fossil from interdune deposits: An example from the Lower Triassic aeolian Tumlin Sandstone, central Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108, 121–138.

Graham, J.R. and Pollard, J.E. (1982). Occurrence of the trace fossil *Beaconites antarcticus* in the Lower Carboniferous fluviatile rocks of County Mayo, Ireland. Palaeogeography, *Palaeoclimatology, Palaeoecology*, 38, 257–268.

Grassé, P.P. (1984). *Termitologia, Tome II*. Paris: Masson.

Grassé, P.P. (1986). Evolution as seen through insects. *Bulletin of the Society of Entomology of France*, 91, 5–18.

Grassle, J.F. (1985). Hydrothermal vent animals: distribution and biology. *Science*, 229, 713–717.

Grazhdankin, D. (2004). Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology*, 30, 179–221.

Green, R.H. and Hobson, K.D. (1970). Spatial and temporal structure in a temperate intertidal community with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). *Ecology*, 51, 999–1011.

Grimaldi, D.A. (1999). Co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Gardens*, 86, 373–406.

Grimaldi, D.A. and Engel, M.S. (2005). *Evolution of the Insects*. Cambridge, UK: Cambridge University Press.

Grimm, K.A. and Föllmi, K.B. (1994). Doomed pioneers: Allochthonous Crustacean tracemakers in anaerobic basinal strata, Oligo-Miocene San Gregorio Formation, Baja California Sur, Mexico. *Palaios*, 9, 313–334.

Grotzinger, J.P., Bowring, S.A., Saylor, B.Z. and Kaufman, A.J. (1995). Biostratigraphic and geochronologic constraints on early animal evolution. *Science*, 270, 598–604.

Gruszczynski, M. (1979). Ecological succession in Upper Jurassic hardgrounds from central Poland. *Acta Palaeontologica Polonica*, 24, 429–450.

Haberland, W. and Grebe, W.H. (1957). Prehistoric footprints from El Salvador. *American Antiquity*, 22, 282–285.

Habersetzer, J., Richter, G., and Storch, G. (1994). Paleoecology of early middle Eocene bats from Messel, FRG; aspects of flight, feeding and echolocation. In *Fifth International Theriological Congress; Symposium on Mammalian Evolutionary Paleoecology*, ed. S. Legendre and R.K. Stucky, Amsterdam: Harwood Academic Publishers, pp. 235–260.

Habgood, K.S., Hass, H. and and Kerp, H. (2003). Evidence for an early terrestrial food web: coprolites from the Early Devonian Rhynie chert. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 94, 371–389.

Hagadorn, J.W. and Belt, E.S. (2008). Stranded in upstate New York: Cambrian medusae from the Potsdam Sandstone. *Palaios*, 23, 424–441.

Hagadorn, J.W., Fedo, C.M., Waggoner, B.M. (2000). Early Cambrian Ediacaran-type fossils from California. *Journal of Paleontology*, 74, 731–740.

Hagadorn, J.W., Dott, R.H. and Damrow, D. (2002). Stranded on an Upper Cambrian shoreline: Medusae from Central Wisconsin. *Geology*, 30, 147–150.

Haines, P.W. (2000). Problematic fossils in the late Neoproterozoic Wonoka Formation, South Australia. *Precambrian Research*, 100, 97–108.

Hakes, W.G. (1976). Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *The University of Kansas Paleontological Contributions*, 63, 1–46.

Hakes, W.G. (1985). Trace fossils from brackish-marine shales, Upper Pennsylvanian of Kansas, U.S.A. In *Biogenic Structures: their use in interpreting depositional environments* ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 21–35.

Halffter, G. and Edmonds, W.D. (1982). The nesting behaviour of dung-beetles. An Ecological and Evolutive Approach. *Publicaciones del instituto de Ecología de México*, 10, 1–176.

Hallam, A., (1970). *Gyrochorte* and other trace fossils in the Forest Marble (Bathonian) of Dorset, England. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 189–200.

Hallam, A. (1975). Preservation of trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 55–63.

Hallam, A. and Wignall, P.B. (1997). *Mass Extinctions and their Aftermath*. Oxford, UK: Oxford University Press.

Hammer, Ø. (1998). Computer simulation of the evolution of foraging strategies: application to the ichnological record. *Palaeontologia Electronica*, 1, 21.

Hanken, N.M., Bromley, R.G. and Miller, J. (1996). Plio-Pleistocene sedimentation in coastal grabens, north-east Rhodes, Greece. *Geological Journal*, 31, 271–298.

Hanken, N.M., Bromley, R.G. and Thomsen, E. (2001). Trace fossils of the bivalve *Panopea faujasi*, Pliocene, Rhodes, Greece. *Ichnos*, 8, 117–130.

Hanor, J.S. and Marshall, N.F. (1971). Mixing of sediment by organisms. *School of Geoscience Miscellaneous Publications, Lousiana State University*, 71, 127–135.

Hansen, C.D. and MacEachern, J.A. (2007). Application of the asymmetric delta model to along-strike facies variations in a mixed wave- and river-influenced delta lobe, Upper Cretaceous Basal Belly River Formation, Central Alberta. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 1–16.

Häntzschel, W. (1975). Trace fossils and Problemática. In *Treatise on Invertebrate Paleontology, Part W, Miscellanea*, *Supplement* 1, ed. C. Teichert, Lawrence, KS: Geological Society of America and University of Kansas Press, 1–269.

Häntzschel, W. and Frey, R.W. (1978). Bioturbation. In *The Encyclopedia of Sedimentology*, ed. R.W. Fairdbridge amd J. Bourgeois, Stroudsburg, Dowden: Hutchinson & Ross, pp. 68–71.

Harada, T. and Noto, T. (1984). Volcanic calamity season. *Bulletin of the Gunma Prefecture Museum of History*, 5, 1–21.

Harper, E.M., Forsythe, G.T.W. and Palmer, T.J. (1999). A fossil record full of holes: The Phanerozoic history of drilling predation: Comment and Reply. *Geology*, 27, 959–960.

Harrison, B. (1977). The effect of sand ripples on the small-scale distribution of the interstitial meiobenthos with particular reference to the harpacticoid copepods. *Proceedings 3rd International Meiofauna Conference*, Abstract.

Harvey, A.M., Mather, A.E. and Stokes, M. (2005). Alluvial fans: geomorphology, sedimentology, dynamics – introduction. A review of alluvial-fan research. *Geological Society, London, Special Publications*, 251, 1–7.

Hasiotis ST. (2002). *Continental trace fossils*. Society for Sedimentary Geology Short Course Notes, 51.

Hasiotis, S.T. (2003). Complex ichnofossils of solitary to social organisms: Understanding their evolution and roles in terrestrial paleoecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 259–320.

Hasiotis, S.T. (2004). Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. *Sedimentary Geology*, 167, 177–268.

Hasiotis, S.T. and Bown, T.M. (1992). Invertebrate trace fossils: the backbone of continental ichnology. In *Trace Fossils: Their Paleobiological Aspects*, ed. C. Maples, and R. West, R., *Paleontological Society Short Course Notes*, 5, 64–104.

Hasiotis, S.T. and Dubiel, R.F. (1993). Continental trace fossils of the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. In *The Nonmarine Triassic*, ed. S.G. Lucas and M. Morales, *Bulletin of the New Mexico Museum of Natural History and Science*, 3, 175–178.

Hasiotis, S.T. and Dubiel, R.F. (1995). Termite (Insecta: Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos*, 4, 119–130.

Hasiotis, S.T. and Honey, J.G. (2000). Paleohydrologic and stratigraphic significance of crayfish burrows in Continental deposits: examples from several Paleocene laramide basins in the Rocky Mountains. *Journal of Sedimentary Research*, 70, 127–139.

Hasiotis, S.T. and Mitchell, C.E. (1993). A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures. *Ichnos*, 2, 291–314.

Hasiotis, S.T., Mitchell, C.E. and Dubiel, R.F. (1993a). Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish? *Ichnos*, 2, 315–333.

Hasiotis, S.T., Aslan, A. and Bown, T.M. (1993b). Origin, architecture, and paleoecology of the early Eocene continental ichnofossil *Scaphichnium hamatum*: integration of ichnology and paleopedology. *Ichnos*, 3, 1–9.

Hasiotis, S.T., Kirkland, J.I. and Callison, G. (1998). Crayfish fossils and burrows, Upper Jurassic Morrison Formation, western Colorado: evolutionary and paleohydrologic implications. *Modern Geology*, Part 1, 22, 481–491.

Hasiotis, S.T., Kraus, M.J. and Demko, T.M. (2007). Climatic Controls on Continental Trace Fossils. In *Trace Fossils: Concepts, Prolems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 172–195.

Haubold, H.H. (1986). Archosaur footprints at the terrestrial Triassic-Jurassic transition. In *The Beginning of the Age of Dinosaurs*, ed. K. Padian, Cambridge, UK: Cambridge University Press, pp. 189–201.

Haubold, H. (1996). Ichnotaxonomie und Klassifikation von Tetrapodenfahrten aus dem Perm. *Hallesches Jahrbuch Geowissenshaft B*, 18, 28–86.

Haubold, H. (1999). Tracks of the Dinosauromorpha from the Early Triassic. *Zentralblatt fr Geologie und Palontologie Teil I*, 1998, 783–795.

Haubold, H. and Katzung, G. (1978) Paleoecology and paleoenvironments of tetrapod footprints from the Rotliegend (Lower Permian) of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 307–323.

Haubold, H. and Klein, H. (2000). Die dinosauroiden Fährten *Parachirotherium–Atreipus–Grallator* aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn, ?Nor) in Franken. *Hallesches Jahrbuch für Geowissenschaften B*, 22, 59–85.

Haubold, H. and Klein, H. (2002). Chirotherien und Grallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria. *Hallesches Jahrbuch für Geowissenschaften B*, 24, 1–22.

Haubold, H. and Lucas, S. G. (2001) Early Permian tetrapod tracks: Preservation, taxonomy, and Euramerican distribution. *Natura Bresciana*, 25, 347–354.

Haubold, H. and Lucas, S.G. (2003). Tetrapod footprints of the Lower Permian Choza Formation at Castle Peak, Texas. *Paläontologische Zeitschrift*, 77, 247–261.

Haubold, H. and Sarjeant, W.A.S. (1973). Tetrapodenfa Èhrten aus den Keele und Enville Groups (Permokarbon: Stefan und Autun) von Shropshireund South Staffordshire, Groûitannien. *Zeitschrift Geologische Wissenschaften*, 8, 895–933.

Haubold, H., Buta, R.J., Rindsberg, A.K. and Kopaska-Merkel, D.C. (2005). Atlas of Union Chapel Mine vertebrate trackways and swimming traces. *Alabama Paleontological Society, Monographs*, 1, 207–276.

Hauck, T.E., Dashtgard, S.E. and Gingras, M.K. (2008). Relationships between organic carbon and Fodinichnia morphology. *Palaios*, 23, 336–343.

Hay, R.L. and Leakey, M.D. (1982). The fossil footprints of Laetoli. *Scientific American*, 246, 38–45.

Hayes, B. (2003). In search of the optimal scumsucking bottomfeeder. *American Scientist*, 91, 392–396.

Hayward, B.W. (1976). Lower Miocene bathyal and submarine canyon ichnocoenoses from Northland, New Zealand. *Lethaia*, 9, 149–162.

Heard, T.G. and Pickering, K.T. (2008). Trace fossils as diagnostic indicators of deep-marine environments, middle EoceneAinsa-Jaca basin, Spanish Pyrenees. *Sedimentology*, 55, 809–844.

Heddle, D. (1967). Versatility of movement and the origin of the asteroids. In *Echinoderm Biology*, ed. N. Millott, *Symposia of the Zoological Society of London*, 20, 125–141.

Heer, O. (1865). *Die Urwelt der Schweiz*. Zurich: Friedrich Schultze.

Heezen, B.C. and Hollister, C.D. (1971). *The Face of the Deep*. New York: Oxford University Press.

Hein, F.J. and Risk, M.J. (1975). Bioerosion of coral heads: inner patch reefs, Florida Reef Tract. *Bulletin of Marine Science*, 25, 133–138.

Hembree, D.I. (2009). Neoichnology of burrowing millipedes: understanding the relationships between ichnofossil morphology, behavior, and sediment properties. *Palaios*, 24, 425–439.

Hembree, D.I. and Hasiotis, S.T. (2007). Biogenic structures produced by the Kenyan sand boa *Eryx colubrinus* (Reptilia: Ophidia: Boidae): modern analog for interpreting continental trace fossils. *Journal of Sedimentary Research*, 77, 389–397.

Hembree, D.I., Martin, L.D. and Hasiotis, S.T. (2004). Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 203, 127–152.

Henbest, L.G. (1960). Fossil spoor and their environmental significance in Morrow and Atoka series, Pennsylvanian, Washington County, Arkansas. *US Geological Survey, Professional Paper*, 400B, 383–385.

Herringshaw, L.G. and Davies, N.S. (2008). Bioturbation levels during the end-Ordovician extinction event: a case study of shallow marine strata from the Welsh Basin. *Aquatic Biology*, 2, 279–287.

Hester, P.M. and Lucas, S.G. (2001). Lacustrine depositional environments of the Upper Triassic Redonda Formation, east-central New Mexico. *New Mexico Geological Society, Guidebook*, 52, 153–16.

Hickman, C.S. (1993). Theoretical design space; a new program for the analysis of structural diversity; Progress in constructional morphology. *Neues Jahrbuch fuer Geologie und Palaeontologie Abhandlugen*, 190, 169–182.

Higgs, R. (1988). Fish trails in the Upper Carboniferous of south-west England. *Palaeontology*, 31, 55–272.

Higgs, W. (2001). *Ichnology in archaeology*. Thesis. York University.

Hirsch, K.E. (1994). The fossil record of vertebrate eggs. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 269–294.

Hobbs, H.H. Jr. (1981). The Crayfishes of Georgia. *Smithsonian Contributions to Zoology*, 318.

Hobday, D.K. and Tavener-Smith, R. (1975). Trace fossils in the Ecca of northern Natal and their *palaeoenvironmental significance*. *Palaeontologia Africana*, 18, 47–52.

Hofmann, H.J. (1967). Precambrian fossils near Elliot Lake, Ontario. *Science*, 156, 500–504

Hofmann, H.J. (1971). Precambrian fossils, pseudofossils, and problemática in Canada. *Geological Survey of Canada, Bulletin*, 189, 1–146.

Hofmann, H.J. (1990). Computer simulation of trace fossils with random patterns, and the use of goniograms. *Ichnos*, 1, 15–22.

Hofman, H.J. (2005). Palaeoproterozoic dubiofossils from India revisited: Vindhyan triploblastic animal burrows or pseudopfossils. *Journal of the Palaeontological Society of India, Golden Jubilee*, 50, 113–120.

Hogue, E.W. and Miller, C.B. (1981). Effects of sediment microtopography on small-scale spatial distribution of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology*, 53, 181–191.

Hölldobler, B. and Wilson, E.O. (1990). *The Ants*. Cambridge, MA: Harvard University Press.

Hollister, C.D., Heezen, B.C. and Nafe, K.E. (1975). Animal traces on the deep-sea floor. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 493–510.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences, USA*, 105, 19060–19065.

Horodyski, R.J. and Knauth, L.P. (1994). Life on land in the Precambrian. *Science*, 263, 494–498.

Hovikoski, J., Lemiski, R., Gingras, M., Pemberton, G. and MacEachern, J.A. (2008). Ichnology and Sedimentology of a Mud-Dominated Deltaic Coast: Upper Cretaceous Alderson Member (Lea Park Fm), Western Canada. *Journal of Sedimentary Research*, 78, 803–824.

Howard, J.D. (1975). The sedimentological significance of trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 131–145.

Howard, J.D. (1978). Sedimentology and trace fossils. In *Trace fossil concepts*, ed. P.B. Basan, *Society for Sedimentary Geology Short Course Notes*, 5, 11–42.

Howard, J.D. and Dörjes, J. (1972). Animal–sediment relationships in two beach-related tidal flats: Sapelo Island, Georgia. *Journal of Sedimentary Petrology*, 42, 608–623.

Howard, J.D. and Frey, R.W. (1975). Regional animal–sediment characteristics of Georgia estuaries. *Senckenbergiana Maritima*, 7, 33–103.

Howard, J.D. and Frey, R.W. (1984). Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah. *Canadian Journal of Earth Sciences*, 21, 200–219.

Howard, J.D. and Reineck, H. (1981). Depositional facies of high-energy beach-to-offshore sequence with low-energy sequence. *American Association of Petroleum Geologists, Bulletin*, 65, 807–830.

Howard, J.D., Elders, C.A. and Heinbokel, J.F. (1975). Estuaries of the Georgia coast, USA. Sedimentology and Biology V. Animal–sediment relationships in estuarine point bar deposits, Ogeechee River, Ossabaw Sound. *Senckenbergiana Maritima*, 7, 181–203.

Howell, C.D. Jr., Bhattacharya, J.P. and MacEachern, J.A. (2007). Bedset sedimentation rates in a Turonian Greenhouse delta front, Wall Creek Member, Frontier Formation, Powder Reiver Basin, Wyoming. In *Ichnological Application to Sedimentological and Sequence Stratigraphic Problems*, ed. J.A. MacEachern, M.K. Gingras, K.L. Bann and S.G. Pemberton, Society for Sedimentary Geology Research Conference, Price, pp. 81–84.

Howell, J.A. and Flint, S.F. (2003). Sequences and systems tracts in the Book Cliffs. In *Sedimentary Record of Sea-Level Change*, ed. A.L. Coe, Cambridge, UK: Cambridge University Press and Open University, pp. 179–197.

Hu, B., Wang, G. and Goldring, R. (1998). *Nereites* (or *Neonereites*) from Lower Jurassic lacustrine turbidites of Henan, central China. *Ichnos*, 6, 203–209.

Hua, H., Pratt, B.R. and Zhang, L.Y. (2003). Borings in *Cloudina* shells: Complex predatory-prey dynamics in the Terminal Neoproterozoic. *Palaios*, 18, 454–459.

Hubbard, S.M. and Shultz, M.R. (2008). Deep burrows in submarine fan-channel deposits of the Cerro Toro Formation (Cretaceous), Chilean Patagonia: Implications for firmground development and colonization in the deep-sea. *Palaios*, 23, 223–232.

Hudson, J.D. (1990). Salinity from faunal analysis and geochemistry. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 406–410.

Hunt, A.P. and Lucas, S.G. (2006a). Permian tetrapod ichnofacies. In *Non-marine Permian biostratigraphy and Biocronology*, ed. S.G. Lucas, G. Cassinis and J.W. Schneider, *Geological Society Special Publication*, 265, 137–156.

Hunt, A.P. and Lucas, S.G. (2006b). The taphonomy of the Cleveland-Lloyd Dinosaur Quarry, Upper Jurassic Morrison Formation, Utah: a re-evaluation. In *Paleontology and Geology of the Upper Jurassic Morrison Formation*, ed. J.R. Foster and S.G. Lucas, *New Mexico Museum of Natural History and Science Bulletin*, 36, 57–65.

Hunt, A.P. and Lucas, S.G. (2006c). Triassic-Jurassic tetrapod ichnofacies. In *The Triassic–Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 12–22.

Hunt, A.P. and Lucas, S.G. (2007). Tetrapod ichnofacies: a new paradigm. *Ichnos*, 14, 59–68.

Hunt, A.P., Chin, K. and Lockley, M.G. (1994). The paleobiology of coprolites. In *The Paleobiology of Trace Fossils*, ed. S.K. Donovan, London: John Wiley, pp. 221–240.

Hunt, A.P., Lucas, S.G. and Lockley, M.G. (1998). Taxonomy, stratigraphic and facies significance of vertebrate coprolites of the Upper Triassic Chinle Group, western United States. *Ichnos*, 5, 225–234.

Hunt, A.P., Lucas, S.G. and Lockley, M.G. (2004a). Large pelycosaur footprints from the Lower Pennsylvanian of Alabama, USA. *Ichnos*, 11, 39–44.

Hunt, A.P., Lucas, S.G., Calder, J.H., van Allen, H.E.K., George, E., Gibling, M.R., Herbert, B.L., Mansky, C. and Reid, D.R. (2004b). Tetrapod footprints from Nova Scotia; the Rosetta Stone for Carboniferous tetrapod ichnology. *Geological Society of America, Abstracts with Programs*, 36, 66.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A. (2005). Early Permian tetrapod tracksites in New Mexico. In: *The Permian of Central New Mexico*, ed. S.G. Lucas, K.E. Zeigler and J.A. Spielmann, *New Mexico Museum of Natural History and Science Bulletin*, 31, 46–48.

Hunter, M.A. and Lomas, S.A. (2003). Reconstructing the Siluro-Devonian coastline of Gondwana: insights from the sedimentology of the Port Stephens Formation, Falkland Islands. *Journal of the Geological Society, London*, 160, 459–476.

Ingle, J.C. (1980). Cenozoic paleobathymetry and depositional history of selected sequences within the Southern California Continental Borderland. *Cushman Found Special Publication*, 19, 163–195.

Ishigaki, S. (1989). Footprints of swimming sauropods from Morocco. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 83–86.

Ivantsov, A.Y. and Malakhovskaya, Y.E. (2002). Giant traces of Vendian animals. *Doklady Earth Sciences A*, 385, 618–622.

Jablonski, D. (1995). Extinction in the fossil record. In *Extinction Rates*, ed. R.M. May and J.H. Lawton, Oxford, UK: Oxford University Press, pp. 25–44.

Jaglarza, P. and Uchman, A. (2010). A hypersaline ichnoassemblage from the Middle Triassic carbonate ramp of the Tatricum domain in the Tatra Mountains, Southern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 71–81.

James, N.P., Kobluk, D.R. and Pemberton, S.G. (1977). The oldest macroborers: Lower Cambrian of Labrador. *Science*, 197, 980–983.

Janicke, V. (1969). Untersuchungen ueber den Biotop der Solnhofener Plattenkalke. Investigations of the biotope of the Solnhofen limestones. *Mitteilungen der Bayerischen Staatssammlung fuer Palaeontologie und Historische Geologie*, 9, 117–180.

Jansson, A.M. (1967). Food-web of Cladophora-belt Fauna. *Helgolander Wissenschaftliche Meeresuntersuchungen*, 15, 574–578.

Jenkins, R.J.F. (1995). The problems and potential of using animal fossils and trace fossils in terminal Proterozoic biostratigraphy. *Precambrian Research*, 73, 51–69.

Jensen, S. (1990). Predation by early Cambrian trilobites on infaunal worms – evidence from the Swedish Mickwitzia Sandstone. *Lethaia*, 23, 29–42.

Jensen, S. (1997). Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. *Fossils and Strata*, 42, 1–111.

Jensen, S. (2003). The Proterozoic and earliest trace fossil record; Patterns, problems and perspectives. *Integrative and Comparative Biology*, 43, 219–228.

Jensen, S. and Bergström, J. (2000). *Cheiichnus gothicus* igen. et. isp. n., a new *Bergaueria*-like arthropod trace fossil from the lower Cambrian of Vastergotland, Sweden. *Geologiska Föreningens I Stockholm Förhandlingar*, 122, 293–296.

Jensen, S. and Mens, K. (1999). Lower Cambrian shallow-water occurrence of the branching "deep-water" type of trace fossil *Dendrorhaphe* from the Lontova Formation, eastern Latvia. *Paläontologische Zeitschrift*, 73, 187–193.

Jensen, S. and Runnegar, B.N. (2005). A complex trace fossil from the Spitskop Member (terminal Ediacaran–? Lower Cambrian) of southern Namibia. *Geological Magazine*, 142, 561–569.

Jensen, S., Gehling, J.G. and Droser, M.L. (1998). Ediacara-type fossils in Cambrian sediments. *Nature*, 393, 567–569.

Jensen, S., Saylor, B.Z., Gehling, J.G. and Germs, G.J.B. (2000). Complex trace fossils from the terminal Proterozoic of Namibia. *Geology*, 28, 143–146.

Jensen, S., Gehling, J.G., Droser, M.L. and Grant, S.W.F. (2002). A scratch circle origin for the medusoid fossil *Kullingia*. *Lethaia*, 35, 291–299.

Jensen, S., Droser, M.L. and Gehling, J.G. (2005). Trace fossil preservation and the early evolution of animals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 220, 19–29.

Jensen, S., Droser, M.L. and Gehling, J.G. (2006). A critical look at the Ediacaran trace fossil record. In *Neoproterozoic Geobiology and Paleobiology*, ed. J. Kaufman and S. Xiao, Topics in Geobiology, 27, 115–157.

Johnson, E.W., Briggs, D.E.G., Suthren, R.J. Wright, J.L. and Tunncliff, S.P. (1994). Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake district. *Geological Magazine*, 131, 395–406.

Johnson, M.E. (1988). Why are ancient rocky shores so uncommon? *Journal of Geology*, 96, 469–480.

Johnson, M.E. (2006). Uniformitarianism as a guide to rocky-shore ecosystems in the geological record. *Canadian Journal of Earth Sciences*, 43, 1119–1147.

Johnson, R.G. (1967). Salinity of interstitial water in a sandy beach. *Limnology and Oceanography*, 12, 1–7.

Johnston, P.A., Eberth, D.A., and Anderson, P.K. (1996). Alleged vertebrate eggs from Upper Cretaceous red beds, Gobi Desert, are fossil insect (Coleoptera) pupal chambers: *Fictovichnus* new ichnogenus. *Canadian Journal of Earth Sciences*, 33, 511–525.

Johnstone, P.D., Mustard, P.S. and MacEachern, J.A. (2006). The basal unconformity of the Nanaimo Group, southwestern British Columbia: a Late Cretaceous storm-swept rocky shoreline. *Canadian Journal of Earth Sciences*, 43, 1165–1181.

Jones, S.E. and Jago, C.F. (1993). In situ assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology*, 115, 133–142.

Jones, B. and Pemberton, S.G. (1989). Sedimentology and ichnology of a Pleistocene unconformity-bounded, shallowing-upward carbonate sequence: the Ironshore Formation, Salt Creek, Grand Cayman. *Palaios*, 4, 343–355.

Jones, C.G., Lawton, J.H. and Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.

Jorgensen, B.B. (1996). Bacteria and marine biogeochemistry. In *Marine Geochemistry, 2nd edn*, ed. H.D. Schulz and M. Zabel, Berlin: Springer, pp. 169–206.

Kanazawa, K. (1992). Adaptation of test shape for burrowing and locomotion in spatangoid echinoids. *Palaeontology*, 35, 733–750.

Kanazawa, K. (1995). How spatangoids produce their traces: relationship between burrowing mechanism and trace structure. *Lethaia*, 28, 211–219.

Kauffman, E.G. and Hart, M.B. (1996). Cretaceous bio-events. In *Global Events and Event Stratigraphy*, ed. O.H. Walliser, Berlin: Springer, pp. 285–312.

Keighley, D.G. and Pickerill, R.K. (1994). The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology*, 37, 305–337.

Keighley, D.G. and Pickerill, R.K. (1997). Systematic ichnology of the Mabou and Cumberland Groups (Carboniferous) of western Cape Breton Island, eastern Canada, 1: burrows, pits, trails, and coprolites. *Atlantic Geology*, 33, 181–215.

Keighley, D.G. and Pickerill, R.K. (2003). Ichnocoenoses from the Carboniferous of eastern Canada and their implications for the recognition of ichnofacies in nonmarine strata. *Atlantic Geology*, 39, 1–22.

Keller, G. (2001). The end-Cretaceous mass extinction in the marine realm: Year 2000 assessment. *Planetary and Space Science*, 49, 817–830.

Keller, G. (2003). Biotic effects of impacts and volcanism. *Earth and Planetary Science Letters*, 215, 249–264.

Kelley, P.H. and Hansen, T.A. (2001). The Mesozoic marine revolution. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 94–97.

Kelly, S.R.A. and Bromley, R.G. (1984). Ichnological nomenclature of clavate borings. *Palaeontology*, 27, 793–807.

Kennedy, W.J. (1967). Burrows and surface traces from the Lower Chalk of southern England. *British Museum (Natural History), Geology Bulletin*, 15, 127–167.

Kennedy, W.J. (1970). Trace fossils in chalk environments. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 263–282.

Kennedy, W.J. (1975). Trace fossils in carbonate rocks. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, Berlin: Springer-Verlag, pp. 377–398.

Kennedy, W.J. and Garrison, R.E. (1974). Morphology and genesis of nodular chalks and hardgrounds in the Upper Cretaceous of southern England. *Sedimentology*, 22, 311–386.

Kern, J. P. (1980). Origin of trace fossils in Polish Carpathian flysch. *Lethaia*, 13, 347–372.

Kern, J.P. and Warme, J.E. (1974). Trace fossils and bathymetry of the Upper Cretaceous Point Loma Formation, San Diego, California. *Geological Society of America, Bulletin*, 85, 893–900.

Kidwell, S.M. and Brenchley, P.J. (1994). Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction? *Geology*, 22, 1139–1143.

Kim, J.Y. and Paik, I.S. (1997). Nonmarine *Diplocraterion luniforme* (Blanckenhorn 1916) from the Hasandong Formation (Cretaceous) of the Jinju area, Korea. *Ichnos*, 5, 131–138.

Kim, J.Y., Keighley, D.G., Pickerill, R.K., Hwang, W. and Kim, K.-S. (2005). Trace fossils from marginal lacustrine deposits of the Cretaceous Jinju Formation, southern coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 218, 105–124.

Kim, J.Y., Kim, S.H., Kim, K.S. and Lockley, M.G. (2006). The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): more evidence of high avian diversity in East Asia. *Cretaceous Research*, 27, 56–69.

Kim, J.Y., Kim, K.S. and Lockley, M.G. (2008a). Hominid ichnology: tracking our own origins. *Ichnos*, 15, 103–105.

Kim, J.Y., Kim, K.S., Lockley, M.G. and Matthews, N. (2008b). Hominid ichnotaxonomy: An exploration of a neglected discipline. *Ichnos*, 15, 126–139.

Kim, S.K., Kim, J.Y., Kim, S.H., Lee, C.Z. and Lim, J.D. (2009). Preliminary Report on Hominid and Other Vertebrate Footprints from the Late Quaternary Strata of Jeju Island, Korea. *Ichnos*, 16, 1–11.

Kineke, G.C., Sternberg, R.W., Trowbridge, J.H. and Rockwell, G.W. (1996). Fluid-mud processes on the Amazon continental shelf. *Continental Shelf Research*, 16, 667–696.

King, M.J. and Benton, M.J. (1996). Dinosaurs in the Early and Mid Triassic? The footprint evidence from Britain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 122, 213–225.

King, M.J., Sarjeant, W.A.S., Thompson, D.B. and Tresise, G. (2005). A revised systematic ichnotaxonimy and review of the vertebrate footprint ichnofamily Chirotheriidae from the British Triassic. *Ichnos*, 12, 241–299.

Kinne, O. (1964). Non-genetic adaptation to temperature and salinity. *Helgolander wissenschaftliche Meeresuntersuchungen*, 9, 443–458.

Kitchell, J.A. (1979). Deep-sea foraging pathways: an analysis of randomness and resource exploitation. *Paleobiology*, 5, 107–125.

Kitchell, J.A., Kitchell, J. F., Clark, D.L. and Dangeard, L. (1978a). Deep-sea foraging behavior: its bathymetric potential in the fossil record. *Science*, 200, 1289–1291.

Kitchell, J.A., Kitchell, J.F., Johnson, G.L. and Hunkins, K.L. (1978b). Abyssal traces and megafauna: comparison of productivity, diversity, and density in the Arctic and Antarctic. *Paleobiology*, 4, 171–180.

Klein, G. de V. (1971). A sedimentary model for determining paleotidal range. *Geological Society of America Bulletin*, 82, 2585–2592.

Klein, G. de V. (1977). *Clastic Tidal Facies*. Champaign, IL: CEPCO.

Klein, R., Mokady, O. and Loya, Y. (1991). Bioerosion in ancient and contempary coral of the genus *Porites*: patterns and palaeoenvironmental implications. *Marine Ecology Progress Series (Halsten- bek)*, 77, 245–251.

Knaust, D. (1997). Die Karbonatrampe am SE-Rand des Persischen Golfes (Vereinigte Arabische Emirate): Resentes Analogon für den Unteren Muschelkalk der Germanischen Trias? *Greifswalder Geowissenschaftliche Beiträge*, 5, 101–123.

Knaust, D. (2004a). The oldest Mesozoic nearshore *Zoophycos*: evidence from the German Triassic. *Lethaia*, 37, 297–306.

Knaust, D. (2004b). Cambro-Ordovician trace fossils from the SW-Norwegian Caledonides. *Geological Journal*, 39, 1–24.

Knaust, D. (2007). Invertebrate trace fossils and ichnodiversity in shallow-marine carbonates of the German Middle Triassic (Muschelkalk). In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publications*, 88, 223–240.

Knaust, D. (2008). Complex behavioural pattern as an aid to identify the producer of *Zoophycos* from the Middle Permian of Oman. *Lethaia*, 42, 146–154.

Knaust, D. (2009). Characterisation of a Campanian deep-sea fan system in the Norwegian Sea by means of ichnofabrics. *Marine and Petroleum Geology*, 26, 1199–1211.

Knecht, R.J., Benner, J.S., Rogers, D.C. and Ridge, J.C. (2009). *Surculichnus bifurcauda* n. igen., n. isp., a trace fossil from Late Pleistocene glaciolacustrine varves of the Connecticut River Valley, USA, attributed to notostracan crustaceans based on neoichnological experimentation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 232–239.

Kneer, D., Asmus, H., Ahnelt, H. and Vonk, J.A. (2008). Records of *Austrolethops wardi* Whitley (Teleostei: Gobiidae) as an inhabitant of burrows of the thalassinid shrimp *Neaxius acanthus* in tropical seagrass beds of the Spermonde Archipelago, Sulawesi, Indonesia. *Journal of Fish Biology*, 72, 1095–1099.

Knoll, A.H., Golubic, S., Green, J. y Swett, K. (1986). Organically preserved microbial endoliths from the late Proterozoic of East Greenland. *Nature*, 321, 856–857.

Knoll, A., Walter, M., Narbonne, G. and Chirstie-Blick, N. (2006). The Ediacaran Period: a new addition to the geologic time scale. *Lethaia*, 39, 13–30.

Knox, G.A. (1986). *Estuarine Ecosystems: A Systems Approach*. Boca Raton, FL: CRC Press.

Knox, L.W. and Miller, M.F. (1985). Environmental control of trace fossil morphology. In *Biogenic Structures: Their Use in Interpreting Depositional Environments*, ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 167–176.

Kobluk, D.R., James, N.P. and Pemberton, S.G. (1978). Initial diversification of macroboring ichnofossils and exploitation of macroboring niche in the lower Paleozoic. *Paleobiology*, 4, 163–170.

Komar, P.D. (1976). *Beach Processes and Sedimentation: Englewood Cliffs*. Upper Saddle River, NJ: Prentice Hall.

Kotake, N. (1989). Paleoecology of the *Zoophycos* producers. *Lethaia*, 22, 327–341.

Kotake, N. (1991). Non-selective surface deposit feeding by the *Zoophycos* producers. *Lethaia*, 24, 379–385.

Kotake, N. (1992). Deep sea echiurans: possible producers of *Zoophycos*. *Lethaia*, 25, 311–316.

Kotake, N. (1994). Population paleoecology of the *Zoophycos* producing animal. *Palaios*, 9, 84–91.

Kotake, N. (1997). Ethological interpretation of the trace fossil *Zoophycos* in the Hikoroichi Formation (Lower Carboniferous), southern Kitakami Mountains, Northeast Japan. *Paleontological Research*, 1, 15–28.

Kotake, N. (2007). *Macaronichnus* isp. associated with *Piscichnus waitemata* in the Miocene of Yonaguni-jima Island, southwest Japan. In *Trace Fossils, Concepts, Problems, Prospects*, ed. W. Miller, III, Amsterdam: Elsevier, pp. 492–500.

Kowalewski, M., Dulai, A. and Fürsich, F.T. (1998). A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology*, 26, 1091–1094.

Kowalewski, M., Dulai, A. and Fürsich, F.T. (1999). A fossil record full of holes: the Phanerozoic history of drilling predation – Reply to comment. *Geology*, 27, 959–960.

Koy, K. and Plotnick, R.E. (2007). Theoretical and experimental ichnology of mobile foraging. In *Trace Fossils: Concepts, Problems and Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 428–441.

Koy, K. and Plotnick, R.E. (2010). Ichnofossil morphology as a response to resource distribution: insights from modern invertebrate foraging. *Palaeogeography Palaeoclimatology Palaeoecology*, 292, 272–281.

Kozur, H.W. and Lemone, D.V. (1995). New terrestrial arthropod trackways from the Abo Member (Sterlitamakian, late Sakmarian, late Wolfcampian) of the Shalem Colony section, Robledo Mountains, New Mexico. In *Early Permian Footprints and Facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 107–113.

Kozur, H.W., Krainer, K. and Mostler, H. (1996). Ichnology and Sedimentology of the Early Permian deep-water deposits from the Lercara-Roccapalumba Area (Western Sicily, Italy). *Facies*, 34, 123–150.

Kramer, J.M., Erickson, B.R., Lockley, M.G., Hunt, A.P. and Braddy, S.J. (1995). Pelycosaur predation in the Permian: Evidence from *Laoporus* trackways from the Coconino Sandstone with a description of a new ichnospecies of *Permichnium*. In *Early Permian footprints and facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 245–249.

Krapovickas, V. (2010). El Rol de las trazas fósiles de tetrápodos en los modelos de icnofacies continentales en ambientes de climas áridos – semiáridos. PhD dissertation, Universidad de Buenos Aires, Buenos Aires.

Krapovickas, V., Mángano, M.G., Mancuso, A., Marsicano, C.A. and Volkheimer, W. (2008). Icnofaunas triásicas en abanicos aluviales distales: evidencias de la Formación Cerro Puntudo, Cuenca Cuyana, Argentina. *Ameghiniana*, 45, 463–472.

Krapovickas, V., Ciccioli, P.L., Mángano, M.G., Marsicano, C.A. and Limarino, C.O. (2009). Paleobiology and paleoecology of an arid–semiarid Miocene South American ichnofauna in anastomosed fluvial deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 284, 129–152.

Kraus, M.J. and Hasiotis, S.T. (2006). Significance of different modes of rhizolith preservation to interpreting paleoenvironmental and paleohydrologic settings: examples from Paleogene paleosols, Bighorn Basin, Wyoming, USA. *Journal of Sedimentary Research*, 76, 633–646.

Książkiewicz, M. (1970). Observations on the ichnofauna of the Polish Carpathians. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 283–322.

Książkiewicz, M. (1977). Trace fossils in the flysch of the Polish Carpathians. *Paleontologica Polonica*, 36, 1–200.

Kuban, G.J. (1989). Elongate dinosaur tracks. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 57–82.

Kumar, A., Gopolan, K. and Rajagopalan, G. (2000). Mesoproterozoic Age of the Vindhyan Sediments, Central India from Glauconite Rb-Sr Systematics. *Journal of Conference Abstracts*, 5, 608.

Labandeira, C.C. (1997). Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences*, 26, 329–377.

Labandeira, C.C. (1998). Plant–insect associations from the fossil record. *Geotimes*, 43, 18–24.

Labandeira, C.C. (2000). The paleobiology of pollination and its precursors. In *Phanerozoic Terrestrial Ecosystems*, ed. R.A. Gastaldo and W.A. DiMichele, *Paleontological Society Papers*, 6, 233–269.

Labandeira, C.C. (2002). The history of associations between plants and animals. In *History of Plant–Animal Interactions*, ed. C. Herrera and O. Pellmyr, Oxford, UK: Blackwell Science, pp. 26–74.

Labandeira, C.C. (2006). The four phases of plant–arthropod associations in deep time. *Geologica Acta*, 4, 409–438.

Labandeira, C.C. (2007). The origin of herbivory on land: The initial pattern of live tissue consumption by arthropods. *Insect Science*, 14, 259–274.

Labandeira, C.C., Phillips, T.L. and Norton, R.A. (1997). Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. *Palaios*, 12, 319–353.

Labandeira, C.C., Johnson, K.R. and Wilf, P. (2002a). Impact of the terminal Cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences, USA*, 99, 2061–2066.

Labandeira, C.C., Johnson, K.R. and Lang, P. (2002b). A preliminary assessment of insect herbivory across the Cretaceous/Tertiary boundary: extinction and minimal rebound. In *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains-An Integrated Continental Record at the End of the Cretaceous*, ed. J.H. Hartman, K.D. Johnson and D.T. Nichols, Boulder, CO: Geological Society of America, pp. 297–327.

Lamond, R.E., and Tapanila, L. (2003). Embedment cavities in lacustrine stromatolites: Evidence of animal interactions from Cenozoic carbonates in USA and Kenya. *Palaios*, 18, 445–453.

Landing, E. (1994). Precambrian-Cambrian boundary global stratotyperatified and a new perspective of Cambrian time. *Geology*, 22, 179–182.

Landing, E. and Brett, C.E. (1987). Trace fossils and regional significance of a Middle Devonian (Givetian) discomformity in southwestern Ontario. *Journal of Paleontology*, 61, 205–230.

Lanes, S., Manceñido, M. and Damborenea, S. (2007). *Lapispira*: a double helicoidal burrow from Jurassic marine nearshore environments. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, MG. Mángano, J.F. Genise and N.G. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 59–77.

Lanier, W.P., Feldman, H.R. and Archer, A.W. (1993): Tidal sedimentation from a fluvial to estuarine transition, Douglas Group, Missourian-Virgilian, Kansas. *Journal of Sedimentray Petrology*, 63, 860–873.

Larson, D.W. and Rhoads, D.C. (1983). The evolution of infaunal communities and sedimentary fabrics. In *Biotic Interactions in Recent and Fossil Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenum Press, pp. 627–648.

Larsonneur, C. (1994). The Bay of Mont-Saint-Michel: a sedimentation model in a temperate macrotidal environment. *Senckenbergiana Maritima*, 24, 3–63.

Laza, J.H. (2006). Dung-beetle fossil brood balls: The ichnogenera *Coprinisphaera*, Sauer and *Quirogaichnus* (Coprinisphaeridae). *Ichnos*, 13, 217–235.

Leakey, M.D. (1981). Tracks and tools. *Philosophical Transactions Royal Society London B*, 292, 95–102.

Leakey, M.D. (1987). Animals prints and trails. In *Laetoli: a Pliocene site in northern Tanzania*, ed. M. D. Leakey and J.M. Harris, Oxford, UK: Clarendon Press, pp. 451–489.

Leakey, M.D. and Harris, J.M. (1987). *Laetoli: A Pliocene Site in Northern Tanzania*. Oxford, UK: Clarendon Press.

Leakey, M.D. and Hay, R.L. (1979). Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature*, 278, 317–323.

Legarreta, L., Uliana, M.A., Larotonda, C.A. and Meconi, G.R. (1993). Approaches to nonmarine sequence stratigraphy: theoretical models and examples from Argentine basins. In *Subsurface Reservoir Characterisation from Outcrop Observations*, ed. R. Eschard and B. Doliez, Editions Technip, *Collection Colloques et Seminaires*, 51, 125–145.

Legg, I.C. (1985). Trace fossils from a Middle Cambrian deltaic sequence, North Spain. *Society for Sedimentary Geology Special Publication*, 35, 151–165.

Leithold, E.L. and Dean, W.E. (1998). Depositional processes and carbon burial on a Turonian prodelta at the margin of the western interior Seaway. In *Stratigraphy and Palaeoenvironments of the Cretaceous Western Interior seaway, USA*, ed. W.E. Dean and M.A. Arthur, *Society for Sedimentary Geology Concepts in Sedimentology and Palaeontology*, 6, 189–200.

Leonardi, G. (1981). *Brasilichnium elusivum* gen. et sp. nov.: pistas de tetrapodes do Mesozoico guardadas nas colecoes de Museu Nacional de Rio de Janeiro. *Anais Academia Brasileira de Ciencias*, 53, 793–805.

Leonardi, G. (1989). Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, Cambridge, UK: Cambridge University Press, pp. 165–178.

Leszczyński, S. (1991a). Oxygen-related controls on predepositional ichnofacies in turbidites, Guipúzcoan Flysch (Albian-Lower Eocene), Northern Spain. *Palaios*, 6, 271–280.

Leszczyński, S. (1991b). Trace Fossil tiering in flysch sediments: examples form the Guipzcoan flysch (Cretaceous-Paleogene), northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 88, 167–184.

Leszczyński, S. (1992a). Controls on trace fossil distribution in flysch deposits. *Nakladem Uniwersytetu Jagiellonskiego, Rozprawy Habilitacyjne*, 236, 1–120.

Leszczyński, S. (1992b). A generalized model for the development of ichnocoenoses in flysch deposits. *Ichnos*, 2, 137–146.

Leszczyński, S. (1993). A generalized model for the development of ichnocoenoses in flysch deposits. *Ichnos*, 2, 137–146.

Leszczyński, S. and Seilacher, A. (1991). Ichnocoenoses of a turbidite sole. *Ichnos*, 1, 293–303.

Lettley, C.D., Gingras, M.K., Pearson, N.J. and Pemberton, S.G. (2007a). Burrowed stiffgrounds on estuarine point bars: Modern and ancient examples, and criteria for their discrimination from firmgrounds developed along omission surfaces. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentray Geology Short Course Notes*, 52, 325–333.

Lettley, C.D., Pemberton, S.G., Gingras, M.K., Ranger, M.J. and Blakney, B.J. (2007b). Integrating sedimentology and ichnology to shed light on the system dynamics and paleogeography of an ancient riverine estuary. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentray Geology Short Course Notes*, 52, 147–165.

Levin, L.A., Blair, N.E., DeMaster, D.J., Plaia, G., Fornes, W., Martin, C.M. and Thomas, C.J. (1997). Rapid subduction of organic matter by maldanid polychaetes on the North Carolina Slope. *Journal of Marine Research*, 55, 595–611.

Levin, L.A., Blair, N.E., Martin, C.M., DeMaster, D.J., Plaia, G. and Thomas, C.J. (1999). Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *In situ* experiments using 13C-labeled diatom. *Marine Ecology Progress Series*, 182, 37–54.

Levin, L.A., Rathburn, A.E., Gutierrez, D., Munoz, P. And Shankle, A. (2003). Bioturbation by symbiont-bearing annelids in near-anoxic sediments; implications for biofacies models and paleo-oxygen assessments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199, 129–140.

Levi-Setti, R. (1993). *Trilobites*. 2nd edn. Chicago, IL: University of Chicago Press.

Lewis, D.W. and Ekdale, A.A. (1991). Lithofacies relationships in a Late Quaternary gravel and loess fan delta complex, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 81, 229–251.

Lewis, D.W. and Ekdale, A.A. (1992). Composite ichnofabric of a Mid-Tertiary unconformity on a pelagic limestone. *Palaios*, 7, 222–235.

Lewis, J.R. (1961). The littoral zone on a rocky shore. A biological or physical entity. *Oikos*, 12, 280–301.

Lewis, J.R. (1964). *The Ecology of Rocky Shore*. London: English Universities Press.

Li, X. and Droser, M.L. (1999). Lower and Middle Ordovician shell beds from the Basin and Range province of western United States (California, Nevada, and Utah.). *Palaios*, 14, 215–233.

Liebau, A. (1984). Grundlagen der Okobathymetrie. In *Palaobathymetrie*, ed. H. Luterbacher, *Palaontologische Kursbucher*, 2, 149–184.

Lillie, M.C. (1998). Cranial surgery dates back to Mesolithic. *Nature*, 391, 854.

Lim, S.K., Yang, S.Y. and Lockley, M.G (1989). Large dinosaur footprint assemblages from the Cretaceous Jindong Formation of southern Korea. In *Dinosaurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 333–336.

Lin, J.P., Zhao, Y.L., Rahman, I.A., Xiao, S. and Wang, Y. (2010). Bioturbation in Burgess Shale-type *Lagerstätten*. Case study of trace fossil–body fossil association from the Kaili Biota (Cambrian Series 3), Guizhou, China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291, 245–256.

Lindholm, R.M. and Casey, J.F. (1990). The distribution and possible biostratigraphic significance of the ichnogenus *Oldhamia* in the shales of the Blow Me Down Brook Formation, western Newfoundland. *Canadian Journal of Earth Sciences*, 27, 1270–1287.

Little, C. (2000). *The Biology of Soft Shores and Estuaries*. New York: Oxford University Press.

Liu, A.G., Mcllroy, D. and Brasier, M.D. (2010). First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology*, 38, 123–126.

Liu, H.T.H., Kneer, D., Asmus, H. and Ahnelt, H. (2008). The feeding habits of *Austrolethops wardi*, a gobiid fish inhabiting burrows of the thalassinidean shrimp *Neaxius acanthus*. *Estuatine, Coastal and Shelf Science*, 79, 764–767.

Lobza, V. and Schieber, J. (1999). Biogenic sedimentary structures produced by worms in soupy, soft muds: Observations from the Chattanooga Shale (Upper Devonian) and experiments. *Journal of Sedimentary Research*, 69, 1041–1049.

Locklair, R.E. and Savrda, C.E. (1998a). Ichnofossil tiering analysis of a rhythmically bedded chalk-marl sequence in the Upper Cretaceous of Alabama. *Lethaia*, 31, 311–322.

Locklair, R.E. and Savrda, C.E. (1998b). Ichnology of rhytmically bedded Demopolis Chalk (Upper Cretaceous, Alabama): Implication for paleoenvironment, depositional cycle origins, and tracemaker behavior. *Palaios*, 13, 423–438.

Lockley, M.G. (1986). The Paleobiological and paleoenvironmental importance of dinosaur footprints. *Palaios*, 1, 37–47.

Lockley, M.G. (1987). Dinosaur footprints from the Dakota Group of eastern Colorado. *The Mountain Geologist*, 24, 107–122.

Lockley, M.G. (1989). Summary and prospectus. In *Dinosurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 441–447.

Lockley, M.G. (1991). *Tracking Dinosaurs. A New Look at an Ancient World*. Cambridge, UK: Cambridge University Press.

Lockley, M.G. (1992). Comment on “Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin”. *Geology*, 20, 666–667.

Lockley, M.G. (1993). *Siguiendo las huellas de los dinosaurios*. Madrid: McGraw Hill.

Lockley, M.G. (1998). The vertebrate track record. *Nature*, 396, 429–432.

Lockley, M.G. (2001). A decade of dinosaur tracking at Dinosaur Ridge. *Mountain Geologist*, 38, 119–135.

Lockley, M.G. (2003). *A Guide to the Fossil Footprints of the Dinosaur Ridge and Fossil Trace Areas*. Morrison, CO: Friends of Dinosaur Ridge.

Lockley, M.G. (2007). A tale of two ichnologies: The different goals and potentials of Invertebrate and Vertebrate (Tetrapod) Ichnotaxonomy and how they relate to Ichnofacies analysis. *Ichnos*, 14, 39–58.

Lockley, M.G. and Conrad, K. (1989). The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the western USA. In *Dinosurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 121–134.

Lockley, M.G. and Foster, J.R. (2006). Dinosaur and turtle tracks from the Morrison Formation (upper Jurassic) of Colorado National Monument, with observations on the taxonomy of vertebrate swim tracks. In *Geology and Paleontology of the Morrison Formation*, ed. J.R. Foster and S.G. Lucas, *New Mexico Museum of Natural History and Science Bulletin*, 36, 193–198.

Lockley, M.G. and Hunt, A.P. (1994). A review of vertebrate ichnofaunas of the Western Interior United States: evidence and implications. In *Mesozoic Systems of the Rocky Mountain Region, United States*, ed. M.V. Caputo, J.A. Peterson, K.J. Franczyk, Denver, CO: RMS-SEPM, 95–108.

Lockley, M.G. and Hunt, A.P. (1995). *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. New York: Columbia University Press.

Lockley, M.G. and Meyer, C.A. (2000). *Dinosaur Tracks and Other Fossil Footprints of Europe.* New York: Columbia University Press.

Lockley, M.G. and Rainforth. E.C. (2002). The track record of Mesozoic birds and pterosaurs: an ichnological and paleoecological perspective. In *Mesozoic Birds: Above the Heads of Dinosaurs*, ed. L.M. Chiappe and L.M. Witmer, Berkley, CA: University of California Press, pp. 405–418.

Lockley, M.G., Houck, K.J. and Prince, N.K. (1986). North America’s largest dinosaur trackway site: implications for Morrison Formation paleoecology. *Geological Society of America Bulletin*, 97, 1163–1176.

Lockley, M.G., Rindsberg, A.K. and Zeiler, R.M. (1987). The paleoenvironmental significance of the nearshore *Curvolithus* ichnofacies. *Palaios*, 2, 255–262.

Lockley, M.G., Holbrook, J., Hunt, AP., Matsukawa, M. and Meyer, C. (1992). The Dinosaur Freeway: a Preliminary Report on the Cretaceous Megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico. In *Mesozoic of the Western Interior*, ed. R. Flores, *Society for Sedimentary Geology Midyear Meeting, Fieldtrip Guidebook*, 39–54.

Lockley, M.G., Hunt, A.P. and Meyer, C.A. (1994). Vertebrate tracks and the ichnofacies concept: Implications for palaeoecology and palichnostratigraphy. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 241–268.

Lockley, M.G., Hunt, A.P., Haubold, H. and Lucas, S.G. (1995). Fossil footprints in the DeChelly Sandstone of Arizona: with paleoecological observations on the ichnology of dune facies. *Bulletin of New Mexico Museum of Natural History and Science*, 6, 225–233.

Lockley, M.G., Wright, J.L. and Matsukawa, M. (2001). A new look at *Magnoavipes* and so-called big bird tracks from Dinosaur Ridge (Cretaceous, Colorado). *The Mountain Geologist*, 38. 137–146.

Lockley, M.G., Matsukawa, M. and Jianjun, L. (2003). Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. *Ichnos*, 10, 169–177.

Lockley, M.G., Lucas, S.G., Hunt, A.P. and Gaston, R. (2004). Ichnofaunas from the Triassic–Jurassic boundary sequences of the Gateway area, western Colorado: implications for faunal composition and correlation with other areas. *Ichnos*, 11, 89–102.

Lockley, M.G., Matsukawa, M., Ohira, H., Li, J., Wright, J., White, D. and Chen, P. (2006). Bird track from Liaoning Province, China: New insights into avian Evolution during the Jurassic-Cretaceous transition. *Cretaceous Research*, 27, 33–43.

Lockley, M.G., Roberts, G. and Kim, J.Y. (2008a). In the footprints of our ancestors: an overview of the hominid track record. *Ichnos*, 15, 106–125.

Lockley, M.G., Garcia-Vasquez, R., Espinoza, E. and Lucas, S.G. (2008b). America's most famous hominid footprints: history and context of tracks from Nicaragua. *Ichnos*, 15, 55–69.

Löffler, E. and Margules, C. (1980). Wombats detected from space. *Remote Sensing of Environment*, 9, 47–56.

Lohrer, A.M., Thrush, S.F. and Gibbs, M.M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, 431, 1092–1095.

Loope, D.B. (1992). Comment on "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin". *Geology*, 20, 667–668.

Loope, D.B. (2006). Dry-season tracks in dinosaur-triggered grainflows. *Palaios*, 21, 132–142.

Loope, D.B. (2008). Life beneath the surfaces of active Jurassic dunes: Burrows from the Entrada Sandstone of south-central Utah. *Palaios*, 23, 411–419.

López Cabrera, M.I., Olivero, E.B., Carmona, N.B. and Ponce, J.J (2008). Cenozoic trace fossils of the *Cruziana, Zoophycos* and *Nereites* ichnofacies from the Fuegian Andes, Argentina. *Ameghiniana*, 45, 377–392.

Lord, A.R. (1990). The Pleistocene–Holocene transition in southwestern Sweden and the recognition of deglaciation effects in adjacent seas. In Glacimarine Environments: Processes and Sediments, ed. J.A.. Dowdeswell and J.D. Scourse, *Geological Society, London, Special Publications*, 53, 317–328.

Loutit, T.S., Hardenbol, J., Vail, P.R. and Baum, G.R. (1988). Condensed sections: the Key to age determination and correlation of continental margin sequences. In *Sea Level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S.Hastings, C.G.St.C. Kendell, H.W. Posamentier, C.A. Ross and J.C. van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 183–213.

Lovegrove, B.G. and Siegfried, W.R. (1989). Spacing and origins of Mima-like earth mounds in the cape of South Africa. *South African Journal of Science*, 85, 108–112.

Löwemark, L. and Schäfer, P. (2003). Ethological implications from a detailed X-ray radiograph and 14C-study of the modern deep-sea Zoophycos. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 101–21.

Löwemark, L., Schönfeld, J., Werner, F. and Schäfer, P. (2004). Trace fossils as a paleoceanographic tool: evidence from late Quaternary sediments of the southwestern Iberian margin. *Marine Geology*, 204, 27–41.

Löwemark, L., Lin, H.L. and Sarnthein, M. (2006). Temporal variations of the trace fossil *Zoophycos* in a 425 ka long sediment record from the South China Sea: implications for the ethology of the *Zoophycos* producer. *Geological Magazine*, 143, 105–114.

Löwemark, L., Lin, I.T, Wang, C.H. and Schönfeld, J. (2007). A test of the Gradening Hypothesis for the trace fossil *Zoophycos*. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R. Bromley, L.A. Buatois, M.G. Mángano, J. Genise and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 79–86.

Lucas, S.G. (2001). Taphotaxon. *Lethaia*, 34, 30.

Lucas, S.G. (2004). A global hiatus in the Middle Permian tetrapod fossil record. *Stratigraphy*, 1, 47–64.

Lucas, S.G. (2007). Tetrapod footprint biostratigraphy and biochronology. *Ichnos*, 14, 5–38.

Lucas, S.G. and Hunt, A.P. (2006). Permian tetrapod footprint: Bioestratigraphy and biocronology. In *Non-marine Permian biostratigraphy and Biocronology*, ed. S.G. Lucas, G. Cassinis and J.W. Schneider, *Society for Sedimentary Geology Special Publication*, 265, 179–200.

Lucas, S.G. and Lerner, A.J. (2005). Lower Pennsylvanian invertebrate ichnofossils from the Union Chapel Mine, Alabama; a preliminary assessment. *Alabama Paleontological Society, Monographs*, 1, 147–152.

Lucas, S.G. and Lerner, A.J. (2006). Invertebrate ichnofossil assemblages of the Upper Triassic Redonda Formation at Mesa Redonda, East-Central New Mexico. In: *The Triassic-Jurassic Terrestrial Transition*, ed. J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 122–136.

Lucas, S.G., Lozovsky, V.R. and Shishkin, M.A. (1999). Tetrapod footprint from Early Permian redbeds of the northern Caucasus, Russia. *Ichnos*, 6, 277–281.

Lucas, S.G., Morgan, G.S., Hawley, J.W., Love, D.W. and Myers, R.G. (2002). Mammal footprints from the upper Pleistocene of the Tularosa Basin, Doña Ana County, New Mexico. In *Geology of White Sands*, ed. V. Lueth, K.A. Giles, S.G. Lucas, B.S. Kues, R.G. Myers and D. Ulmer-Scholle, *New Mexico Geological Society Guide Book*, 53, 285–288.

Lucas, S.G., Hunt, A.P., Mansky, C. and Calder, J.H. (2004a). The oldest tetrapod footprint ichnofaunas, from the Lower Mississippian Horton Bluff Formation, Nova Scotia, Canada. *Geological Society of America, Abstracts with Programs*, 36, 66.

Lucas, S.G, Lerner, A.J. and Hunt, A.P. (2004b). Permian tetrapod footprints from the Lucero Uplift, central New Mexico, and Permian footprint biostratigraphy. In *Carboniferous–Permian Transition at Carrizo Arroyo, Central New Mexico*, ed. S.G. Lucas and K.E. Ziegler, *New Mexico Museum of Natural History and Science Bulletin*, 25, 291–300.

Lucas, S.G., Lerner, A.J., Hannibal. J.T., Hunt, A.P. and Schneider, J.W. (2005). Trackway of a giant *Arthropleura* from the Upper Pennsylvanian of El Cobre Canyon, New Mexico. *New Mexico Geological Society, 56th Field Conference Guidebook, Geology of the Chama Basin*, pp. 279–282.

Lucas S.G., Lerner A.J., Spielmann, J.A. and Hunt, A.P. (2006a). Invertebrate ichnofossils from the Upper Triassic Bull Canyon Formation, east central New Mexico. In *The Triassic–Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 118–121.

Lucas S.G., Lerner A.J., Milner A.C. and Lockley M.G. (2006b). Lower Jurassic invertebrate ichnofossils from a clastic lake margin, Johnson Farm, Southwestern Utah. In *The Triassic-Jurassic Terrestrial Transition*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 128–136.

Lucas, S.G., Gobetz, K.E., Odier, G.P., McCormick, T. and Egan, C. (2006c). Tetrapod burrows from the Lower Jurassic Navajo Sandstone, southeast Utah. In *The Triassic-Jurassic Terrestrial Transtion*, ed. H.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner and J.I. Kirkland, *New Mexico Museum of Natural History and Science Bulletin*, 37, 147–154.

Lucas, S.G., Spielmann, J.A., Klein, K. and Lerner, A.J. (2010a). Ichnology of the Upper Triassic (Apachean) Redonda Formation, east-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 47, 1–75.

Lucas, S.G., Minter, N. and Hunt, A.P. (2010b). Re-evaluation of alleged bees' nests from the Upper Triassic of Arizona. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 286, 194–201.

Lyell, C. (1830). *Principles of Geology*. London: John Murray.

MacArthur, R.H. and Wilson E.O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

MacEachern, J.A. and Burton, J.A. (2000). Firmground *Zoophycos* in the Lower Cretaceous, Viking Formation Alberta: a distal expression of the *Glossifungites* ichnofacies. *Palaios*, 15, 387–398.

MacEachern, J.A. and Gingras, M. (2007). Recognition of brackish-water trace fossil assemblages in the Cretaceous western interior seaway of Alberta. In *Sediment-Organism Interactions: A Multifaceted Ichnology*, ed. R. Bromley, L.A. Buatois, M.G. Mángano, J. Genise and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 149–194.

MacEachern, J.A. and Pemberton, S.G. (1992). Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton. *Society for Sedimentary Geology Core Workshop*, 17, 57–84.

MacEachern, J.A. and Pemberton, S.G. (1994). Ichnological aspects of incised valley fill systems from the Viking Formation of the Western Canada Sedimentary Basin, Alberta, Canada. In *Incised Valley Systems: Origin and Sedimentary Sequences*, ed. R. Boyd, B.A. Zaitlin and R. Dalrymple, *Society for Sedimentary Geology Special Publication*, 51, 129–157.

MacEachern, J.A. and Pemberton, S.G. (1997). Ichnology: biogenic utility in genetic stratigraphy. *Canadian Society of Petroleum Geologists and Society for Sedimentary Geology Joint Convention (Calgary), Notes Core Conference*, 387–412.

MacEachern, J.A., Raychaudhuri, I. and Pemberton, S.G. (1992). Stratigraphic applications of the *Glossifungites* ichnofacies: delineating discontinuities in the rock record. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 169–198.

MacEachern, J.A., Zaitlin, B.A. and Pemberton, S.G. (1998). High-resolution sequence stratigraphy of early transgressive deposits, Viking Formation, Joffre Field, Alberta, Canada. *American Association of Petroleum Geologists, Bulletin*, 82, 729–756.

MacEachern, J.A., Zaitlin, B.A. and Pemberton, S.G. (1999a). A sharp-based sandstone of the Viking Formation, Joffre Field, Alberta, Canada: criteria for recognition of transgressively incised shoreface complexes. *Journal of Sedimentary Research*, 69, 876–892.

MacEachern, J.A., Stelck, C.R. and Pemberton, S.G. (1999b). Marine and marginal marine mudstone deposition: paleoenvironmental interpretations based on the integration of ichnology, palynology and foraminiferal paleoecology. In *Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic Analysis and Sedimentological Interpretation*, ed. K.M. Bergman and J.W. Snedden, *Society for Sedimentary Geology Special Publication*, 64, 205–225.

MacEachern, J.A., Zaitlin, B.A. and Pemberton, S.G. (1999c). Coarse-grained, shoreline-attached, marginal-marine parasequences of the Viking Formation, Joffre Field, Alberta, Canada. In *Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic Analysis and Sedimentological Interpretation*, ed. K.M. Bergman and J.W. Snedden, *Society for Sedimentary Geology Special Publication*, 64, 273–296.

MacEachern, J.A., Bann, K.L., Bhattacharya, J.P. and Howell, C.D. Jr. (2005). Ichnology of deltas: organism responses to the dynamic interplay of rivers, waves, storms, and tides. In *River Deltas: Concepts, Models, and Examples*, ed. L. Giosan and J.P. Bhattacharya, *Society for Sedimentary Geology Special Publication*, 83, 49–85.

MacEachern, J.A., Bann, K.L., Pemberton, S.G. and Gingras, M.K. (2007a). The Ichnofacies paradigm: High-resolution paleoenvironmental interpretation of the rock record. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 27–64.

MacEachern, J.A., Pemberton, S.G. and Bhattacharya, J.P. (2007b). Ichnological and sedimentological evaluation of the Ferron Sandstone Cycles in Ivie Creek Cores #3 and #11. In *Ichnological Applications to Sedimentological and Sequence Stratigraphic Problems*, ed. J.A. MacEachern, M.K. Gingras, K.L. Bann and S.G. Pemberton, *Society for Sedimentary Geology Research Conference Abstract Volume*, 144–174.

MacEachern, J.A., Pemberton, S.G., Gingras, M.K., Bann, K.L. and Dafoe, L.T. (2007c). Use of trace fossils in genetic stratigraphy. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 110–134.

Mackie, G.L. (2001). *Applied Aquatic Ecosystem Concepts*. Dubuque, IA: Kendall/Hunt.

MacNaughton, R.B. (2007). The application of trace fossils to biostratigraphy. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 135–158.

MacNaughton, R.B. and Narbonne, G.M. (1999). Evolution and ecology of Neoproterozoic-Lower Cambrian trace fossils, NW Canada. *Palaios*, 14, 97–115.

MacNaughton, R.B. and Pickerill, R.K. (1995). Invertebrate ichnology of the nonmarine Lepreau Formation (Triassic), southern New Brunswick, eastern Canada. *Journal of Paleontology*, 69, 160–171.

MacNaughton, R.B. and Pickerill, R.K. (2003). Taphonomy and the taxonomy of trace fossils: a commentary. *Lethaia*, 36, 66–70.

MacNaughton, R.B., Narbonne, G.M., Dalrymple, R.W. (2000). Neoproterozoic slope deposits, Mackenzie Mountains, northwestern Canada: implications for passive-margin development and Ediacaran faunal ecology. *Canadian Journal of Earth Sciences*, 37, 997–1020.

MacNaughton, R.B., Cole, J.M., Dalrymple, R.W., Braddy, S.J., Briggs, D.E.G. and Lukie, T.D. (2002). First steps on land: Arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology*, 5, 391–394.

Macsotay, O. (1967). Huellas problemáticas y su valor paleoecológico en Venezuela. *Geos*, 16, 7–79.

Maerz, R.H. Jr., Kaesler, R.L. and Hakes, W.G. (1976). Trace fossils from the Rock Bluff Limestone (Pennsylvanian, Kansas). *The University of Kansas Paleontological Contributions*, 80, 1–6.

Mafart, B. (2006). Anthropological study of Holocene human footprints of the sebkra El Azrag (Islamic Republic of Mauritania). *Anthropologie*, 110, 766–787.

Magwood, J.P.A. (1992). Ichnotaxonomy: a burrow by any other name? In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Short Courses in Paleontology*, 5, 15–33.

Magwood, J.P.A. and Pemberton, S.G. (1990). Stratigraphic significance of Cruziana: New data concerning the Cambrian–Ordovician ichnostratigraphic paradigm. *Geology*, 18, 729–732.

Main, B.Y. (1982). Adaptations to arid habitats by mygalomorph spiders. In *Evolution of the Flora and Fauna of Arid Australia*, ed. W.R. Barker and P.J.M. Greenslade, Norwood, Australia: Peacock Publications, pp. 273–283.

Malanson, G.P. (1993). *Riparian Lanscapes.* Cambridge, UK: Cambridge University Press.

Mángano, M.G. (2011). Trace-fossil assemblages in a Burgess Shale-type deposit from the Stephen Formation at Stanley Glacier, Canadian Rocky Mountains: Unraveling ecologic and evolutionary controls. In *Proceedings of the International Conference on the Cambrian Explosion*, ed. P.A. Johnston and K.J. Johnston, *Palaeontographica Canadiana*, 31, in press.

Mángano, M.G. and Buatois, L.A. (1991). Discontinuity surfaces in the Lower Cretaceous of the High Andes (Mendoza, Argentina): Trace fossils and environmental implications. *Journal of South American Earth Sciences*, 4, 215–229.

Mángano, M.G. and Buatois, L.A. (1994). Trazas fósiles e icnofábricas en depósitos carbonáticos cretácicos, Las Cuevas, Alta Cordillera de Mendoza. *Ameghiniana*, 31, 55–66.

Mángano, M.G. and Buatois, L.A. (1995a). A conceptual framework for trace fossil lagerstatten. *2nd International Symposium on Lithographic Limestones, Extended Abstracts*, 103–105.

Mángano, M.G. and Buatois, L.A. (1995b). Biotic response to volcanic and sedimentologic processes in a Gondwanic active plate margin basin; the Arenig-Llanvirn Suri Formaiton, Famatina Basin, Northwest Argentina. *Field Trip Guidebook- Pacific section, Society for Sedimentary Geology*, 77, 229–232.

Mángano, M.G. and Buatois, L.A. (1996). Shallow marine event sedimentation in a volcanic arc-related setting: the Ordovician Suri Formation, Famatina Range, northwest Argentina (Famatina System). *Sedimentary Geology*, 105, 63–90.

Mángano, M.G. and Buatois, L.A. (1997). Slope apron deposition in an Ordovician arc-related setting, Chaschuil area, Famatina Basin, Northwest Argentina. *Sedimentary Geology*, 109, 155–180.

Mángano, M.G. and Buatois, L.A. (1999a). Feeding adaptations. In *Encyclopedia of Paleontology, Volume 1*, ed. R. Singer, Chicago: Fitzroy Dearborn Publishers, pp. 458–465.

Mángano, M.G. and Buatois, L.A. (1999b). Ichnofacies models in Early Paleozoic tide-dominated quartzites: onshore–offshore gradients and the classic Seilacherian paradigm. *Acta Universitatis Carolinae*, 43, 151–154.

Mángano, M.G. and Buatois, L.A. (2003a). Trace Fossils. In *Ordovician Fossils of Argentina*, ed. J.L. Benedetto, Cordoba, Spain: Universidad Nacional de Córdoba, Secretaría de Cienciay Tecnología, pp. 507–553.

Mángano, M.G. and Buatois, L.A. (2003b). *Rusophycus leifeiriksson*i en la Formación Campanario: Implicancias paleobiológicas, paleoecológicas y paleoambientales. In *Icnología: Hacia una convergencia entre geología y biología*, ed. L.A. Buatois and M.G. Mángano, *Publicación Especial de la Asociación Paleontológica Argentina*, 9, 65–84.

Mángano, M.G. and Buatois, L.A. (2004a). Ichnology of Carboniferous tide-influenced environments and tidal flat variability in the North American Midcontinent. In *The application of ichnology to palaeoenvironmental and stratigraphic analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 157–178.

Mángano, M.G. and Buatois, L.A. (2004b). Reconstructing Early Phanerozoic intertidal ecosystems: Ichnology of the Cambrian Campanario Formation in northwest Argentina. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils and Strata*, 51, 17–38.

Mángano, M.G. and Buatois, L.A. (2004c). Decoupling of ichnotaxonomic diversification and mixground ecology during the Early Cambrian. In *First International Congress on ichnology, Trelew, Argentina*, ed. L.A. Buatois and M.G. Mángano, Museo Paleontologico Egidio Fureglio, 50.

Mángano, M.G. and Buatois, L.A. (2006). Nemakit-Daldynian ichnofaunas: Evidence of a phylogenetic fuse to the Cambrian explosion? *Geological Society of America Annual Meeting, Abstracts with Program*, 474.

Mángano, M.G. and Buatois, L.A. (2007). Trace fossils in evolutionary paleoecology. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 391–409.

Mángano, M.G. and Buatois, L.A. (2011). Timing of Infaunalization in shallow-marine Early Paleozoic communities in Gondwanan Settings: Discriminating evolutionary and paleogeographic controls. *Palaeontologica Electronica*, 14, in press.

Mángano, M.G. and Caron, J.B. (2008). What can trace fossils tell us about the Burgess Shale? In *Second International Congress on Ichnology, Cracow*, ed. A. Uchman, *Polish Geological Institute Abstract Book*, pp. 73–75.

Mángano, M.G. and Droser, M.L. (2004). The ichnologic record of the Ordovician radiation. In *The Great Ordovician Biodiversification Event*, ed. B.D. Webby, F. Paris, M.L. Droser and I.G. Percival, New York: Columbia University Press.

Mángano, M.G., Buatois, L.A., Wu, X., Sun, J. and Zhang, G. (1994). Sedimentary facies, depositional processes and climatic controls in a Triassic lake, Tanzhuang Formation, western Henan Province, China. *Journal of Paleolimnology*, 11, 41–65.

Mángano, M.G., Buatois, L.A. and Claps, G. (1996a). Grazing trails formed by soldier fly larvae (Diptera, Stratiomyidae) and their paleoenvironmental and paleoecological implications for the fossil record. *Ichnos*, 4, 163–167.

Mángano, M.G., Buatois, L.A. and Aceñolaza, G.F. (1996b). Trace fossils and sedimentary facies from an Early Ordovician tide-dominated shelf (Santa Rosita Formation, northwest Argentina): Implications for ichnofacies models of shallow marine successions. *Ichnos*, 5, 53–88.

Mángano, M.G., Buatois, L.A. and Aceñolaza, F.G. (1996c). Icnología de ambientes marinos afectados por vulcanismo: La Formación Suri, Ordovícico del extremo norte de la sierra de Narváez, Sistema del Famatina. *Asociación Paleontológica Argentina, Publicación Especial*, 4, 69–88.

Mángano, M.G., Buatois, L.A., Maples, C.G. and Lanier, W.P. (1997). *Tonganoxichnus*, a new insect trace fossil from the Upper Carboniferous of eastern Kansas, USA. *Lethaia*, 30, 113–125.

Mángano, M.G., Buatois, L.A., West, R.R. and Maples, C.G. (1998). Contrasting behavioral and feeding strategies recorded by tidal-flat bivalve trace fossils from the Upper Carboniferous of eastern Kansas. *Palaios*, 13, 335–351.

Mángano, M.G., Buatois, L.A., West, R.R. and Maples, C.G. (1999). The origin and paleoecologic significance of the trace fossil *Asteriacites* in the Pennsylvanian of Kansas and Missouri. *Lethaia*, 32, 17–30.

Mángano, M.G., Buatois, L.A., Maples, C.G. and West, R.R. (2000). A new ichnospecies of *Nereites* from Carboniferous tidal-flat facies of eastern Kansas, USA: Implications for the *Nereites-Neonereites* debate. *Journal of Paleontology*, 74, 149–157.

Mángano, M.G., Labandeira, C., Kvale, E. and Buatois, L.A. (2001a). The insect trace fossil *Tonganoxichnus* from the Middle Pennsylvanian of Indiana: Paleobiologic and paleoenvironmental implications. *Ichnos*, 8, 165–175.

Mángano, M.G., Buatois, L.A. and Moya, M.C. (2001b). Trazas fósiles de trilobites de la Formación Mojotoro (Ordovícico inferior-medio de Salta, Argentina): Implicancias paleoecológicas, paleobiológicas y bioestratigráficas. *Revista Española de Paleontología*, 16, 9–28.

Mángano, M.G., Buatois, L.A., West, R.R. and Maples, C.G. (2002a). Ichnology of a Pennsylvannian Equatorial Tidal Flat: the Stull Shale Member at Waverly, Eastern Kansas. *Kansas Geological Survey*, 245, 1–133.

Mángano, M.G., Buatois, L.A. and Rindsberg, A.K. (2002b). Carboniferous *Psammichnites*: systematic re-evaluation, taphonomy and autecology. *Ichnos*, 9, 1–22.

Mángano, M.G., Buatois, L.A. and Muñiz-Guinea, F. (2002c). *Rusophycus moyensis* n. isp. en la transición Cámbrica-Tremadociana del noroeste Argentino: implicancias paleoambientales y bioestratigráficas. *Revista Brasileira de Paleontologia*, 4, 35–44.

Mángano, M.G., Buatois, L.A. and Muñiz-Guinea, F. (2005a). Ichnology of the Alfarcito Member (Santa Rosita Formaiton) of northwestern Argentina: animal–substrate interactions in a lower Paleozoic wave-dominated shallow sea. *Ameghiniana*, 42, 641–668.

Mángano, M.G., Carmona, N.B., Buatois, L.A. and Muñiz-Guinea, F. (2005b). A new ichnospecies of *Arthrophycus* from the Upper Cambrian-lower Tremadocian of northwest Argentina: Implications for the Arthrophycid lineage and potential in ichnostratigraphy. *Ichnos*, 12, 179–190.

Mángano, M.G., Hofmann, R., Elicki, O. and Shinaq, R. (2007). The aftermath of the agronomic revolution: Trace fossils from Lower to Middle Cambrian marginal-marine environments, Hanneh Member, Burj Formation, southern Dead Sea, Jordan. *Quinta Reunion Argentina de Icnologia y Tercera Reunion de Icnologia del Mercosur*, 23.

Mangum, C.P. (1964). Studies on speciation in maldanid polychaetes of the North American Atlantic coast II. Distribution and competitive interaction of five sympatric species. *Limnology and Oceanography*, 9, 12–26.

Manning, P.L. (2008). *T. rex* speed trap. In *Tyrannosaurs rex: The Tyrant King*, ed. K. Carpenter and P.L. Larson, Bloomington, IN: Indiana University Press, pp. 204–231.

Manning, P.L., Margetts, L., Johnson, M.R., Withers, P., Sellers, W.I., Falkingham, P.L., Mummery, P.M., Barret, P.M. and Raymont, D.R. (2009). Biomechanics of dromaeosaur dinosaur claws: Application of x-ray microtomography, nanoidentation and finite element analysis. *Invited paper, Anatomical Record*, 292, 1397–1405.

Manton, S.M. (1977). The *Arthropoda. Habits, Functional Morphology, and Evolution*. Oxford UK: Clarendon Press.

Maples, C.G. and Archer, A.A. (1986). Shoaling-upward sequences and facies-dependent trace fossils in the Monteagle Limestone (Mississippian) of Alabama. *Southeastern Geology*, 27, 35–43.

Maples, C.G. and Archer, A.A. (1989). The potential of Paleozoic nonmarine trace fossils for paleoecological interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 73, 185–195.

Marshall, C.D. (2006). Explaining the Cambrian "explosion" of animals. *Annual Review of Earth and Planetary Science*, 34, 355–384.

Marintsch, E. J., and Finks, R. M. (1982). Lower Devonian ichnofacies at Highland Mills, New York and their gradual replacement across environmental gradients. *Journal of Paleontology*, 56, 1050–1078.

Marsicano, C.A., Arcucci, A., Mancuso, A.C. and Caselli, A. (2004). Early–Middle Triassic tetrapod footprints of southern South America: a phylogenetic approach. *Ameghiniana*, 41, 171–184.

Marsicano, C.A., Domnanovich, N. and Mancuso, A.C. (2007). Dinosaur origins: evidence from the footprint record. *Historical Biology*, 19, 83–91.

Marsicano, C.A., Mancuso, A.C., Palma, R.M. and Krapovickas, V. (2010). Tetrapod tracks in a marginal lacustrine setting (Middle Triassic, Argentina): taphonomy and significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291, 388–399.

Martin, A.J. (1993). Semiquantitative and statistical analysis of bioturbate textures, Sequatchie Formation (Upper Ordovician), Georgia and Tennessee, USA. *Ichnos*, 2, 117–136.

Martin, A.J. (2006a). Resting traces of *Ocypode qudrata* associated with hydration and respiration: Sapelo Island, Georgia, USA. *Ichnos*, 13, 57–68.

Martin, A.J. (2006b). A composite trace fossil of decapod and hymenopteran origin from the Rice Bay Formation (Holocene), San Salvador, Bahamas. *The 12th Symposium on the Geology of the Bahamas and other Carbonate Regions*, pp. 99–112.

Martin, A.J. and Pyenson, N.D. (2005). Behavioral significance of vertebrate trace fossils from the Union Chapel site. *Alabama Paleontological Society, Monographs*, 1, 59–73.

Martin, A.J., Close, J.C. and Simones, G.C. (1994). Theoretical and practical considerations of integrating subsurface ichnological and geophysical data in Late Cretaceous strata, southeastern Atlantic Coastal Plain, USA. *14th International Sedimentological Congress (Recife), Abstracts of Papers*, S52–S53.

Martin, K.D. (2004). A re-evaluation of the relationship between trace fossils and dysoxia. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 141–156.

Martin, L.D. and Bennett, D.K. (1977). The burrows of the Miocene beaver *Paleocastor*, western Nebraska, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 22, 173–193.

Martin, M.A. and Pollard, J.E. (1996). The role of trace fossil (ichnofabric) analysis in the development of depositional models for the Upper Jurassic Fulmar Formation of the Kittiwake Field (Quadrant 21 UKCS). In *Geology of the Humber Group: Central Graben and Moray Firth, UKCS*, ed. A. Hurst, *Geological Society Special Publication*, 114, 163–183.

Martin, M.W., Grazhdankin, D.V., Bowring, S.A., Evans, D.A.D., Fedonkin, M.A. and Kirschvink, J.L. (2000) Age of Neoproterozoic bilaterian body and trace fossils, White Sea, Russia: implications for metazoan evolution. *Science*, 288, 841–845.

Martin, P., Boes, X., Goddeeris, B. and Fagel, N. (2005). A qualitative assessment of the influence of bioturbation in Lake Baikal sediments. *Global Planet Change*, 46, 87–99.

Martinell, J. and Domènech, R. (1995). Bioerosive structures on the Pliocene rocky shores of Catalonia (Spain). *Revista Española de Paleontologia*, 10, 37–44.

Martinius, A.W. and Molenaar, N. (1991). A coral–mollusc (*Goniaraea–Crassatella*) dominated hardground community in a siliciclastic-carbonate sandstone (the Lower Eocene Roda Formation, Southern Pyrenees, Spain). *Palaios*, 6, 142–155.

Martinius, A. W., Kaas, I., Næss, A., Helgesen, G., Kjærefjord, J.M, and Leith, D.A. (2001) Sedimentology of the heterolithic and tide-dominated Tilje Formation (Early Jurassic, Halten Terrace offshore mid-Norway). In *Sedimentary environments Offshore Norway: Palaeozoic to Recent*, ed. O. Martinsen and T. Dreyer, *Norwegian Petroleum Society, Special Publication*, 10, 103–144.

Martinsson, A. (1970). Toponomy of trace fossils. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 323–330.

Mason, T.R. (1980). Formation and diagenesis of Visean trace fossils from Ireland. *Lethaia*, 13, 229–237.

Masselink, G. and Hegge, B.J. (1995). Morphodynamics of meso- and macrotidal beaches. Examples from central Queensland. *Marine Geology*, 129, 1–23.

Masselink, G. and Short, A.D. (1993). The effect of tidal range on beach morphodynamics and morphology: a conceptual beach model. *Journal of Coastal Research*, 9, 785–800.

Mastrolorenzo, G., Petrone, P., Pappalardo, L. and Sheridan, M.F. (2006). The Avellino 3780-yr-B.P. catastrophe as a worst-case scenario for a future eruption at Vesuvius. *Proceedings of the National Academy of Sciences, USA*, 103, 4366–4370.

Matthews, S.C. and Missarzhevsky, V.V. (1975). Small shelly fossils of late Precambrian and Early Cambrian age: a review of recent work. *Journal of the Geological Society, London*, 131, 289–304.

Mata, S.A. and Bottjer, D.J. (2009) The paleoenvironmental distribution of Phanerozoic wrinkle structures. *Earth Science Reviews*, 96, 181–195.

Matz, M.V., Frank, T.M., Marshall, N.J., Widder, E.A. and Johnsen, S. (2008). Giant deep-sea Protist produces bilaterian-like traces. *Current Biology*, 18, 1849–1854.

Mayor, A. and Sarjeant, W.A.S. (2001). The folklore of footprints in stone: From classical antiquity to the present. *Ichnos*, 8, 143–163.

Mayoral, E. and Muñiz, F. (1996). La icnofacies de *Gnathichnus* en el sector suroccidental de la Cuenca del Guadalquivir (Lepe, Huelva, España). *Coloquios de Paleontología*, 48, 71–82.

McCann, T. (1990). Distribution of Ordovician-Silurian ichnofossil assemblages in Wales: Implications for Phanerozoic ichnofaunas. *Lethaia*, 23, 243–255.

McCann, T. (1993). A *Nereites* ichnofacies from the Ordovician–Silurian Welsh basin. *Ichnos*, 3, 39–56.

McCann, T. and Pickerill, R.K. (1988). Flysch trace fossils from the Cretaceous Kodiak Formation of Alaska. *Journal of Paleontology*, 62, 330–348.

McCrea, R.T., Pemberton, S.G. and Currie, P J. (2004). New ichnotaxa of mammal and reptile tracks from the upper Paleocene of Alberta. *Ichnos*, 11, 323–339.

McGhee, G.R. Jr. (1996). *The Late Devonian Mass Extinction*. New York: Columbia University Press.

McGhee, G.R. Jr. (2001). The "multiple impacts hypothesis" for mass extinction: a comparison of the late Devonian and the late Eocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 176, 47–58.

McGhee, G.R. Jr., Sheehan, P.M., Bottjer, D.J. and Droser, M.L. (2004). Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 211, 289–297.

McIlroy, D. (2004a). Some Ichnolgical concepts, methodologies, applications and frontiers. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 3–27.

McIlroy, D. (2004). Ichnofabrics and sedimentary facies of a tide-dominated delta: Jurassic Ile Formation of Kristin Field, Haltenbanken, Offshore Mid-Norway. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, Geological Society Special Publication, 228, 237–272.

McIlroy, D. (2007a). Lateral variability in shallow marine ichnofabrics; implications for the ichnofabric analysis method. *Journal of the Geological Society, London*, 164, 359–369.

McIlroy, D. (2007b). Ichnology of a macrotidal tide-dominated deltaic depositional system: Lajas Formation, Neuquén Province, Argentina. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 195–211.

McIlroy, D. (2008). Ichnological analysis: the common ground between ichnofacies workers and ichnofabric analysts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 332–338.

McIlroy, D. (2010). Biogenic cross-lamination produced by the pistol-shrimp *Alpheus bellulus* in microcosm experiments. *Journal of Sedimentary Research*, 80, 151–154.

McIlroy, D. and Garton, M. (2004). A worm's eye view of the Early Palaeozoic sea floor. *Geology Today*, 20, 224–230.

McIlroy, D. and Logan, G.A. (1999). The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. *Palaios*, 14, 58–72.

McIlroy, D., Worden, R.H. and Needham, S.J. (2003). Faeces, clay minerals and reservoir potential. *Journal of the Geological Society, London*, 160, 489–493.

McIlroy, D., Brasier, M.D. and Lang, A.S. (2009) Smothering of microbial mats by macrobiota: implications for the Ediacara biota. *Journal of the Geological Society*, 166, 1117–1121.

McKeever, P.J. (1991). Trackway preservation in eolian sandstones from the Permian of Scotland. *Geology*, 19, 726–729.

McKeever, P.J. and Haubold, H. (1996). Reclassification of vertebrate trackways from the Permian of Scotland and related forms from Arizona and Germany. *Journal of Paleontology*, 70, 1011–1022.

McLusky, D.S. (1989). *The Estuarine Ecosystem. 2nd edn.* London: Blackie.

Meadows, A., Meadows, P.S. and McLoughlin, P. (1998). Spatial heterogeneity in an intertidal sedimentary environment and it's macrobenthic community. In *Sedimentary Processess in the Intertidal Zone*, ed. K.S. Black, D.M. Patterson and A. Cramp, *Geological Society Special Publication*, 139, 367–388.

Meadow, P.S. and Anderson, J.G. (1968). Micro-organisms attached to marine sand grains. *Journal of the Marine Biology Association of the United Kingdom*, 48, 161–175.

Melchor, R.N. (2001). Icnología y sedimentología de una sucesión lacustre influenciada por tormentas: Formación Los Rastros (Triásico), Talampaya, La Rioja. *Abstracts 4th Reunión Argentina de Icnología and 2nd Reunión de Icnología del Mercosur*, *San Miguel de Tucumán*, 56.

Melchor, R.N. (2004). Trace fossil distribution in lacustrine deltas: examples from the Triassic rift lakes of the Ischigualasto-Villa Union Basin, Argentina. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 335–354.

Melchor, R.N. (2007). Changing lake dynamics and sequence stratigraphy of synrift lacustrine strata in a haf-graben: an example from the Triassic Ischigualasto–Villa Unión Basin, Argentina. *Sedimentology*, 54, 1417–1446.

Melchor, R.N. and Genise, J.F. (2004a). Critical appraisal of vertebrate ichnotaxonomy. *32nd International Geological Congress Italia 2004, Abstracts part 1. International Union of Geological Sciences*, 597.

Melchor, R.N. and Genise, J.F. (2004b). Vertebrate vs. Invertebrate ichnology…or one ichnology. In *First International Congress on Ichnology, Trelew, Argentina*, ed. L.A. Buatois and M.G. Mángano, *Museo Paleontólogico Egidio Feruglio Abstract Book*, 55–56.

Melchor, R.N. and Sarjeant, W.A.S. (2004). Small amphibian and reptile footprints from the Permian Carapacha Basin, Argentina. *Ichnos*, 11, 57–78.

Melchor, R.N., Genise, J.F. and Miquel, S.E. (2002). Ichnology, sedimentology and paleontology of Eocene calcareous paleosols from a palustine sequence, Argentina. *Palaios*, 17, 16–35.

Melchor, R.N., Bellosi, E. and Genise, J.F. (2003). Invertebrate and vertebrate trace fossils from a lacustrine delta: The Los Rastros Formation, Ischigualasto Provincial Park, San Juan, Argentina. In *Icnología: Hacia una Convergencia entre Geología y Biología*, ed. L.A. Buatois and M.G. Mángano, *Asociación Paleontológica Argentina Publicación Especial*, 9, 17–33.

Melchor, R.N., Bedatou, E., Valais, S. de and Genise, J.F. (2006). Lithofacies distribution of invertebrate and vertebrate trace fossil assemblages in an Early Mesozoic ephemeral fluvio- lacustrine system from Argentina: Implications for the *Scoyenia* ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239, 253–285.

Meldrum, D.J., Lockley, M.G., Lucas, S.G. and Mussiba, C. (2011). Ichnotaxonomy of the Laetoli trackways: the earliest hominin footprints. *Journal of African Earth Sciences*, in press.

Mellere, D. and Steel, R.J. (1995). Facies architecture and sequentiality of nearshore and "shelf" sandbodies; Haystack Mountains Formation, Wyoming, USA. *Sedimentology*, 42, 551–574.

Metz, R. (1991). Scratch circles from the Towaco Formation (Lower Jurassic), Riker Hill, Roseland, New Jersey. *Ichnos*, 1, 233–235.

Metz, R. (1993). A new ichnospecies of *Spongeliomorpha* from the Late Triassic of New Jersey. *Ichnos*, 2, 259–262.

Metz, R. (1995). Ichnologic study of the Lockatong Formation (Late Triassic), Newark Basin, southeastern Pennsylvania. *Ichnos*, 4, 43–51.

Metz, R. (1996). Newark Basin ichnology: The Late Triassic Perkasie Member of the Passaic Formation, Sanatoga, Pennsylvania. *Notheastern Geology and Environmental Sciences*, 18, 118–129.

Metz, R. (2000). Triassic Trace Fossils from Lacustrine Shoreline Deposits of the Passaic Formation, Douglassville, Pennsylvania. *Ichnos*, 7, 243–318.

Miall, A.D. (1995). Whither stratigraphy? *Sedimentary Geology*, 100, 5–20.

Miall, A.D. (1996). *The Geology of Fluvial Deposits*. Berlin: Springer-Verlag.

Michener, C.D. (1979). Biogeography of the bees. *Annals of the Missouri Botanical Garden*, 66, 277–347.

Mietto, P., Avanzini, M. and Rolandi, G. (2003). Human footprints in Pleistocene volcanic ash. *Nature*, 422, 133.

Mikuláš, R. (1990). The ophiuroid *Taeniaster* as a tracemaker of *Asteriacites*, Ordovician of Czechoslovakia. *Ichnos*, 1, 133–137.

Mikuláš, R. (1992). The ichnogenus *Asteriacites*: paleoenvironmental trends. *Věstnik Ceského geologického ústavu*, 67, 423–433.

Mikuláš, R. (1995). Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic). *Journal of the Czech Geological Society*, 40, 37–45.

Mikuláš, R. (1997). Ethological interpretation of the ichnogenus *Pragichnus* Chlupáč, 1987 (Ordovician, Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie*, *Monatshefte*, 2, 93–108.

Mikuláš, R. (1998). Ordovician of the Barrandian area: Reconstruction of the sedimentary basin, its benthic communities and ichnoassemblages. *Journal of the Czech Geological Society*, 43, 143–159.

Mikuláš, R. (2003): The *Mermia* Ichnofacies across the fossilization barrier: a comparison of the Permian Krkonoše Piedmont Basin (Czech Republic) and modern flood sediments at Prague. VII International Ichnofabric Workshop, Program, Abstracts, pp. 44–45.

Mikuláš, R, (2008). Xylic substrates at the fossilization barrier: oak trunks (*Quercus* sp.) in the Holocene sediments of the Labe River, Czech Republic. In *Current Developments in Bioerosion*, ed. M. Wisshak and L. Tapanila, Berlin: Springer-Verlag, pp. 415–429.

Mikuláš, R. and Cílek, V. (1998). Terrestrial insect bioerosion and the possibilities of its fossilization. *Ichnos*, 5, 325–333.

Mikuláš, R. and Genise, J.F. (2003). Traces within traces: holes, pits and galleries in walls and fillings of insect trace fossils in paleosols. *Geologica Acta*, 1, 339–348.

Miller, G.D. (1986). The sediments and trace fossils of the Rough Rock Group on Cracken Edge, Derbyshire. *Mercian Geologist*, 10, 189–202.

Miller, M.F. (1984). Distribution of biogenic structures in Paleozoic non–marine and marine–margin sequences: an actualistic model. *Journal of Paleontology*, 58, 550–570.

Miller, M.F. (1991). Morphology and paleoenvironmental distribution of Paleozoic *Spirophyton* and *Zoophycos*: implications for the *Zoophycos* ichnofacies. *Palaios*, 6, 410–425.

Miller, M.F. (2000). Benthic aquatic ecosystems across the Permian–Triassic transition: record from biogenic structures in fluvial sandstones, central Transantarctic Mountains. *Journal of African Earth Sciences*, 31, 157–164.

Miller, M.F. and Byers, C.W. (1984). Abundant and diverse early Paleozoic infauna indicated by the stratigraphic record. *Geology*, 12, 40–43.

Miller, M.F. and Collinson, J.W. (1994). Trace fossils from Permian and Triassic sandy braided stream deposits, Central Transantarctic Mountains. *Palaios*, 9, 605–610.

Miller, M.F. and Johnson, K.G. (1981). *Spirophyton* in alluvial-tidal facies of the Catskill deltaic complex: possible biological control of ichnofossil distribution. *Journal of Paleontology*, 55, 1016–1027.

Miller, M.F. and Labandeira, C.C. (2003). Slow crawl across the salinity divide: Delayed colonization of freshwater ecosystems by invertebrates. *GSA Today*, 12, 4–10.

Miller, M.F. and Knox, L.W. (1985). Biogenic structures and depositional environments of a Lower Pennsylvanian coal-bearing sequence, northern Cumberland Plateau, Tennessee, USA. In *Biogenic Structures: their use in interpreting depositional environments*, ed. H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 67–97.

Miller, M.F. and Smail, S.E. (1997). A semiquantitative method for evaluating bioturbation on bedding planes. *Palaios*, 12, 391–396.

Miller, M.F. and White, D.S. (2007). Ecological and evolutionary controls on the composition of marine and lake ichnofacies. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 531–544.

Miller, M.F. and Woodrow, D.L. (1991). Shoreline deposits of the Catskill deltaic complex, Schoharie Valley, New York. *Bulletin of the New York State Museum*, 469, 153–177.

Miller, M.F., Collinson, J.W. and Frisch, R.A. (1991). Depositional setting and history of a Permian post–glacial black shale: Mackellar Formation, Central Transantarctic Mountains. In *Gondwana Seven Proceedings, Sao Paulo*, ed. H. Ulbrich and A.C. Rocha Campos, pp. 201–215.

Miller, M.F., McDowell, T.A., Smail, S.E., Shyr, Y. and Kemp, N.R. (2002). Hardly used habitats: dearth and distribution of burrowing in Paleozoic and Mesozoic stream and lake deposits. *Geology*, 30, 527–530.

Miller, W., III. (1991a). Paleoecology of graphoglyptids. *Ichnos*, 1, 305–312.

Miller, W., III. (1991b). Intrastratal trace fossil zonation, Cretaceous flysch of northern California. *Ichnos*, 1, 161–171.

Miller, W., III (1996). Sabellariid polychaete squatters in *Teredolites*: possible source of composite ichnotaxa in xylic substrates. *Ichnos*, 4, 317–319.

Miller, W., III. (1998). Complex marine trace fossils. *Lethaia*, 31, 29–32.

Miller, W., III. (2002). Complex trace fossils as extended organisms: a proposal. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 3, 147–158.

Miller, W., III. (2003). Paleobiology of complex trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 3–14.

Miller, W., III. and D'Alberto, L. (2001), Paleoethologic implication of *Zoophycos* from Late Cretaceous and Paleocene limestone of the Venetian Prealps, northeastern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 237–247.

Miller, W., III and Vokes, E.H. (1998). Large *Phymatoderma* in Pliocene slope deposits, Northwestern Ecuador: associated ichnofauna, fabrication, and behavioral ecology. *Ichnos*, 6, 23–45.

Milner, G.R. and Smith, V.G. (2005). Carnivore alteration of human bone from a late prehistoric site in illinois. *American. Journal of Physical Anthropology*, 79, 43–49.

Milton, S.J. and Dean, W.R.J. (1990). Mima-like mounds in the southern and western Cape: Are the origins so mysterious? *South African Journal of Science*, 86, 207–208.

Minter, N.J. and Braddy, S.J. (2006a). Walking and jumping with Palaeozoic apterygote insects. *Palaeontology*, 49, 827–835.

Minter, N.J. and Braddy, S.J. (2006). The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA. *Palaeontology*, 49, 1123–1142.

Minter, N.J. and Braddy, S.J. (2009). Ichnology of an Early Permian tidal flat: The Robledo Mountains Formation of the Robledo Mountains, Southern New Mexico, USA. *Special Papers in Palaeontology*, 82, 1–107.

Minter, N.J., Buatois, L.A., Lucas, S.G., Braddy, S.J. and Smith, J.A. (2006). Spiral-shaped Graphoglyptids from an Early Permian Intertidal Flat. *Geology*, 34, 1057–1060.

Minter, N.J., Braddy, S.J., and Davis, R.B. (2007a). Between a rock and a hard place: arthropod trackways and ichnotaxonomy. *Lethaia*, 40, 365–375.

Minter, N.J., Krainer, K., and Lucas, S.G. (2007b). Paleoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA. *Palaeogeography, Paleoclimatology, palaeoecology*, 246, 390–423.

Moloney, C.L., Levin, S.A., Chiariello, N.R. and Buttel, L. (1992). Pattern and scale in a serpentine grassland. *Theoretical Population Biology*, 41, 257–276.

Monaco, P. (1995). Relationships between trace-fossil communities and substrate characteristics in some Jurassic pelagic deposits in the Umbria-Marche Basin, central Italy. *Geobios, Memoire Special*, 18, 299–311.

Monaco, P. and Giannetti, A. (2002). Three-dimensional burrow systems and taphofacies in shallowing-upward parasequences, lower Jurassic carbonate platform (Calcari Grigi, Southern Alps, Italy). *Facies*, 47, 57–82.

Montague, C.L., Bunker, S.M., Haines, E.B., Pace, M.L. and Wetzel, R.L. (1981). Aquatic macroconsumers. In *The Ecology of Salt Marsh*, ed. L.R. Pomeroy and R.G. Wiegert, Springer-Verlag, New York, 69–85.

Montague, K.E., Walton, A.W. and Hasiotis, S.T. (2010). Euendolithic microborings in basalt glass fragments in hyaloclastites: Extending the ichnofabric index to microbioerosion. *Palaios*, 25, 393–399.

Moore, D.G. and Scruton, P.C. (1957). Minor internal structures of some recent unconsolidated sediments. *American Association of Petroleum Geologists, Bulletin*, 41, 2723–2751.

Morales, M. and Haubold, H. (1995). Tetrapod tracks from the Lower Permian DeChelly Sandstone of Arizona: Systematic description. In *Early Permian footprints and facies*, ed. S.G. Lucas and A.B. Heckert, *New Mexico Museum of Natural History and Science Bulletin*, 6, 251–261.

Moran, D.P. and Reaka, M.L. (1988). Bioerosion and the availability of shelter for benthic reef organisms. *Marine Ecology Progress Series*, 44, 249–263.

Moreno, F., Vegas, R. and Marcos, A. (1976). Sobre la edad de las series Ordovicicas y Cambricas relacionadas con la discordancia “Sárdica” en el anticlinal de Valdelacasa (Monetes de Toledo, España). *Breviora Geologica Astúrica*, 20, 8–16.

Morrissey, L.B. and Braddy, S.J. (2004). Terrestrial trace fossils from the Lower Old Red Sandstone, southeast Wales. *Geological Journal*, 39, 315–336.

Morrissey, L.B., Braddy S.J., Bennett J.P., Marriott S.B. and Tarrant P.R. (2004). Fish trails from the Lower Old Red Sandstone of Tredomen Quarry, Powys, southeast Wales. *Geological Journal*, 39, 337–358.

Morrow, J.R. and Hasiotis, S.T. (2007). Endobenthic response through mass extinction episodes: Predictive models and observed patterns. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Elsevier, Amsterdam, 575–611.

Mountney, N.P. (2004). The sedimentary signature of desert systems and their response to environmental change. *Geology Today*, 20, 101–106.

Mountney, N.P. (2006). Eolian facies models. In *Facies Models Revisited*, ed. H. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 19–83.

Mueller-Dombois, D. and Ellenberg, H. (1980). Methods available for vegetation classification and their suitability for various purposes. In *The IBP Survey of Conservation Sites: An Experimental Study*, ed. A.R. Clapham, IBP Internat’l Series No. 24, Cambridge University Press, 26–54.

Mulder, T. and Syvitski, J.P.M. (1995). Turbidity currents generated at river mouths during exceptional discharges to the world oceans. *Journal of Geology*, 103, 285–299.

Müller, A.H. (1962). Zur Ichnologie, Taxiologie und Okologie fossiler Tiere. *Freiberger Forschungshefte C*, 366, 7–27.

Müller, A.H. (1966). Neue Lebensspuren (Vestigia invertebratorum) aus dem Karbon und der Trias Mitteldeutschlands. *Geologie*, 15, 712–725.

Muñiz, F., Mayoral, E. and Martín, M. (1995). Pistas fósiles intergradacionales en el Mioceno superior del sector suroccidental de la cuenca del Guadalquivir. *Jornadas de Paleontología, Actas*, 11, 119–122.

Muñoz, N.G. (1986). Bioclastic carbonates of Margarita Island, Venezuela, as a key to exploration. *Carbonates and Evaporites*, 1, 13–23.

Muñoz, N.G. (1994). Engineering application of trace fossil analysis for oil reservoir quality and for a dam site in Venezuela. *14th International Sedimentological Congress (Recife)*, *Abstracts of Papers*, S54–S55.

Muñoz, N.G., Casas, J.E., Moreno, J. and Yoris, F. (1997). Flysch Eoceno de La Isla de Margarita y sus Facies Turbidíticas. 8º *Congreso Geológico Venezolano and* 1º *Latinoamericano de Sedimentología*, *Excursión No*. 2, 39.

Musiba, C., Mabula, A., Selvaggio, M. and Magori, C. (2008). Pliocene animal trackways at Laetoli: Research and conservation potential. *Ichnos*, 15, 166–178.

Mustoe, G.E. (2002). Eocene bird, reptile, and mammal tracks from the Chuckanut Formation, Northwest Washington. *Palaios*, 17, 403–413.

Murray, J.M.H., Meadows, A. and Meadows, P.S. (2002). Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. *Geomorphology*, 47, 15–30.

Mutti, E. (1979). Turbidites et cones sous-marins profonds. *Sedimentation detritique (fluviatile, littorale et marine)*, *Institut de Geologie de l’University de Fribourg*, *Short Course*, 353–419.

Mutti, E. (1985). Turbidite systems and their relations to depositional sequences. In *Provenance of Arenites*, ed. G.G. Zuffa, Dordrecht: D. Reidel Publishing Company, pp. 65–93.

Mutti, E. (1992). *Turbidite Sandstones*. Parma, Italy: AGIP-Istituto di Geología, Università di Parma.

Mutti E. and Normark, W.R. (1991). An integrated approach to the study of turbidite systems. In *Seismic Facies and Sedimentary Processes of Modern and Ancient Submarine Fans*, ed. P. Weimer and M.H. Link, New York: SpringerVerlag, pp. 75–106.

Mutti, E. and Ricci Lucchi, F. (1972). Turbidite facies and facies associations. In *Examples of Turbidite Facies and Facies Association from Selected Formations of the Northern Apennines*, ed. E. Mutti, G.C. Parea, F. Ricci Lucchi, M. Sagri, G. Zanzucchi, G. Ghibaudo and S. Iaccarino, *Ninth International Congress on Sedimentology, A-11 of Fieldtrip Guidebook*, 21–36.

Mutti, E, Davoli, G., Tinterri, R. and Zavala, C. (1996). The importance of ancient fluvio-deltaic systems dominated by catastrophic flooding in tectonically active basins. *Memorie di Scienze Geologiche, Universita di Padova*, 48, 233–291.

Mynt, M. (2001). *Psilonichnus quietis* isp. nov. from the Eocene Iwaki formation, Shiramizu group, Joban coal field, Japan. *Ichnos*, 8, 1–14.

Mynt, M. (2007). The *Psilonichnus* Ichnofacies: An example from the Iwaki Formation, Shiramizu Group, Joban Coal Field, Japan. In *Applied Ichnology*, ed. J.A. MacEachern, K.L. Bann, M.K. Gingras, and S.G. Pemberton, *Society for Sedimentary Geology Short Course Notes*, 52, 335–342.

Myrow, P.M. (1992). Pot and gutter casts from the Chapel Island Formation, southeast Newfoundland. *Journal of Sedimentary Petrology*, 62, 992–1007.

Myrow, P.M. (1995). *Thalassinoides* and the enigma of Early Paleozoic open-framework burrow Systems. *Palaios*, 10, 58–74.

Naiman, R.J., Decamps, H., Pastor, J. and Johnston, C.A. (1988). The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society*, 7, 289–306.

Naiman, R.J., Décamps, H. and McClain, M.E. (2005). *Riparia: Ecology, Conservation and Management of Streamside Communities.* San Diego: Elsevier.

Nair, N.B. and Ansell, A.D. (1968). The mechanism of boring in *Zirphaea crispata* (L) (Bivalvia: Pholadidae). *Proceedings of the Royal Society*, *Series B*, 170, 155–173.

Nara, M. (1995). *Rosselia socialis*: a dwelling structure of a probable terebellid polychaete. *Lethaia*, 28, 171–178.

Nara, M. (1997). High-resolution analytical method for event sedimentation using *Rosselia socialis*. *Palaios*, 12, 489–494.

Nara, M. (2002). Crowded *Rosselia socialis* in Pleistocene inner shelf deposits: benthic Paleoecology during rapid sea-level rise. *Palaios*, 17, 268–276.

Nara, M., Akiyama, H. and Itani, G. (2008). Macrosymbiotic association of the myid bivalve *Cryptomya* with thalassinidean shrimps: Examples from modern and Pleistocene tidal flats of Japan *Palaeogeography, Palaeoclimatology, Palaeoecology*, 261, 100–104.

Narbonne, G.M. (1984). Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada. *Journal of Paleontology*, 58, 398–415.

Narbonne, G.M. (2004). Modular construction of Early Ediacaran complex lifeforms. *Science*, 305, 1141–1144.

Narbonne, G.M. (2005). The Ediacara Biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences*, 33, 421–442.

Narbonne, G. M. and Aitken, J. D. (1990). Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada. *Palaeontology*, 33, 945–980.

Narbonne, G.M. and Gehling, J.G. (2003). Life after snowball: the oldest complex Ediacaran fossils. *Geology*, 31, 27–30.

Narbonne, G.M., Myrow, P.M. and Anderson, M.M. (1987). A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Canadian Journal of Earth Sciences*, 24, 1277–1293.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences, USA*, 105, 19052–19059.

Neal, E.G. and Roper, T.J. (1991). The environmental impact of badgers (*Meles meles*) and their sets. In *The Environmental Impact of Burrowing Animals and Animal Burrows*, ed. P.S. Meadows and A. Meadows, *Symposia of the Zoological Society of London*, 63.

Needham, S.J., Worden, R.H. and Cuadros, J. (2006). Sediment ingestion by worms and the production of bio-clays; a study of macrobiological enhanced weathering and early diagenetic processes. *Sedimentology*, 53, 567–579.

Neef, G. (2004a). Non-marine ?Late Silurian–Early Devonian trace fossils, Darling Basin, western New South Wales. *Alcheringa*, 28, 389–399.

Neef, G. (2004b). Devonian arthropod trackways from the fluvial Revendale Formation, western New South Wales. *Alcheringa*, 28, 401–402.

Neira, C., Sellanes, J., Levin L.A. and Arntz, W.E. (2001). Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. *Deep-Sea Research*, 48, 2453–2472.

Nesbitt, E.A. and Campbell, K.A. (2002). A new *Psilonichnus* ichnospecies attributed to mud-shrimp *Upogebia* in estuarine settings. *Journal of Paleontology*, 76, 892–901.

Nesbitt, E.A. and Campbell. K.A. (2006). The paleoenvironmental significance of *Psilonichnus*. *Palaios*, 21, 187–196.

Neto de Carvalho, C. (2006). Roller coaster behavior in the *Cruziana Rugosa* group from Penha Garcia (Portugal): implications for the feeding program of trilobites. *Ichnos*, 13, 255–265.

Netto, R.G. (1989). Paleoicnologia das sequencias eólicas sotopostas a Formacao Botucatu no Rio Grande do Sul. *Acta Geologica Leopoldensia*, 28, 31–44.

Netto, R.G. and Grangeiro, M.E. (2009). Neoichnology of the seaward side of Peixe Lagoon in Mostardas, southernmost Brazil: the *Psilonichnus* ichnocoenosis revisited. *Revista Brasileira de Paleontologia*, 12, 211–224.

Netto, R.G. and Martini da Rosa, C.L. (2001). A biota vendiana da sub-bacia de Santa Bárbara, Bacia do Camaquã. *17 Congresso Brasileiro de Paleontologia, Sociedade Brasileira de Paleontologia, Boletim de Resumos, Rio Branco*, 94.

Netto, R.G. and Rossetti, D.F. (2003). Ichnology and salinity fluctuations: a case study in the Early Miocene (Lower Barreiras Succession) of São Luís Basin, Maranhão, Brazil. *Revista Brasileira de Paleontologia*, 6, 5–18.

Netto, R.G., Buatois, L.A., Mángano, M.G., and Balistieri, P. (2007). *Gyrolithes* as a multipurpose burrow: an ethologic approach. *Revista Brasileira de Paleontologia*, 10, 157–168.

Neumann, A.C. (1966). Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography*, 11, 92–108.

Neumann, C. and Wisshak, M. (2006). A foraminiferal parasite on the sea urchin *Echinocorys*: ichnological evidence from the Late Cretaceous (Lower Maastrichtian, northern Germany). *Ichnos*, 13, 185–190.

Newell, R.C. (1979). *Biology of Intertidal Animals*. Kent, UK: Marine Ecological Surveys Ltd.

Nichol, R. (1982). Fossilized human footprints in Rangitoto ash on Motutapu Island. *Geological Society of New Zealand Newsletter*, 51, 11–13.

Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. and Ahlberg, P.E. (2010). Tetrapod trackways from the early Middle Devonian period of Poland. *Nature*, 463, 43–48.

Noffke, N. (1999). Erosional remnants and pockets evolving from biotic–physical interactions in a Recent lower supratidal environment. *Sedimentary Geology*, 123, 175–181.

Noffke, N. (2010). *Geobiology: Microbial Mats in Sandy Deposits from the Archaean Era to Today*. Berlin: Springer-Verlag.

Noffke, N., Gerdes, G., Klenke, T. and Krumbein, W.E. (1996). Microbially induced sedimentary structures – examples from modern sediments of siliciclastic tidal flats. *Zentralblatt für Geologie und Paläontologie Teil I*, 1/2, 307–316.

Nogueira, M.S. and Netto, R.G. (2001). Icnofauna da Formação Rio do Sul (Grupo Itararé, Permiano da bacia do Paraná) na Pedreira Itaú Itauna, Santa Catarina, Brasil. *Acta Geologica Leopoldensia*, 52/53, 397–406.

Norris, R.D. (2001). Impact of K-T boundary events on marine life. In *Palaeobiology II*, ed. D.E.G. Briggs and P.G. Crowther, Oxford, UK: Blackwell Science, pp. 229–231.

Nygaard, E. (1983). *Bathichnus* and its significance in the trace fossil association of Upper Cretaceous chalk, Mors, Denmark. *Danmarks Geologiske Undersøgelse Arbog*, 1982, 107–137.

O'Clair, C.E. and Zimmerman, S.T. (1987). Biogeography and ecology of intertidal and shallow subtidal communities. In *The Gulf of Alaska: Physical Environment and Biological Resources*, ed. D.W. Hood and S.T. Zimmerman, Springfield, VA: National Technical Information Service, pp. 305–344.

Olivero, D. and Gaillard, C. (1996). Paleoecology of Jurassic *Zoophycos* from south-eastern France. *Ichnos*, 4, 249–260.

Olivero, E.B., Buatois, L.A. and Scasso, R.A. (2004). *Paradictyodora antarctica*: a new complex vertical spreite trace fossil from the Upper Cretaceous–Paleogene of Antarctica and Tierra del Fuego, Argentina. *Journal of Paleontology*, 78, 783–789.

Olivero, D. and Gaillard, C. (2007). A constructional model for *Zoophycos*. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 466–477.

Olivero, E.B., and López Cabrera, M.I. (2005). *Patagonichnus*: a new trace fossil from the Miocene of Patagonia. A probable fodinichnion of gregarious polychaetes. *Ameghiniana*, 42, 277–294.

Olivero, E.B. and López Cabrera, M.I. (2010). *Tasselia ordamensis*: a biogenic structure of probable deposit-feeding and gardening maldanid polychaetes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 336–348.

Olivero, E.B., Ponce, J.J., Marsicano, C.A. and Martinioni, D.R. (2007). Depositional settings of the basal López de Bertodano Formation, Maastrichtian, Antarctica. *Revista de la Asociación Geológica Argentina*, 62, 521–529.

Olivero, E.B., López, M.I., Malumián, N. and Torres Carbonell P.J. (2010). Eocene graphoglyptids from shallow-marine, highenergy, organic-rich, and bioturbated turbidites, Fuegian Andes, Argentina. *Acta Geologica Polonica*, 60, 77–91.

Olóriz, F. and Rodríguez-Tovar, F.J. (1999). Análisis paleoicnológico del perfil de Puerto Lorente (Kimmeridgense, Sierra de Cazorla, Prebético Externo). *Revista Española de Paleontología nro extraordinario*, 15–28.

Olóriz, F. and Rodríguez-Tovar, F.J. (2002). Trace-fossils and minor discontinuities in a marl limestone rhythmite, Lower–Middle Kimmeridgian, southern Spain. *Geobios*, 35, 581–593.

Olsen, P.E. (1980). Fossil great lakes of the Newark Supergroup in New Jersey. In *Field Studies of New Jersey Geology and Guide to Field Trips*, ed. W.M. Manspeizer, New York State Geological Association, 52nd Annual Meeting, Rutgers University, 352–398.

Olsen, P.E. (1989). Newark Basin, New Jersey. In *Tectonic, Depositional, and Paleoecologic History of Early Mesozoic Rift Basins, Eastern North America*, ed. PE. Olsen, R. Schliche, and P.J. Gore, *International Geological Congress Field Trip Guidebook*, T-351, 2.

Olsen, P.E. and Huber, P. (1998). The oldest Late Triassic footprint assemblage from North America (Pekin Formation, Deep River basin, North Carolina, USA). *Southeastern Geology*, 38, 77–90.

Olsen, P.E., Remington, C.L. and Cornet, B. (1978). Cyclic change in Late Triassic lacustrine communities. *Science*, 201, 729–732.

Olsen, P.E., Shubin, N.H. and Anders, M.H. (1987). New Early Jurassic tetrapod assemblages constrain Triassic–Jurassic tetrapod extinction event. *Science*, 237, 1025–1029.

Olsen, P.E., Smith, J.B. and McDonald, N.G. (1998). Type material of the species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, USA). *Journal of Vertebrate Paleontology*, 18, 586–601.

Olszewski, T. (1996). Segregation of bivalves and brachiopods in the upper Paleozoic: the influence of ecology on macroevolutionary history.In *Abstracts of Papers*, Washington DC: North American Paleontological Convention (NAPC-96), pp. 295.

Onac, B.P., Ettinger, K., Kearns, J. and Balasz, I.I. (2005). A modern, guano-related occurrence of foggite, CaAl(PO4)(OH)2·H2O and churchite-(Y), YPO4·2H2O in Cioclovina Cave, Romania. *Mineralogy and Petrology*, 85, 291–302.

Orłowski, S. (1992). Trilobite trace fossils and their stratigraphical significance in the Cambrian sequence of the Holy Cross Mountains, Poland. *Geological Journal*, 27, 15–34.

Orłowski, S., Radwański, A. and Roniewicz, P. (1970). The trilobite ichnocoenoses in the Upper Cambrian sequence of the Holy Cross Mountains. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 345–360.

Orłowski, S., Radwański, A. and Roniewicz, P. (1971). Ichnospecific variability of the Upper Cambrian Rusophycus from the Holy Cross Mts. *Acta Geologica Polonica*, 21, 341–348.

Orr, P.J. (1994). Trace fossil tiering within event beds and preservation of frozen profiles: An example from the lower Carboniferous of Menorca. *Palaios*, 9, 202–210.

Orr, P.J. (1996). The ichnofauna of the Skiddaw Group (Early Ordovician) of the Lake District, England. *Geological Magazine*, 133, 193–216.

Orr, P.J. (2001). Colonization of the deep-marine environment during the early Phanerozoic: The ichnofaunal record. *Geological Journal*, 36, 265–278.

Orr, P.J. (2003). Ecospace utilization in early Phanerozoic deep-marine environments: deep bioturbation in the Blakely Sandstone (Middle Ordovician), Arkansas, USA. *Lethaia*, 36, 97–106.

Ortí, F., Rosell, L., Anadón, P. (2003). Deep to shallow lacustrine evaporates in the Libros Gypsum (southern Teruel Basin, Miocene, NE Spain): an occurrence of pelletal gypsum rhythmites. *Sedimentology*, 50, 361–386.

Orton, G.J. and Reading, H.G. (1993). Variability of deltaic processes in terms of sediment supply, with particular emphasis on grainsize. *Sedimentology*, 40, 475–512.

Oschmann, W. (1993). Environmental oxygen fluctuations and the adaptive response of marine benthic organisms. *Journal of the Geological Society, London*, 150, 187–191.

Osgood, R.G. Jr. (1970). Trace fossils of the Cincinnati area. *Palaeontographica Americana*, 6, 281–444.

Osgood, R.G. Jr. (1975). The paleontological significance of trace fossils. In *The Study of Trace Fossils: A Synthesis of Principles, Problems and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 87–108.

Ott, J.A., Fuchs, B., Fuchs, R. and Malasek, A. (1976). Observations on the biology of *Callianassa stebbingi* Borrodaille and *Upogebia litoralis* Risso and their effect upon the sediment. *Senckenbergiana Maritima*, 8, 61–79.

Owen, J. (1980). *Feeding Strategy*. Oxford, UK: Oxford University Press.

Ozalas, K., Savrda, C.E. and Fullerton, R.R. Jr. (1994). Bioturbated oxygenation-event beds in siliceous facies; Monterey Formation (Miocene), California. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 112, 63–83.

Pak, R. and Pemberton, S.G. (2003). Ichnology of the Yeoman Formation. *Summary of Investigation 2003, v.1, Saskatchewan Geological Survey, Saskatchewan Industry and Resources, Miscelaneous Report 2003–4.1, CD-ROM Paper*, A-3, 16.

Palmer, J.D. (1967). Daily and tidal components in the persistent rhythmic activity of the crab, *Sesarma*. *Nature*, 215, 64–66.

Palmer, J.D. (1995). *The Biological Rhythms and Clocks of Intertidal Animals*. New York: Oxford University Press.

Palmer, T.J. (1978). Burrows at certain omission surfaces in the Middle Ordovician of the Upper Mississippi Valley. *Journal of Paleontology*, 52, 109–117.

Papentin, F. (1973). A Darwinian evolutionary system III: experiments on the evolution of feeding patterns. *Journal of Theoretical Biology*, 39, 431–445.

Papentin, F. and Röder, H. (1975). Feeding patterns: the evolution of a problem and a problem of evolution. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 184–191.

Pashin, J.C. (2005). Pottsville stratigraphy and the Union Chapel Lagerstaette. *Alabama Paleontological Society, Monographs*, 1, 39–58.

Pattison, S.A.J. (2005). Storm-influenced prodelta turbidite complex in the lower Kenilworth Member at Hatch Mesa, Book Cliffs, Utah, USA: implications for shallow marine facies models. *Journal of Sedimentary Research*, 75, 420–439.

Pattison, S.A.J., Ainsworth, R.B. and Hoffman, T.A. (2007). Evidence of across shelf transport of fine-grained sediments: turbidite-filled shelf channels in the Campanian Aberdeen Member, Book Cliffs, Utah, USA. *Sedimentology*, 54, 1033–1063.

Pearson, D.L. (1988). Biology of tiger beetles. *Annual Reviews*, 33, 123–147.

Pearson, T.H. (1980). Macrobenthos of fjords. In *Fjord Oceanography*, ed. H.J. Freeland, D.M. Farmer and C.E. Kings, New York: Plenum Press, pp. 569–602.

Pearson, T.H. (2001). Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography and Marine Biology Annual Reviews*, 39, 233–267.

Pearson, N.J. and Gingras, M.K. (2006). An ichnological and sedimentological facies model for muddy point-bar deposits. *Journal of Sedimentary Research*, 76, 771–782.

Pearson, N.J., Gingras, M.K., Armitage, I.A. and Pemberton, S.G., (2007). The Significance of Atlantic Sturgeon Feeding Excavations, Mary's Point, Bay of Fundy, New Brunswick, Canada. *Palaios*, 22, 457–464.

Pemberton, S.G. and Frey, R.W. (1982). Trace fossil nomenclature and the *Planolites–Palaeophycus* dilemma. *Journal of Paleontology*, 56, 843–881.

Pemberton, S.G. and Frey, R.W. (1984a). Ichnology of storm–influenced shallow marine sequence: Cardium Formation (Upper Cretaceous) at Seebe, Alberta. In *The Mesozoic of middle North America*, ed. D.F. Stott and D.J. Glass, *Canadian Society of Petroleum Geologists Memoir*, 9, 281–304.

Pemberton, S.G. and Frey, R.W. (1984b). Quantitative methods in ichnology; spatial distribution among populations. *Lethaia*, 17, 33–49.

Pemberton, S.G. and Frey, R.W. (1985). The *Glossifungites* ichnofacies: modern examples from the Georgia coast, USA. In *Biogenic Structures: Their use in interpreting depositional environments*, ed., H.A. Curran, *Society for Sedimentary Geology Special Publication*, 35, 237–259.

Pemberton, S.G. and Frey, R.W. (1991). William Buckland and his "coprolitic vision". *Ichnos*, 1, 317–325.

Pemberton, S.G. and Gingras M.K. (2005). Classification and characterizations of biogenically enhanced permeability. *American Association of Petroleum Geologists, Bulletin*, 89, 1493–1517.

Pemberton, S.G. and Jones, B. (1988). Ichnology of the Pleistocene Ironshore Formation, Grand Cayman Island, British West Indies. *Journal of Paleontology*, 62, 495–505.

Pemberton, S.G. and MacEachern, J.A. (1995). The sequence stratigraphic significance of trace fossils: Examples from the Cretaceous foreland basin of Alberta, Canada. In *Sequence Stratigraphy of Foreland Basin Deposits: Outcrop and Subsurface Examples from the Cretaceous of North America*, ed. J.C. Van Wagoner and G. Bertram, *American Association of Petroleum Geologists Memoir*, 64, 429–475.

Pemberton, S.G. and MacEachern J.A. (1997). The ichnological signature of storm deposits: The use of trace fossils in event stratigraphy. In *Paleontological Events. Stratigraphic, Ecological and Evolutionary Implications*, ed. C.E. Brett and G.C. Baird, New York: Columbia University Press, pp. 73–109.

Pemberton, S.G. and Magwood, J.P.A. (1990). A unique occurrence of *Bergaueria* in the Lower Cambrian Gog Group near Lake Louise, Alberta. *Journal of Paleontology*, 64, 436–440.

Pemberton, S.G. and Wightman, D.M. (1992). Ichnological characteristics of brackish water deposits. In *Applications of ichnology to petroleum exploration: A core workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 141–167.

Pemberton, S.G., Kobluk, D.R., Yeo, R.K. and Risk, M.J. (1980). The boring *Trypanites* at the Silurian–Devonian disconformity in southern Ontario. *Journal of Paleontology*, 54, 1258–1266.

Pemberton, S.G., Frey, R.W. and Bromley, R.G. (1988). The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences*, 25, 886–892.

Pemberton, S.G., Frey, R.W. and Saunders, T.D.A. (1990). Trace fossils. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 355–362.

Pemberton, S.G., Frey, R.W., Ranger, M.J. and MacEachern, J.A. (1992a). The conceptual framework of ichnology. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 1–32.

Pemberton, S.G., MacEachern, J.A. and Frey, R.W. (1992b). Trace fossils facies models: environmental and allostratigraphic significance. In *Facies Models and Sea Level Changes*, ed. R.G. Walker and N.P. James, Geological Association of Canada, 47–72.

Pemberton, S.G., Van Wagoner, J.C. and Wach, G.D. (1992c). Ichnofacies of a wave-dominated shoreline. In *Applications of ichnology to petroleum exploration: A core workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 339–382.

Pemberton, S.G., MacEachern, J.A. and Ranger, M.J. (1992d). Ichnology and event stratigraphy: the use of trace fossils in recognizing tempestites. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 85–118.

Pemberton, S.G., Spila, M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, D. and Sinclair, I.K. (2001). *Ichnology & Sedimentology of Shallow to Marginal Marine Systems. Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin. Geological Association of Canada Short Course Notes*, 15, St. John's.

Pemberton, S.G., MacEachern, J.A. and Saunders, T. (2004). Stratigraphic applications of substrate-specific ichnofacies: delineating discontinuities in the fossil record. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 29–62.

Pemberton, S.G., MacEachern, J.A., Bann, K.L., Gingras, M.K. and Saunders, T.D.A. (2006). High-latitudinal versus low-latitude: Capturing the elusive signal using trace fossil suites from the ancient record. *Abstracts American Association of Petroleum Geologists 2006 Annual Convention, Houston*, 84.

Pemberton, S.G., Pulham, A., MacEachern, J.A. and Saunders, T.D.A. (2007). The ichnology and sedimentology of the Ferron Sandstone cores of Muddy Creek Canyon, Emery County, SE Utah, USA. In *Ichnological Applications to Sedimentological and Sequence Stratigraphic Problems*, ed. J.A. MacEachern, M.K. Gingras, K.L. Bann and S.G. Pemberton, *Society for Sedimentary Geology Research Conference, Price, Abstract Volume*, 175–209.

Pemberton, S.G., MacEachern, J.A., Gingras, M.K. and Saunders, T.D.A. (2008). Biogenic chaos: cryptobioturbation and the work of sedimentologically friendly organisms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 273–279.

Penland, S. and Suter, J.R. (1989). The geomorphology of the Mississippi River Chenier Plain. *Marine Geology*, 90, 231–258.

Perkins, E.J. (1974). *The Biology of Estuaries and Coastal Waters*. London: Academic Press.

Perry, C.T. (2000). Macroboring of Pleistocene coral communities, Falmouth Formation, Jamaica. *Palaios*, 15, 483–491.

Perry, C.T. and Bertling, M. (2000). Temporal and spatial patterns of coral reef macroboring since the Mesozoic. In *Carbonate Platform Systems: Components and Interactions*, ed. E. Insalaco, P. Skelton and T. Palmer, *Geological Society Special Publication*, 178, 33–50.

Perry, C.T. and Hepburn, L.J. (2008). Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: taphonomic signatures of reef accretion and reef depositional events. *Earth Science Reviews*, 86, 106–144.

Perry, C.T. and Macdonald, I.A. (2002). Impacts of light penetration on the bathymetry of reef microboring communities: Implications for the development of microendolithic trace assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 186, 101–113.

Peterson, K.J. (2005). Macroevolutionary interplay between planktic larvae and benthic predators. *Geology*, 33, 929–932.

Peterson, K.J., Cotton, J.A., Gehling, J.G. and Pisani, D. (2008). The Ediacaran emergence of bilaterians: congruence between the genetic and the geological fossil records. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 1435–1443.

Pflüger, F. (1999). Matground structures and redox facies. *Palaios*, 14, 25–39.

Pharo, C.H. and Carmack, E.C. (1979). Sedimentation processes in a short residence-time intermontane lake, Kamlooops Lake, British Columbia. *Sedimentology*, 26, 523–541.

Pianka, E.R. (1970). On r- and K-selection. *American Naturalist*, 104, 592–597.

Pickerill, R.K. (1981). Trace fossils in a Lower Palaeozoic submarine canyon sequence-the Siegas Formation of northwestern New Brunswick, Canada. *Maritime Sediments and Atlantic Geology*, 17, 36–59.

Pickerill, R.K. (1990). Nonmarine *Paleodictyon* from the Carboniferous Albert Formation of southern New Brunswick. *Atlantic Geology*, 26, 157–163.

Pickerill, R.K. (1992). Carboniferous nonmarine invertebrate ichnocoenoses from southern New Brunswick, eastern Canada. *Ichnos*, 2, 21–36.

Pickerill, R.K. (1994). Nomenclature and taxonomy of invertebrate trace fossils. In *The Palaeobiology of Trace Fossils*, ed. S.K. Donovan, Chichester, UK: John Wiley & Sons, pp. 3–42.

Pickerill, R.K. (1995). Deep-water marine *Rusophycus* and *Cruziana* from the Ordovician Lotbiniere Formation of Quebec. *Atlantic Journal*, 31, 103–108.

Pickerill, R.K. and Brenchley, P.J. (1991). Benthic macrofossils as paleoenvironmental indicators in marine siliciclastic facies. *Geoscience Canada*, 18, 119–138.

Pickerill, R.K and Fillion, D. (1983). On the Tremadoc–Arenig and Lower–Upper Tremadoc boundaries in the Bell Island Group, Conception Bay, eastern Newfoundland. *Maritime Sediments and Atlantic Geology*, 19, 21–30.

Pickerill, R.K. and Narbonne, G.M. (1995). Composite and compound ichnotaxa: a case example from the Ordovician of Québec, eastern Canada. *Ichnos*, 4, 53–69.

Pickerill, R.K. and Williams, P.P. (1989). Deep burrowing in the early Palaeozoic deep sea: examples from the Cambrian(?) – Early Ordovician Meguma Group of Nova Scotia. *Canadian Journal of Earth Science*, 26, 1061–1068.

Pickerill, R.K., Fillion, D. and Harland, T.L. (1984). Middle Ordovician trace fossils in carbonates of the Trenton Group between Montreal and Quebec city, St. Lawrence lowland, eastern Canada. *Journal of Paleontology*, 58, 416–439.

Pickerill, R.K., Romano, M. and Meléndez, B. (1984). Arenig trace fossils from the Salamanca area, western Spain. *Geological Journal*, 19, 249–269.

Pickering, K.T., Hiscott, R. and Hein, F.J. (1989). *Deep-marine Environments: Clastic Sedimentation and Tectonics*. London: Unwin Hyman.

Pieńkowski, M.H. (1983). Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. *Marine Ecology Progress Series*, 11, 141–150.

Pieńkowski, G. and Niedźwiedzki, G. (2009) Invertebrate trace fossil assemblages from the Lower Hettangian of Sołtyków, Holy Cross Mountains, Poland. *Volumina Jurassica*, 6, 109–13.

Pierce, C. (1992). Effects of pocket gopher burrowing on archaeological deposits: a simulation approach. *Geoarchaeology*, 7, 185–208.

Pirazzoli, P.A., Thommeret, J., Thommeret, Y., Laborel, J. and Montaggioni, L. (1982). Crustal block movements from Holocene shorelines: Crete and Antikythira (Greece). *Tectonophysics*, 86, 27–43.

Pirmez, C., Beaubouef, R.T., Friedmann, S.J. and Mohrig, D.C. (2000). Equilibrium profile and base level in submarine channels: examples from Late Pleistocene systems and implications for the architecture of deepwater reservoirs. In *Deepwater Reservoirs of the World*, ed. P. Weimer, R.M. Slatt, J. Coleman, N.C. Rosen, H. Nelson, A.H. Bouma, M.J. Styzen and D.T. Lawrence, *Society for Sedimentary Geology, Gulf Coast Section, 20th Annual Research Conference*, 782–805.

Pirrone, C.A., Buatois, L.A. and Bromley, R.G. (2010). Naming trace fossils in bones. *Latin American Symposium on Ichnology, Abstract Volume*, p. 52.

Plink-Björklund, P. and Steel, R. (2004). Initiation of turbidity currents: evidence for hyperpycnal flow turbidites in Eocene Central Basin of Spitsbergen. *Sedimentary Geology*, 165, 29–52.

Plint, A.G. (1988). Sharp-based shoreface sequences and "offshore bars" in the Cardium Formation of Alberta: their relationship to relative changes in sea-level. In *Sea-Level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross and J.C. Van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 357–370.

Plint, A.G. (2000). Sequence stratigraphy and paleogeography of a Cenomanian deltaic complex; the Dunvegan and lower Kaskapau formations in subsurface and outcrop, Alberta and British Columbia, Canada. *Bulletin of Canadian Petroleum Geology*, 48, 43–79.

Plint, A.G. and Nummedal, D. (2000). The falling stage systems tract: recognition and importance in sequence stratigraphic analysis; sedimentary responses to forced regressions. In *Sedimentary Responses to Forced Regressions*, eds. D. Hunt and R.L. Gawthorpe. *Geological Society Special Publications*, 172, 1–17.

Plint, A.G., and Pickerill, R.K. (1985). Non-marine *Teredolites* from the middle Eocene of southern England. *Lethaia*, 18, 341–347.

Plotnick, R.E. (2007). Chemoreception, odor landscapes, and foraging in ancient marine landscapes. *Palaeontologia Electronica*, 10.

Plotnick, R.E. (2009). Movement Paleoecology and the taphonomy of behavior. *9th North American Paleontological Convention Abstracts, University of Cincinati, Cincinati*, 309.

Plotnick, R.E. and Koy, K. (2005). Let us prey: simulations of grazing traces in the fossil record. 8*th International Conference on GeoComputation, Ann Arbor*.

Plotnick, R.E., Dornbos, S.Q. and Chen, J. (2010). Information landscapes and sensory ecology of the Cambrian Radiation. *Paleobiology*, 36, 303–317.

Pollard, J.E. (1988). Trace fossils in coal-bearing sequences. *Journal of the Geological Society, London*, 145, 339–350.

Pollard, J.E. (1985). *Isopodichnus*, related arthropod traces and notostracans from Triassic fluvial sediments. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 76, 273–285.

Pollard, J.E. and Hardy, P.G. (1991). Trace fossils from the Westphalian D of Writhlington Geological Nature Reserve, nr. Radstock, Avon. *Proceedings of the Geologists Association*, 102, 169–178.

Pollard, J.E. and Walker, E. (1984). Reassessment of sediments and trace fossils from Old Red Sandstone (Lower Devonian) of Dunure, Scotland, described by John Smith (1909). *Geobios*, 17, 567–576.

Pollard, J.E., Goldring, R. and Buck, S.G. (1993). Ichnofabrics containing *Ophiomorpha*: significance in shallow-water facies interpretation. *Journal of the Geological Society of London*, 150, 149–164.

Pollard, J.E., Steel, R.J. and Undersrud, E. (1982). Facies sequences and trace fossils in lacustrine/fan delta deposits, Hornelen Basin (M. Devonian), western Norway. *Sedimentary Geology*, 32, 63–87.

Pomeroy, L.R., Darley, W.M., Dunn, E.L., Gallagher, J.L., Haines, E.B. and Whitney, D.M. (1981). Primary production. In *Ecology of a Salt Marsh*, ed. L.R. Pomeroy and W. Wiegert, New York: Springer-Verlag, pp. 39–67.

Ponce, J.J. and Carmona, N.B. (2010). Miocene deep-marine hyperpycnal channel-levee complexes Tierra del Fuego, Argentina: facies associations and architectural elements. In *Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology*, 61, in press.

Ponce, J.J., Olivero, E.B., Martinioni, D.R. and López Cabrera, M.I. (2007). Sustained and episodic gravity flow deposits and related bioturbation patterns in Paleogene turbidites (Tierra del Fuego, Argentina). In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise and R.N. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 253–266.

Porębski, S.J. and Steel, R.J. (2006). Deltas and sea-level change. *Journal of Sedimentary Research*, 76, 390–403.

Posamentier, H.W. (2001). Lowstand alluvial bypass systems: Incised vs. unincised. *American Society of Petroleum Geologists, Bulletin*, 85, 1771–1793.

Posamentier, H.W. and Allen, G.P. (1993). Siliciclastic sequence stratigraphic patterns in foreland ramp-type basins. *Geology*, 21, 455–458.

Posamentier, H.W. and Allen, G.P. (1999). Siliciclastic sequence stratigraphy: concepts and applications. *Society for Sedimentary Geology Concepts in Sedimentology and Paleontology*, 7.

Posamentier, H.W. and Kolla, V. (2003). Seismic geomorphology and stratigraphy of depositional elements in deep-water settings. *Journal of Sedimentary Research*, 73, 367–388.

Posamentier, H.W. and Vail, P.R. (1988). Eustatic controls on clastic deposition II: sequence and system tract models. In *Sea-level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross and J.C. van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 125–154.

Posamentier, H.W. and Walker, R.G. (2006). Deep-water turbidites and submarine fans. In *Facies Models Revisited*, ed. H.W. Posamentier and R.G. Walker, *Society for Sedimentary Geology Special Publication*, 84, 397–520.

Posamentier, H.W., Jervey, M.T. and Vail, P.R. (1988). Eustatic controls on clastic deposition I: conceptual framework. In *Sea-level Changes: An Integrated Approach*, ed. C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross and J.C. van Wagoner, *Society for Sedimentary Geology Special Publication*, 42, 109–124.

Posamentier, H.W., Allen, G.P., James, D.P. and Tesson, M. (1992). Forced regressions in a sequence stratigraphic framework: concepts, examples, and exploration significance. *American Association of Petroleum Geologists, Bulletin*, 76, 1687–1709.

Potter, P.E., Maynard, J.B. and Depetris, P.J. (2005). *Mud and Mudstone: Introduction and overview.* Berlin: Springer.

Powichrowski, L.K. (1989). Trace fossils from the Helminthoid Flysch (Upper Cretaceous-Palaeocene) of the Ligurian Alps (Italy): development of deep marine ichnoassociations in fan and basin plain environments. *Eclogae Geologicae Helvetiae*, 82, 385–411.

Prantl, F. (1945). Two new problematic trails from the Ordovician of Bohemia. *Académie Tchéque des Sciences, Bulletin International, Classe des Sciences Mathematiques et Naturelles et de la Médecine*, 46, 49–59.

Prather, B.E., Booth, J.R., Steffens, G.S. and Craig, P.A. (1998). Classification, lithologic calibration and stratigraphic succession of seismic facies of intraslope basins, deep-water Gulf of Mexico. *American Association of Petroleum Geologists, Bulletin*, 82, 701–728.

Pratt, B. (1998). Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. *Lethaia*, 31, 73–88.

Prave, A.R. (2002). Life on land in the Proterozoic: evidence from the Torridonian rocks of northwest Scotland. *Geology*, 30, 811–814.

Price, S. and McCann, T.M. (1990). Environmental significance of *Arenicolites* ichnosp. in Pliocene lake deposits of southwest Turkey. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, H11, 687–694.

Prince, N.K. and Lockley, M.G. (1989). The sedimentology of the Purgatoire tracksite region, Morrison Formation of southeastern Colorado. In *Dinosurs Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, New York: Cambridge University Press, pp. 155–163.

Pryor, W.A. (1975). Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. *Geological Society of America Bulletin*, 86, 1244–1254.

Pruss, S. and Bottjer, D.J. (2004). Early Triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-Permian mass extinction. *Palaios*, 19, 551–564.

Pruss, S., Fraiser, M. and Bottjer, D.J. (2004). Proliferation of Early Triassic wrinkle structures: implications for environmental stress following the end-Permian mass extinction. *Geology*, 32, 461–464.

Pruss, S.B., Corsetti, F.A. and Bottjer, D.J. (2005). Environmental trends of Early Triassic biofabrics: implications for understanding the aftermath of the end-Permian mass extinction. In *Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Toward an Integrated Approach*, ed. J.D. Morrow, D.J. Over and P.B. Wignall, Amsterdam: Elsevier, pp. 313–332.

Quiroz, L.I., Buatois, L.A., Mángano, M.G., Jaramillo, C.A. and Santiago, N. (2010). Is the trace fossil *Macaronichnus* an indicator of temperate to cold waters? Exploring the paradox of its occurrence in tropical coasts. *Geology*, 38, 651–654.

Radwański, A. (1969). Lower Tortonian transgression onto the southern slopes of the Holy Cross Mountains. *Acta Geologica Polonica*, 19, 1–164.

Radwański, A. (1977). Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 227–264.

Radwański, A. and Roniewicz, P. (1963). Upper Cambrian trilobite ichnocoenosis from Wielka Wisniowka (Holy Cross Mountains, Poland). *Acta Palaeontologica Polonica*, 8, 259–280.

Radwański, A. and Roniewicz, P. (1972). A long trilobite trackway, *Cruziana semiplicata* Salter, from the Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area (Franconia, south-eastern Germany). *Paläontologische Zeitschrift*, 75, 71–96.

Rahmani, R.A. (1988). Estuarine tidal channel and nearshore sedimentation of a Late Cretaceous epicontinental sea, Drumheller, Alberta, Canada. In *Tide-influenced Sedimentary Environments*, ed. P.L. Boer, A. van Gelder and S.D. Nio, Dordrecht: D. Reidel, pp. 433–471.

Raichlen, D.A., Pontzer, H. and Sockol, M. (2008). The Laetoli footprints and early hominin locomotor kinematics. *Journal of Human Evolution*, 54, 112–117.

Ranger, M.J. and Pemberton, S.G. (1988). Marine influence in the McMurray Formation in the Primrose area, Alberta. In *Sequences, Stratigraphy, Sedimentology: Surface and Subsurface*, ed. P.D. James and D.A. Leckie, *Canadian Society of Petroleum Geologists Memoir*, 15, 439–450.

Ranger, M.J. and Pemberton, S.G. (1992). The sedimentology and ichnology of estuarine point bars in the McMurray Formation of the Athabasca Oil Sands Deposit, northeastern Alberta, Canada. In *Applications of Ichnology to Petroleum Exploration: A Core Workshop*, ed. S.G. Pemberton, *Society for Sedimentary Geology Core Workshop*, 17, 401–421.

Rasmussen, B., Bose, P.K., Sarkar, S., Banerjee, S., Fletcher, I.R. and McNaughton, N.J. (2002a). 1.6 Ga U-Pb zircon age for the Chorhat Sandstone, lower Vindhyan, India: possible implications for early evolution of animals. *Geology*, 30, 103–106.

Rasmussen, B., Bengtson, S., Fletcher, I.R. and McNaughton, N. (2002b). Discoidal impressions and trace-like fossils more than 1200 million years old. *Science*, 296, 1112–1115.

Ratcliffe, B.C. and Fagerstrom, J.A. (1980). Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance. *Journal of Paleontology*, 54, 614–630.

Raup D.M. (1979). Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science*, 206, 217–218.

Raup D.M. (1992). Large-body impact and extinction in the Phanerozoic. *Paleobiology*, 18, 80–88.

Raup, D.M. and Seilacher, A. (1969). Fossil foraging behaviour: computer simulation. *Science*, 166, 994–995.

Ray, J.S., Martin, M.W., Veizer, J. and Bowring, S.A. (2002). U-Pb zircon dating and Sr isotope systematics of the Vindhyan Supergroup, India. *Geology*, 30, 131–134.

Reading, H.G. and Richards, M. (1994). Turbidite systems in deep-water basin margins classified by grain size and feeder system. *American Association of Petroleum Geologists, Bulletin*, 78, 792–822.

Reese, E.S. (1966). The complex behavior of echinoderms. In *Physiology of Echinodermata*, ed. R.A. Boolootian, New York: Interscience Publishers, pp. 157–218.

Reineck, H.-E. (1958). Longitudinale schrägschicht in Watt. *Geologische Rundschau*, 47, 73–82.

Reineck, H.-E. (1963). Sedimentgefüge im Bereich der südliche Nordsee. *Abhandlungen Senckenbergischen Naturforsche de Gesellschaft*, 505, 1–138.

Reineck, H.-E. (1967). Layered sediments of tidal flat beaches, and shelf bottoms of the North Sea. In *Estuaries*, ed. G.H. Lauff, *American Association for the Advancement of Science Special Publication*, 83, 191–206.

Reinson, G.E. (1984). Barrier island and associated stand-plain systems. In *Facies Models, Second edition*, ed. R.G. Walker, *Geological Association of Canada, Geoscience Canada Reprint Series*, 1, 119–140.

Reise, K. (1985). *Tidal Flat Ecology: An Experimental Approach to Species Interactions. Ecological Studies* 54. Berlin: Springer-Verlag.

Reise, K. and Volkenborn, N. (2004). Large worms as ecosystem engineers in intertidal Sediments. In *Proceedings of the Sysmposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments from Individual Behaviour to their Roles as Ecosystem Engineers*, Japan: Nagasaki University Press, 95.

Remane, A. and Schlieper, C. (1971). *Biology of Brackish Water*. New York: John Wiley and Sons.

Retallack, G.J. (1990). *Soils of the Past*. London: Unwin-Hyman.

Retallack, G.J. (1996). Early Triassic therapsid footprints from the Sydney basin, Australia. *Alcheringa* 20, 301–314

Retallack, G.J. (2001). *Scoyenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. *Palaeontology*, 44, 209–235.

Retallack, G.J. and Feakes, C.R. (1987). Trace fossil evidence for Late Ordovician animals on land. *Science*, 235, 61–63.

Rhoads, D.C. (1974). Organism-sediment relations in the muddy sea floor. *Oceanography and Marine Biology Annual Review*, 12, 263–300.

Rhoads, D.C. (1975). The paleoecological and environmental significance of trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 147–160.

Rhoads, D.C. and Germano, J.D. (1982). Characterization of organism–sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (Remote System). *Marine Ecology Progress Series*, 8, 115–128.

Rhoads, D.C. and Morse, J.W. (1971). Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia*, 4, 413–428.

Rhoads, D.C. and Young, D.K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structures. *Journal of Marine Research*, 28, 150–178.

Richter, R. (1928). Psychische reaktionen fossiler tiere. *Palaeobiologica*, 1, 225–245.

Richter, G. and Baszio, S. (2001). Traces of a limnic food web in the Eocene Lake Messel: a preliminary report based on fish coprolite analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 345–368.

Richter, G. and Wedmann, S. (2005). Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 223, 147–161.

Riggs, S.R., Ambrose, W.G. Jr., Cook, J.W., Snyder, S.W. and Snyder, S.W. (1998). Sediment production on sediment-starved continental margins: The interrelations between hard bottoms, sedimentological and benthic community processes, and storm dynamics. *Journal of Sedimentary Research*, 68, 155–168.

Rindsberg, A.K. (1990a). Ichnological consequences of the 1985 International Code of Zoological Nomenclature. *Ichnos*, 1, 59–63.

Rindsberg, A.K. (1990b). Freshwater to marine trace fossils of the Mary Lee Coal zone and overlying strata (Westphalian A), Pottsville Formation of northern Alabama. In *Carboniferous Coastal Environments and Paleocommunities of the Mary Lee Coal Zone, Marion and Walker Counties, Alabama*, ed. R.A. Gastaldo, T.M. Demko and Y. Liu, A *Guidebook for Field Trip VI: Southeastern Section, Geological Society of America, Tuscaloosa, Alabama, Geological Survey of Alabama*, pp. 82–95.

Rindsberg, A.K. (1992). Holocene ichnology of eastern Mississippi Sound, Alabama. *Circular-Geological Society of Alabama, Report*, 167, 1–75.

Rindsberg, A.K. (1994). Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous Formations. *Geological Survey of Alabama Bulletin*, 158, 1–107.

Rindsberg, A.K. (2005). Gas-escape structures and their paleoenvironmental significance at the Steven C. Minkin Paleozoic Footprint Site (Early Pennsylvanian, Alabama). In *Pennsylvanian Footprints in the Black Warrior Basin of Alabama*, ed. R.D. Buta, A.K. Rindsberg, and D.C. Kopaska-Merkel, *Alabama Paleontological Society Monograph*, 1, 177–183.

Rindsberg, A.K. and Martin, A.J. (2003). *Arthrophycus* in the Silurian of Alabama (USA) and the problem of compound trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 187–219.

Rine, J.M. and Ginsburg, R.N. (1985). Depositional facies of a mud shoreface in Suriname, South America: a mud analogue to sandy nearshore marine deposits. *Journal of Sedimentary Petrology*, 55, 633–652.

Risk, M.J. and Tunnicliffe, V.J. (1978). Intertidal spiral burrows: *Paraonis fulgens* and *Spiophanes wigleyi* in the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology*, 48, 1287–1292.

Röder, H. (1971). Gangsysteme von *Paraonis fulgens* Levinsen 1883 (Polychaeta) in ökologischer, ethologischer und aktuopaläontologischer Sicht. *Senckenbergiana Maritima*, 3, 3–51.

Röder, H. (1977). Zur Beziehung zwischen Konstruktion und Substrat bei mechanisch bohrenden Bohrmuscheln (Pholadidae, Teredinidae). *Senckenbergiana Maritima*, 9, 105–213.

Roberts, D.L. (2008). Last interglacial hominid and associated vertebrate fossil trackways in coastal eolianites, South Africa. *Ichnos*, 15, 190–207.

Roberts, G. (2009). Ephemeral, subfossil mammalian, avian and hominid footprints within Flandrian sediment exposures at Formby Point, Sefton Coast, North West England. *Ichnos*, 16, 33–48.

Rodriguez-Aranda, J.P. and Calvo, J.P. (1998). Trace fossils and rhizoliths as a tool for sedimentological and palaeoenvironmental analysis of ancient continental evaporite successions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 140, 383–399.

Rodriguez-de la Rosa, R.A., Aguillon-Martinez, M.C., Lopez-Espinoza, J. and Eberth, D.A. (2004). The fossil record of vertebrate tracks in Mexico. *Ichnos*, 11, 27–37.

Rodríguez-Tovar, F.J. (2005). Fe-oxide spherules infilling *Thalassinoides* burrows at the Cretaceous-Paleogene (K–P) boundary: Evidence of a near-contemporaneous macrobenthic colonization during the K–P event. *Geology*, 33, 585–588.

Rodriguez-Tovar, F.J. and Delgado, J. (2006). Cuantificación del grado de consolidación del substrato: aplicacion en analisis icnológicos. *Ameghiniana*, 43, 503–508.

Rodríguez-Tovar, F.J. and Uchman, A. (2004a). Ichnotaxonomic analysis of the Cretaceous/Palaeogene boundary interval in the Agost section, south-east Spain. *Cretaceous Research*, 25, 635–647.

Rodríguez-Tovar, F.J. and Uchman, A. (2004b). Trace fossils after the K–T boundary event from the Agost section, SE Spain. *Geological Magazine*, 141, 429–440.

Rodríguez-Tovar, F.J. and Uchman, A. (2006). Ichnological analysis of the Cretaceous-Palaeogene boundary interval at the Caravaca section, SE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242, 313–325.

Rodriguez-Tovar, F.J. and Uchman, A. (2008). Bioturbational disturbance of the Cretaceous-Palaeogene (K-Pg) boundary layer: Implications for the interpretation of the K–P boundary impact event. *Geobios*, 41, 661–667.

Rodriguez-Tovar, F.J., Martinez-Ruiz, F. and Bernasconi, S.M. (2006). Use of high resolution ichnological and stable isotope data for assessing completeness of a K–P boundary section, Agost, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237, 137–146.

Rodríguez-Tovar, F.J., Pérez-Valera, F. and Pérez-López, A. (2007). Ichnological analysis in high-resolution sequence stratigraphy: The *Glossifungites* ichnofacies in Triassic successions from the Betic Cordillera (southern Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 198, 293–307.

Rodríguez-Tovar, F.J., Uchman, A., Payros, A., Orue-Etxebarria, X., Apellaniz, E. and Molina, E. (2010a). Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285, 50–65.

Rodríguez-Tovar, F. J, Morgado, A. and Lozano, J.A. (2010b). Using ichnofossils to characterize chert tools: a preliminary study from Southern Iberia. *Geoarchaeology: An International Journal*, 25, 514–526.

Rodríguez-Tovar, F. J, Morgado, A. and Lozano, J.A. (2010c). Ichnological analysis: a non-destructive tool in archaeology. *Lethaia*, 43, 587–590.

Rogers, D.A. (1990). Probable tetrapod tracks rediscovered in the Devonian of Scotland. *Journal of the Geological Society, London*, 147, 746–748.

Rokas, A., Krüger, D. and Carroll, S.B. (2005). Animal evolution and the molecular signature of radiations compressed in time. *Science*, 310, 1933–1938.

Rona, P.A., Seilacher, A., de Vargas, C., Gooday, A.J., Bernhard, J. M., Bowser, S., Vetriani, C., Wirsen, C.O., Mullineaux, L., Sherrell, R., Grassle, J.F., Low, S. and Lutz, R.A. (2009). A living fossil on the deep-sea floor. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 56, 1700–1712.

Root, R.B. (1967). The niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs*, 37, 317–350.

Roubik, D.W. (1989). *Ecology and Natural History of Tropical Bees*. New York: Cambridge University Press.

Roubik, D.W. and Michener, C.D. (1980). The seasonal cycle and nests of *Epicharis zonata*, a bee whose cells are below the wet-season water table (Hymenoptera, Anthophoridae). *Biotropica*, 12, 56–60.

Runnegar, B. (1992a). Proterozoic metazoan trace fossils. In *The Proterozoic Biosphere*, ed. J.W. Schopf and C. Klein, Cambridge, UK: Cambridge University Press, pp. 1009–1015.

Runnegar, B. (1992b). Oxygen and the early evolution of the Metazoa. In *Metazoan life Without Oxygen*, ed. C. Bryant, London: Chapman & Hall, pp. 65–87.

Ruppert, E.E., Fox, R.S. and Barnes, R.D. (2004). *Invertebrate Zoology: A Functional Evolutionary Approach.* Belmont, CA: Thomson-Brooks/Cole.

Rydell, J., Hammarlund, J. and Seilacher, A. (2001). Trace fossil associations in the Swedish Mickwitzia sandstone (Lower Cambrian): did trilobites really hunt for worms? *Geologiska Föreningens i Stockholm Förhandlingar [GFF]*, 123, 247–250.

Rytel, M.M. (1962). Trephinations in ancient Peru. *Polish Medical Sciences Historical Bulletin*, 5, 42–45.

Sadler, C.J. (1993). Arthropod trace fossils from the Permian De Chelly Sandstone, northeastern Arizona. *Journal of Paleontology*, 67, 240–249.

Salimullah, A.R.M. and Stow, D.A.V. (1995). Ichnofacies recognition in turbidites/hemiturbidites using enhaced FMS images: examples from ODP Leg 129. *The Log Analyst*, 36, 38–48.

Sanders, H.L. (1968). Marine benthic diversity: a comparative study. *American Naturalist*, 102, 243–282.

Sanders, H.L. (1969). Marine benthic diversity and the stability-time hypothesis. *Brookhaven Symposia on Biology*, 22, 71–81.

Sanders, H.L., Mangelsdorf, P.C. and Hampson, G.R. (1965). Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limnology and Oceanography*, 10, R216-R229.

Sands, W.A. (1969). The association of termites and fungi. In *Biology of Termites, Volume 1*, ed. K. Krishna, and F.M. Weesner, New York: Academic Press, pp. 495–524.

Sands, W.A. (1987). Ichnocoenoses of probable termite origin from Laetoli. In *Laetoli: A Pliocene Site in Northern Tanzania*, ed. M.D. Leakey, and J.M. Harris, Oxford, UK: Clarendon Press, pp. 409–433.

Sarjeant, W.A.S. (1967). Fossil footprints from the Middle Triassic of Nottinghamshire and Derbyshire. *Mercian Geologist*, 2, 327–341.

Sarjeant, W.A.S. (1975). Plant trace fossils. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer-Verlag, pp. 51–69.

Sarjeant, W.A.S. (1996). Pisadas en las arenas del tiempo: Pisadas de vertebrados y la interpretación de paleoambientes sedimentarios. Perspectiva histórica y principales aplicaciones. *Asociación Paleontológica Argentina, Publicación Especial*, 4, 31–46.

Sarjeant, W.A.S. and Langston, W. Jr. (1994). Vertebrate footprints and invertebrate traces from the Chadronian (late Eocene) of Trans-Pecos Texas. *Texas Memorial Museum Bulletin*, 36, 1–86.

Sarjeant, W.A.S. and Mossman, D.J. (1978). Vertebrate footprints from the Carboniferous sediments of Nova Scotia: a historical review and description of newly discovered forms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23, 279–306.

Sarjeant, W.A.S. and Reynolds, R.E. (1999). Camel and horse footprints from the Miocene of California. *San Bernadino County Museum Association Quarterly*, 46, 3–19.

Sarjeant, W.A.S., Reynolds, R.E. and Kissell-Jones, M.M. (2002). Fossil creodont and carnivore footprints from California, Nevada, and Wyoming. In *Between the Basins: Exploring the Western Mojave and Southern Basin and Range Province*, ed. R.E Reynolds, Fullerton, CA: California State University, pp. 37–50.

Sarkar, S. and Chaudhuri, A.K. (1992). Trace fossils in Middle to Late Triassic fluvial redbeds, Pranhita-Godavari Valley, south India. *Ichnos*, 2, 7–19.

Savazzi, E. (1982). Shell sculpture and burrowing in the bivalves *Scapharca inaequivalvis* and *Acanthocardia tuberculata*. *Stuttgarter Beiträge zur Naturkunde Serie A*, 353, 1–12.

Savazzi, E. (1991). Burrowing in the inarticulate brachiopod *Lingula anatina*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 85, 101–106.

Savrda, C.E. (1991a). *Teredolites*, wood substrates, and sea-level dynamics. *Geology*, 19, 905–908.

Savrda, C.E. (1991b). Ichnology in sequence stratigraphic studies: an example from the Lower Paleocene of Alabama. *Palaios*, 6, 39–53.

Savrda, C.E. (1992). Trace fossils and benthic oxygenation. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 172–196.

Savrda, C. (1993). Ichnosedimentologic evidence for a noncatastrophic origin of Cretaceous–Tertiary boundary sand in Alabama. *Geology*, 21, 1075–1078.

Savrda, C.E. (1998). Ichnology of the Bridge Creek Limestone Member: Evidence for temporal and spatial variations in paleo-oxygenation in The Western Interior Seaway. In *Stratigraphy and Paleoenvironments of the Western Interior Seaway along the Kansas-Colorado-Utah Drilling Transect*, ed. W.E. Dean and M.A. Arthur, *Society for Sedimentary Geology Concepts in Sedimentology and Paleontology*, 6, 127–136.

Savrda, C.E. (2002). Equilibrium responses reflected in a large *Conichnus* (Upper Cretaceous Eutaw Formation, Alabama, USA). *Ichnos*, 9, 33–40

Savrda, C.E. (2007a). Trace fossils and marine benthic oxygenation. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 149–158.

Savrda, C.E. (2007b). Taphonomy of trace fossils. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 92–109.

Savrda, C.E. and Bottjer, D.J. (1986). Trace fossil model for reconstruction of paleo-oxygenation in bottom waters. *Geology*, 14, 3–6.

Savrda, C.E. and Bottjer, D.J. (1987). Trace fossils as indicators of bottom-water redox conditions in ancient marine environments. In *New Concepts in the Use of Biogenic Sedimentary Structures for Paleoenvironmental Interpretation*, ed. D.J. Bottjer, *Society for Sedimentary Geology Pacific Section, Volume and Guidebook*, 52, 3–26.

Savrda, C.E. and Bottjer, D.J. (1989). Trace fossil model for reconstructing oxygenation histories of ancient marine bottom waters: application to Upper Cretaceous Niobrara Formation, Colorado. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 74, 49–74.

Savrda, C.E. and Bottjer, D.J. (1991). Oxygen-related biofacies in marine strata: an overview and update. In *Modern and Ancient Continental Shelf Anoxia*, ed. R.V. Tyson and T.H. Pearson, *Geological Society Special Publication*, 58, 201–219.

Savrda, C.E. and Bottjer, D.J. (1994). Ichnofossils and ichnofabrics in rhythmically bedded pelagic/hemipelagic carbonates: recognitions and evaluation of benthic redox and scour cycles. In *Orbital Forcing and Cyclic Sequences*, ed. P. de Boer and D.G. Smith, *International Association of Sedimentologists Special Publication*, 19, 195–210.

Savrda, C.E. and King, D.T. Jr. (1993). Log-ground and *Teredolites* largerstätte in a transgressive sequence, Upper Cretaceous (Lower Campanian) Mooreville Chalk, central Alabama. *Ichnos*, 3, 69–77.

Savrda, C.E. and Nanson, L.L. (2003). Ichnology of fair-weather and storm deposits in an Upper Cretaceous estuary (Eutaw Formation, western Georgia, USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 202, 67–83.

Savrda, C.E. and Ozalas, K. (1993). Preservation of mixed-layer ichnofabrics in oxygenation-event beds. *Palaios*, 8, 609–613.

Savrda, C.E., and Smith, M.W. (1996). Behavioural implications of branching and tube-lining in *Teredolites*. *Ichnos*, 4, 191–198.

Savrda, C.E. and Uddin, A. (2005). Large *Macaronichnus* and their behavioural implications (Cretaceous Eutaw Formation, Alabama, USA). *Ichnos*, 12, 1–9.

Savrda, C.E., Bottjer, D.J. and Seilacher, A. (1991). Redox-related benthic events. In *Cycles and Events in Stratigraphy*, ed. G. Einsele, W. Ricken and A. Seilacher, Berlin: Springer-Verlag, pp. 524–541.

Savrda, C.E., Ozalas, K., Demko, T.H., Hichison, R.A. and Scheiwe, T.D. (1993). Log-grounds and the ichnofossil *Teredolites* in transgressive deposits of the Clayton Formation (Lower Paleocene), Western Alabama. *Palaios*, 8, 311–324.

Savrda, C.E., Locklair, R.E., Hall, J.K., Sadler, M.T., Smith, M.W. and Warren, J.D. (1998). Ichnofabrics, ichnocoenoses, and ichnofacies implications of an Upper Cretaceous tidal-inlet sequence (Eutaw Formation, Central Alabama). *Ichnos*, 6, 53–74.

Savrda, C.E., Blanton-Hooks, A.D. Collier, J.W., Drake, R.A., Graves, R.L., Hall, A.G., Nelson, A.I., Slone, J.C., Williams, D.D. and Wood, H.A. (2000). *Taenidium* and associated ichnofossils in fluvial deposits, Cretaceous Tuscaloosa Formation, eastern Alabama, southeastern U.S.A. *Ichnos* 7, 227–242.

Savrda, C.E., Browning, J.V., Krawinkel, H., and Hesselbo, S.P. (2001). Firmground ichnofabrics in deep-water sequence stratigraphy, Tertiary Clinoform-toe Deposits, New Jersey Slope. *Palaios*, 16, 294–305.

Savrda, C.E., Counts, J., McCormick, O., Urash, R. and Williams, J. (2005). Log-grounds and *Teredolites* in transgressive deposits, Eocene Tallahatta Formation (southern Alabama, USA). *Ichnos*, 12, 47–57.

Scarboro, D.D. and Tucker, M.E. (1995). Amphibian footprints from the mid-Carboniferous of Northumberland, England: sedimentological context, preservation and significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 113, 335–349.

Scasso, R.A. and Bellosi, E.S. (2004). Cenozoic continental and marine trace fossils at the Bryn Gwyn Paleontological Park, Chubut. In *First International Congress on Ichnology, Trelew, Argentina*, ed. R.A. Scasso and E.S. Bellosi, *Museo Paleontológico Egidio Feruglio, Bryn Gwyn Guidebook*, 1–19.

Scasso, R., Olivero, E.B. and Buatois, L.A. (1991). Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine fan/shelf depositional system (Upper Cretaceous, James Ross Island, Antarctica). *Journal of South American Earth Science*, 4, 239–260.

Schaeffer-Novelli, Y., Cintron-Molero, G. and Soares, M.L.G. (2002). Mangroves as indicators of sea level change in the muddy coasts of the world. In *Muddy Coasts of the World: Processes, Deposits and Function*, ed. T. Healy, Y. Wang and J.-A. Healy, Amsterdam: Elsevier, 245–262.

Schäfer, W. (1962). *Aktuo-Paläontologie nach Studien in der Nordsee*. Frankfurt am Main: Waldemar Kramer.

Schäfer, W. (1972). *Ecology and Palaeoecology of Marine Environments*. Chicago, IL: University of Chicago Press.

Schatz, E.R., M.G. Mángano, L.A. Buatois and Limarino, C.O. (2011). Life in the Late Paleozoic Ice Age: trace fossils from glacially influenced deposits in a late Carboniferous Fjord-valley of Western Argentina. *Journal of Paleontology*, 85, 502–518.

Schieber, J. (1999). Microbial mats in terrigenous clastics: The challenge of identification in the rock record. *Palaios*, 14, 3–12.

Schieber, J. (2002). The role of an organic slime matrix in the formation of pyritized burrow trails and pyrite concretions. *Palaios*, 17, 104–109.

Schieber, J. (2003). Simple gifts and buried treasures; implications of finding bioturbation and erosion surfaces in black shales. *The Sedimentary Record*, 1, 4–8.

Schieber, J., Bose, P.K., Eriksson, P.G., Banerjee, S., Sarkar, S., Altermann, W. and Catuneanu, O. (2007). *Atlas of Microbial Mat Features Preserved Within the Siliciclastic Rock Record. Atlases in Geology 2*. Amsterdam: Elsevier.

Schimper, W.P. and Schenk, A. (1890). Palaeophytologie. In *Handbuch de Palaeontologie, Teil II*, ed. K.A. Zittel, Leipzig: Oldenbourg, pp. 958.

Schlager, W. (2005). Carbonate Sedimentology and Sequence Stratigraphy. *Society for Sedimentary Geology Concepts in Sedimentology and Paleontology*, 8.

Schlirf, M. (2000). Upper Jurassic trace fossils from the Boulonnais (northern France). *Geologica et Palaeontologica*, 34, 145–213.

Schlirf, M. and Uchman, A. (2005). Revision of the ichnogenus *Sabellarifex* Richter, 1921 and its relationship to *Skolithos* Haldeman, 1840 and *Polykladichnus* Fürsich, 1981. *Journal of Systematic Palaeontology*, 3, 115–131.

Schlirf, M., Uchman, A. and Kümmel, M. (2001). Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area

(Franconia, south-eastern Germany). *Paläontologische Zeitschrift*, 75, 71–96.

Schoener, T.W. (1987). A brief history of optimal foraging ecology. In *Foraging Behavior*, ed. A.C. Kamil, J.R. Krebs and H.R. Pulliam, New York: Plenum Press, pp. 5–68.

Scholle, P.A., Arthur, M.A. and Ekdale, A.A. (1983). Pelagic environment. In *Sandstone Depositional Environments*, ed. P.A. Scholle and D. Spearing, *American Association of Petroleum Geologists Memoir*, 31, 220–291.

Schram, F.R., Feldmann, R.M. and Copeland, M.J. (1978). The Late Devonian Paleaopalaemonidae and the earliest decapod crustaceans. *Journal of Paleontology*, 52, 1375–1387.

Schuppers, J.D. (1993). Quantification of turbidite facies in a reservoir-analogous submarine fan channel sandbody, south-central Pyrinees, Spain. In *The Geological Modelling of Hydrocarbon Reservoirs and Outcrop Analogues*, ed. S.S. Flint and I.D. Bryant, *International Association of Sedimentologists Special Publication*, 15, 99–112.

Scott, A.C. (1992). Trace-fossils of plant–arthropod interactions. In *Trace Fossils*, ed. C.G. Maples and R.R. West, *Paleontological Society Short Course Notes*, 5, 197–223.

Scott, J.J., Renaut, R.W, Buatois, L.A. and Mángano, M.G. (2007a). Saline lake ichnology: Examples of shoreline fluctuations from the Green River Formation, Wyoming, USA and the Kenya Rift. *5th Annual Meeting of the Mercosur, Ushuaia*, 30.

Scott, J.J., Renaut, R.W., Owen, R.B., Sarjeant, W.A.S., (2007b). Biogenic activity, trace formation, and trace taphonomy in the marginal sediments of saline, alkaline Lake Bogoria, Kenya Rift Valley. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J. Genise, and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 309–330.

Scott, J.J., Renaut, R.W. and Owen, B.R. (2008). Preservation and Paleoenvironmental Significance of a Footprinted Surface on the Sandai Plain, Lake Bogoria, Kenya Rift Valley. *Ichnos*, 15, 208–231.

Scott, J.J., Renaut, R.W., Owen, R.B. and Buatois, L.A. (2009). Trace fossils in exhumed surfaces around saline lakes: an example from Lake Bogoria, Kenya Rift Valley. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 176–198.

Scott, J.J., Renaut, R.W. and Owen, R.B. (2010). Taphonomic controls on animal tracks at saline, alkaline Lake Bogoria, Kenya Rift Valley: impact of salt efflorescence and clay mineralogy *Journal of Sedimentary Research*, 80, 639–665.

Scrivner, P.J. and Bottjer, D.J. (1986). Neogene avian and mammalian tracks from Death Valley National Monurnent, Califomia: their context, classification and preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 57, 285–331.

Seike, K. (2008). Burrowing behaviour inferred from feeding traces of the opheliid polychaete *Euzonus* sp. as response to beach morphodynamics. *Marine Biology*, 153, 1199–1206.

Seike, K. (2009). Influence of beach morphodynamics on the distribution of the opheliid polychaete *Euzonus* sp. and its feeding burrows on a sandy beach: paleoecological and paleoenvironmental implications for the trace fossil *Macaronichnus segregatis*. *Palaios*, 24, 799–808.

Seike, K. and Curran, A.H. (2010). Burrow morphology of the Bahamian land crab *Gecarcinus lateralis. Workshop on Crustacean Bioturbation, Fossil and Recent*, ed. J.M. Gibert de, F. Muñiz, E. Mayoral, Z. Belaústegui, *Abstract Volume*, 91–94.

Seilacher, A. (1953a). Studien zur Palichnologie. I. Über die Methoden der Palichnologie. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 96, 421–452.

Seilacher, A. (1953b). Studien zur Palichnologie. II. Die fossilen Ruhespuren (Cubichnia). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 98, 87–124.

Seilacher, A. (1954). Die Geologische Bedeutung Fossiler Lebensspuren. *Zeitschrift Deutschen Geologische Gesellschaft*, 105, 214–227.

Seilacher, A. (1955a). Spuren und Lebensspuren der Trilobiten. In *Beitrage zur Kenntnis des Kambriums in der Salt Range (Pakistan)*, ed. O.H. Schindewolf and A. Seilacher, *Akademie der Wissenschaften und der Literatur zu Mainz, Mathematisch–Naturwissenschaftliche Klasse, Abhandlungen*, 10, 342–372.

Seilacher, A. (1955b). Spuren und Fazies im Unterkambrium. In *Beitrage zur Kenntnis des Kambriums in der Salt Range (Pakistan)*, ed. O.H. Schindewolf and A. Seilacher, *Akademie der Wissenschaften und der Literatur zu Mainz, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen*, 10, 373–399.

Seilacher, A. (1956). Der Beginn des Kambriums als biologische Wende. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 103, 155–180.

Seilacher, A. (1958). Zur ökologische n Charakteristik von Flysch und Molasse. *Eclogae Geologicae Helvetiae*, 51, 1062–1078.

Seilacher, A. (1960). Lebensspuren als Leitfossilien. *Geologische Rundschau*, 49, 41–50.

Seilacher, A. (1962). Paleontological studies on turbidite sedimentation and erosion. *Journal of Geology*, 70, 227–234.

Seilacher, A. (1963a). Umlagerung und Rolltransport von Cephalopodengehäuse. *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 11, 593–615.

Seilacher, A. (1963b). Lebensspuren und sakinitatsfazies. *Fortschritte in der Geologie Rheinland und Westfalen*, 10, 81–94.

Seilacher, A. (1964a). Biogenic sedimentary structures. In *Approaches to Paleoecology*, ed. J. Imbrie, and N. Newell, Chichester, UK: John Wiley & Sons, pp. 296–316.

Seilacher, A. (1964b). Sedimentological classification and nomenclature of trace fossils. *Sedimentology*, 3, 256–253.

Seilacher, A. (1967a). Fossil behaviour. *Scientific American*, 217, 72–80.

Seilacher, A. (1967b). Bathymetry of trace fossils. *Marine Geology*, 5, 413–428.

Seilacher, A. (1968). Sedimentationprozesse in Ammonitengehäusen. *Akademie der Wissenschaften und der Literatur in Mainz, Abhandlungen der mathematisch-naturwissenschaftlichen Klasse*, Jahrgang 1967, 191–204.

Seilacher, A. (1970). *Cruziana* stratigraphy of "non–fossiliferous" Palaeozoic sandstones. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 447–476.

Seilacher, A. (1974). Flysch trace fossils: evolution of behavioural diversity in the deep-sea. *Neues Jahrbuch für Geologie und Palaontologie, Monatshefte*, 233–245.

Seilacher, A. (1977a). Pattern analysis of *Paleodictyon* and related trace fossils. In *Trace Fossils 2*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 9, 289–334.

Seilacher, A. (1977b). Evolution of trace fossil communities. In *Patterns of Evolution*, ed. A. Hallam, Amsterdam: Elsevier, pp. 359–376.

Seilacher, A. (1978). Use of trace fossils for recognizing depositional environments. In *Trace Fossil Concepts*, ed. P.B. Basan, *Society for Sedimentary Geology Short Course Notes*, 5, 167–181.

Seilacher, A. (1984). Late Precambrian and Early Cambrian Metazoa: Preservational or real extinctions? In *Patterns of Change in Earth Evolution*, ed. H.D. Holland and A.F. Trendall, Berlin: Springer-Verlag, pp. 159–168.

Seilacher, A. (1985). Trilobite paleobiology and substrate relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 76, 231–237.

Seilacher, A. (1986). Evolution of behavior as expressed in marine trace fossils. In *Evolution of Animal Behavior: Paleontological and Field Approaches*, ed. J.A. Kitchell and M.H. Nitecki, New York: Oxford University Press, pp. 62–87.

Seilacher, A. (1989). Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia*, 22, 229–239.

Seilacher, A. (1990a). Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology*, 3, 289–311.

Seilacher, A. (1990b). Paleozoic trace fossils. In *The Geology of Egypt*, ed. R. Said, Rotterdam: A.A. Balkema, pp. 649–670.

Seilacher, A. (1992a). An updated *Cruziana* stratigraphy of Gondwanan Palaeozoic sandstones. In *The Geology of Lybia 5*, ed. M.J. Salem, Amsterdam: Elsevier, pp. 1565–1580.

Seilacher, A. (1992b). Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society, London*, 149, 607–613.

Seilacher, A. (1994). How valid is *Cruziana* stratigraphy? *Geologische Rundschau*, 83, 752–758.

Seilacher, A. (1996). Evolution of burrowing behaviour in Silurian trilobites: ichnosubspecies of *Cruziana acacensis*. In *The Geology of the Sirt Basin. Volumes I-III*, ed. M.J. Salem, Amsterdam: Elsevier, pp. 523–530.

Seilacher, A. (1997). *Fossil Art*. Drumheller: The Royal Tyrrell Museum of Paleontology.

Seilacher, A. (1999). Biomat-related lifestyles in the Precambrian. *Palaios*, 14, 86–93.

Seilacher, A. (2000). Ordovician and Silurian arthrophycid ichnostratigraphy. In *Geological Exploration in Murzuk Basin*, ed. M.A. Sola and D. Worsley, Amsterdam: Elsevier, pp. 237–258.

Seilacher, A. (2005). Silurian trace fossils from Africa and Argentina mapping a trans-Gondwanan seaway? *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 129–141.

Seilacher, A. (2007a). *Trace Fossil Analysis*. Heidelberg: Springer-Verlag.

Seilacher, A. (2007b). Principles of ichnostratigraphy. In *Sediment–Organism Interactions: A Multifaceted Ichnology*, ed. R.G. Bromley, L.A. Buatois, M.G. Mángano, J. Genise and R. Melchor, *Society for Sedimentary Geology Special Publication*, 88, 53–56.

Seilacher, A. (2008). Biomats, biofilms, and bioglue as preservational agents for arthropod trackways: *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270, 252–257.

Seilacher, A. and Alidou, S. (1988). Ordovician and Silurian trace fossils from northern Benin (W-Africa). *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 431–439.

Seilacher, A. and Crimes, P.T. (1969). "European" species of trilobite burrows in eastern Newfoundland. In *North Atlantic Geology and Continental drift*, ed. M. Kay, *American Association of Petroleum Geologists Memoir*, 12, 145–148.

Seilacher, A. and Pflüger, F. (1994). From biomats to benthic agriculture: A biohistoric revolution. In *Biostabilization of sediments*, ed. W.E. Krumbein, D.M. Peterson and L.J. Stal, Odenburg: Bibliotheks und Informationssystem der Carl von Ossietzky Universität, pp. 97–105.

Seilacher, A. and Seilacher, E. (1994). Bivalvian trace fossils: A lesson from actuopaleontology. *Courier Forschungsinstitut Institut Senckenberg*, 169, 5–15.

Seilacher, A., Reif, W.-E. and Westphal, F. (1985). Sedimentological, ecological and temporal paterns of fossil Lagerstätten. *Royal Society of London Philosophical Transactions, B*, 311, 5–23.

Seilacher, A., Bose, P.K. and Pflüger, F. (1998). Triploblastic animals more than 1 billion years ago: Trace fossil evidence from India. *Science*, 282, 80–83.

Seilacher, A., Lüning, S., Martin, M., Klitzsch, E., Khoja, A. and Craig, J. (2002). Ichnostratigraphic correlation of Lower Paleozoic clastics in the Kufra Basin (SE Libia). *Lethaia*, 35, 257–262.

Seilacher, A., Grazhdankin, D. and Legouta, A. (2003). Ediacaran biota: The dawn of animal life in the shadow of giant protists. *Paleontological Research*, 7, 43–54.

Seilacher, A., Cingolani, C. and Varela, R. (2004). Ichnostratigraphic correlation of Early Palaeozoic sandstones in North Africa and Central Argentina. In *Geology of NW Libya*, ed. M.J. Salem and T.M. Oun, Libya: Earth Science Society of Libya, 1, 275–292.

Seilacher, A., Buatois, L.A., Mángano, M.G. (2005). Trace fossils in the Ediacaran-Cambrian transition: Behavioural diversification, ecological turnover and environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227, 323–356.

Seilacher-Drexler, E. and Seilacher, A. (1999). Undertraces of sea pens and moon sails and possible counterparts. *Neues Jahrbuch Geologie und Paläontologie, Monatshefte*, 9, 521–540.

Seiple, W. (1981). The ecological significance of the locomotor activity rhythms of *Sesarma cinereum* and *Sesarma reticulatum*. *Crustaceana*, 40, 5–15.

Sellers, W.I. and Manning, P.L. (2007). Estimating maximum running speeds using evolutionary robotics. *Proceedings of the Royal Society, Series B: Biological Sciences*, 274, 2711–2716.

Selley, R.C. (1970). Ichnology of Paleozoic sandstones in the Southern Desert of Jordan: A study of trace fossils in their sedimentologic context. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 477–488.

Sellwood, B.W. (1971). A *Thalassinoides* burrow containing the crustacean *Glyphaea udressieri* (Meyer) from the Bathonian of Oxfordshire. *Palaeontology*, 14, 589–581.

Sepkoski, J.J. Jr. (1981). A factor analytic description of the marine fossil record. *Paleobiology*, 7, 36–53.

Sepkoski, J.J. Jr. (1988). Alpha, beta, or gamma: where does all the diversity go? *Paleobiology*, 14, 221–234.

Sepkoski, J.J. Jr. (1991). A model of onshore–offshore change in faunal diversity. *Paleobiology*, 17, 58–77.

Sepkoski, J.J. Jr. (1992). A compendium of fossil marine animal families. second edition. *Milwaukee Public Museum Contributions in Biology and Geology*, 83, 1–156.

Sepkoski, J.J. Jr. (1995). The Ordovician radiations: diversification and extinction shown by global genus-level taxonomic data. *7th International Symposium on the Ordovician System, Society for Sedimentary Geology, Pacific Section*, 393–396.

Sepkoski, J.J. Jr. (1997). Biodiversity: past, present, and future. *Journal of Paleontology*, 71, 533–539.

Sepkoski, J.J. Jr. and Miller, A.I. (1985). Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In *Phanerozoic Diversity Patterns: Profiles in Macroevolution*, ed. J.W. Valentine, Princeton, NJ: Princeton University Press, pp. 153–190.

Sepkoski, J.J. Jr. and Sheehan, P.M. (1983). Diversification, faunal change, and community replacement during the Ordovician radiations. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenum Press, pp. 673–718.

Sereno, P.C. and Novas, F.E. (1992). The complete skull and skeleton of an early dinosaur. *Science*, 258, 1137–1140.

Shanley, K.W., McCabe, P.J. and Hettinger, R.D. (1992). Tidal influence in Cretaceous fluvial strata from Utah, USA: a key to sequence stratigraphic interpretation, *Sedimentology*, 39, 905–930.

Shapiro, R.S. (2007). Stromatolites: a 3.5-billion-year ichnologic record. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 382–390.

Shaw, J. and Lesemann, J.E. (2003). Subglacial outburst floods and extreme sedimentary events in the Labrador Sea. In *Extreme Depositional Environments: Mega End Members in Geologic Time*, ed. M.A. Chan and A.W. Archer, *Geological Society of America, Special Paper*, 370, 25–41.

Sheehan, P.M. (2001). History of marine biodiversity. *Geological Journal*, 36, 231–249.

Sheehan, P.M. and Schiefelbein, D.R.J. (1984). The trace fossil *Thalassinoides* from the Upper Ordovician of the eastern Great Basin: deep burrowing in the Early Paleozoic. *Journal of Paleontology*, 58, 440–447.

Shen, B., Xiao, S., Dong, L., Zhou, C. and Liu, J. (2007). Problematic macrofossils from Ediacaran successions in the North China and Chaidam blocks: implications for their evolutionary roots and biostratigraphic significance. *Journal of Paleontology*, 81, 1396–1411.

Shi, G.R. and Weldon, E.A. (2002). Permian stratigraphy, sedimentology and paleontology of the southern Sydney Basin, eastern Australia. *First International Palaeontological Congress, IPC2002 Australasia, Pre−4 Field Excursion Guidebook, Daekin University, School of Ecology and Environment, Technical Paper*, 1, 1–65.

Shinn, E.A. (1968). Burrowing in recent lime sediments of Florida and the Bahamas. *Journal of Paleontology*, 42, 879–894.

Short, A.D. (1991). Macro-meso tidal beach morphodynamics, an overview. *Journal of Coastal Research*, 7, 417–436.

Shu, D.G., Conway Morris, S., Han, J., Li, Y., Zhang, X.L., Hua, H., Zhang, Z.F., Liu, J. N., Guo, J.F., Yao, Y. and Yasui, K. (2006). Lower Cambrian vendobionts from China and early diploblast evolution. *Science*, 312, 731–734.

Shultz, M.R. and Hubbard, S.M. (2005). Sedimentology, stratigraphic architecture and ichnology of gravity-flow deposits partially ponded in a growth-fault-controlled slope minibasin, Tres Pasos Formation (Cretaceous), Southern Chile. *Journal of Sedimentary Research*, 75, 440–453.

Sidi, F.H., Nummedal, D., Imbert, P., Darman, H. and Posamentier, H.W. (2003) (eds.). *Tropical deltas of Southeast Asia: Sedimentology, stratigraphy and petroleum geology*. *Society for Sedimentary Geology Special Publication*, 76.

Sidor, C.A., Miller M.F. and Isbell, J.L. (2008). Tetrapod burrows from the Triassic of Antarctica. *Journal of Vertebrate Paleontology*, 28, 277–284.

Siggerud, E.I.H., and Steel, R.J. (1999). Architecture and trace-fossil characteristics of a 10,000–20,000 year, fluvial-to-marine sequence, SE Ebro Basin, Spain. *Journal of Sedimentary Research*, 69, 365–383.

Signor, P.W. III and Brett, C.E. (1984). The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology*, 10, 229–245.

Simpson, E.L. (1991), An exhumed, Lower Cambrian tidal flat: the Antietam Formation, central Virginia, U.S.A. In *Clastic Tidal Sedimentology*, ed. D.G. Smith, G.E. Reinson, B.A. Zaitlin and R.A. Rahmani, *Canadian Society of Petroleum Geology, Memoir*, 16, 123–134.

Simpson, S. (1957). On the trace fossil *Chondrites*. *Quarterly Journal Geological Society of London*, 112, 475–479.

Simpson, S. (1970). Notes on *Zoophycos* and *Spirophyton*. In *Trace Fossils*, ed. T.P. Crimes and J.C. Harper, *Geological Journal Special Issue*, 3, 505–514.

Skilleter, G.A. and Peterson, C.H. (1994). Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. *Oecologia*, 100, 268–278.

Slobodkin, L.B. and Sanders, H.L. (1969). On the contribution of environmental predictability to species diversity. *Brookhaven Symposia on Biology*, 22, 82–95.

Smith, A.B. and Crimes, T.P. (1983). Trace fossils formed by heart urchins: a study of *Scolicia* and related traces. *Lethaia*, 16, 79–92.

Smith, C.R., Levin, L.A., Hoover, D.J., McMurtry, G. and Gage, J.D. (2000). Variations in bioturbation across the oxygen minimum zone in the northwest Arabian Sea. In *Benthic Processes in the Deep Arabian Sea: Biogeochemistry, Biodiversity and Ecology, Deep Sea Research Part II*, ed. J.D. Gage, L.A. Levin and G.A. Wolff, *Tropical Studies in Oceanography*, 47, 227–257.

Smith, D.C. and Douglas, A.E. (1987). *The Biology of Symbiosis*. London: Edward Arnold Publishers Ltd.

Smith, J.J. and Hasiotis, S.T. (2008). Traces and burrowing behaviors of the cicada nymph *Cicadetta calliope*: neoichnology and paleoecological significance of extant soil-dwelling insects. *Palaios*, 23, 503–513.

Smith, J.J., Hasiotis, S.T., Kraus, M.J. and Woody, D. (2008a). *Naktodemasis bowni*: new ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Bighorn Basin, Wyoming. *Journal of Paleontology*, 82, 267–278.

Smith, J.J., Hasiotis, S.T., Kraus, M.J. and Woody, D.T. (2008b). Relationship of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Wyoming, during the Paleocene-Eocene Thermal Maximum. *Palaios*, 23, 683–699.

Smith, P.R., Harper, A.S. and Wood, M.F. (1982). Nonmarine trace fossils in the Mio–Pliocene Ridge Basin Group, southern California. In *Geologic History of Ridge Basin, Southern California*, ed. J.C. Cromwell and M.H. Link, *Society for Sedimentary Geology Pacific Section*, 253–258.

Smith, R. (2004). Silled sub-basins to connected tortuous corridors: Sediment distribution systems on topographically complex subaqueous slopes. In *Confined Turbidite Systems*, ed. S.A. Lomas and P. Joseph, *Geological Society Special Publication*, 222, 23–43.

Smith, R.M.H. (1987). Helical burrow casts of Therapsid origin from the Beaufort Group (Permian) of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 60, 155–170.

Smith, R.M.H. (1993). Sedimentology and ichnology of floodplain paleosurfaces in the Beaufort Group (Late Permian), Karoo Sequence, South Africa. *Palaios*, 8, 339–357.

Smith, R.M.H., Mason, T.R. and Ward, J.D. (1993). Flash–flood sediments and ichnofacies of the Late Pleistocene Homeb Silts, Kuiseb River, Namibia. *Sedimentary Geology*, 85, 579–599.

Smith, R.M.H., Marsicano, C.A., Wilson, J.A. (2009). Sedimentology and paleoecology of a diverse early Jurassic tetrapod tracksite in Lesotho, Southern Africa. *Palaios*, 24, 672–684.

Snelgrove, P.V.R. and Butman, C.A. (1994). Animal–sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology Annual Review*, 32, 111–177.

Soja, C.M. (1991). Silurian trace fossils in carbonate turbidites from the Alexander arc of southeastern Alaska. *Ichnos*, 1, 173–182.

Solan, M. and Wigham, B.D. (2005). Biogenic particle reworking and bacterial–invertebrate interactions in marine sediments. In *Interactions Between Macro- and Microorganisms in Marine Sediments*, ed. E. Kristensen, J.E. Kostka and R.R. Haese, Washington DC: American Geophysical Union, pp. 105–124.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. and Srivastava, D.S. (2004a). Extinction and ecosystem function in the marine benthos. *Science*, 306, 1177–1180.

Solan, M., Wigham, B.D., Hudson, I.R., Kennedy, R., Coulon, C.H., Norling, K., Nilsson, H.C. and Rosenberg, R. (2004b). *In situ* quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. *Marine Ecology Progress Series*, 271, 1–12.

Solan, M., Batty, P., Bulling, M.T. and Godbold, J.A. (2008). How biodiversity affects ecosystem processes: Implications for ecological revolutions and benthic ecosystem function. *Aquatic Biology*, 2, 289–301.

Solan, M., Godbold, J.A., Symstad, A., Flynn D.F.B. and Bunker, D. (2009). Biodiversity–ecosystem function research and biodiversity futures: Early bird catches the worm or a day late and a dollar short? In *Biodiversity, Ecosystem Functioning and Human Wellbeing: An Ecological and Economic Perpective*, ed. S. Naeem, D.E. Bunker, A. Hector, M. Loreau and C. Perrings, Oxford, UK: Oxford University Press, pp. 30–45.

Soler-Gijón, R. and Moratalla, J.J. (2001). Fish and tetrapod trace fossils from the Upper Carboniferous of Puertollano, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 171, 1–28.

Spaargaren, D.H. (1979). Hydrodynamic properties of benthic marine crustacean. *Marine Ecology*, 1, 351–359.

Spaargaren, D.H. (1995). A functional model for describing the responses to salinity stress in aquatic animals. *Comparative Biochemistry and Physiology A*, 111, 501–506.

Sperling, E.A. and Vinther, J. (2010). A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolutiom and Development*, 12, 201–209.

Spila, M.V., Pemberton, S.G. and Sinclair, I.K. (2005). Comparison of marine and brackish/stressed ichnological signatures in the Ben Nevis amd Avalon Formations, Jeanne d'Arc Basin. In *Petroleum Resources and Reservoirs of the Grand Banks, Eastern Canadian Margin*, ed. R.N. Hiscott and A.J. Pulham, *Geological Association of Canada Special Paper*, 43, 73–94.

Squires, R.L. and Advocate, D.M. (1984). Meniscate burrows from Miocene lacustrine–fluvial deposits, Diligencia Formation, Oro copia Mountains, southern California. *Journal of Paleontology*, 58, 593–597.

Stanley, K.O. and Fagerstrom, J.A. (1974). Miocene invertebrate trace fossils from a braided river environment, Nebraska, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 15, 63–82.

Stanley, D.C.A. and Pickerill, R.K. (1993). *Fustiglyphus annulatus* from the Ordovician of Ontario, Canada, with a systematic review of the ichnogenera *Fustiglyphus* Vialov 1971 and *Rhabdoglyphus* Vassoievich 1951. *Ichnos*, 3, 57–67.

Stanley, D.C.A. and Pickerill, R.K. (1998). Systematic ichnology of the Late Ordovician Georgian Bay Formation of Southern Ontario, Eastern Canada. *Royal Ontario Museum, Life Sciences Contributions*, 162, 1–56.

Stanley, S.M. (1970). Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America, Memoir*, 25, 1–269.

Stearley, R.F. and Ekdale, A.A. (1989). Modern marine bioerosion by macroinvertebrates, Northern Gulf of California. *Palaios*, 4, 453–467.

Steele-Petrovic, H.M. (1979). The physiological differences between articulate brachiopods and filter-feeding bivalves as a factor in the evolution of marine level-bottom communities. *Palaeontology*, 22, 101–134.

Stössel, I. (1995). The discovery of a new Devonian tetrapod trackway in SW Ireland. *Journal of the Geological Society of London*, 152, 407–413.

Stow, D.A.V. (1985). Deep-sea clastics: Where are we and where are we going? In *Sedimentology Recent Developments and Applied Aspects*, eds. P. J. Brenchley and B. P. J. Williams. *Geological Society of London, Special Publication*, 18, 67–93.

Stow, D.A.V. and Wetzel, A. (1990). Hemiturbidite: a new type of deep-water sediment. *Proceedings Ocean Drilling Program, Scientific Results*, 116, 25–34.

Stow, D.A.V., Reading, H.G. and Collinson, J.D. (1996). Deep seas. In *Sedimentary Environments*, ed. H.G. Reading, Oxford, UK: Blackwell Science, pp. 395–454.

Strother, P.K. (2000). Cryptospores: the origin and early evolution of the terrestrial flora. In *Phanerozoic Terrestrial ecosyStems*, ed. R.A. Gastaldo and W.A. DiMichele, *The Paleontological Society Papers*, 6, 3–20.

Strother, P.K., Al-Hajri, S. and Traverse, A. (1996). New evidence of land plants from the lower Middle Ordovician of Saudi Arabia. *Geology*, 24, 55–58.

Strother, P.K. and Beck, J.H. (2000). Spore-like microfossils from Middle Cambrian strata: expanding the meaning of the term cryptospore. In *Pollen and Spores: Morphology and Biology*, ed. M.M. Harley, C.M. Morton and S. Blackmore, Kew, London: Royal Botanic Gardens, pp. 413–424.

Sturm, H. (1955). Beiträge zur Ethologie einiger mitteldeutscher Machiliden. *Zeitschrift für Tierpsychologie*, 12, 337–363.

Sutcliffe, O.E. (1997). An ophiuroid trackway from the Lower Devonian Hunsrück Slate, Germany. *Lethaia*, 30, 33–39.

Suwa, G. (1984). Could *Australopithecus afarensis* have made the hominid tracks at Laetoli? *Journal of Physical Anthropology*, 963, 224–225.

Swinbanks, D.D. and Murray, J.W. (1981). Biosedimentological zonation of Boundary Bay tidal flats, Fraser River Delta, British Columbia. *Sedimentology*, 28, 201–237.

Systra, Y.J. and Jensen, S. (2006). Trace Fossils from the Dividalen Group of northern Finland with remarks on early Cambrian trace fossil provincialism. *Geologiska Föreningens I Stockholm Förhandlingar*, 128, 321–325.

Syvitski, J.P., Burrell, D.C. and Skei, J.M. (1987). *Fjords: Processes and Products*. New York: Springer-Verlag.

Szajna, M.J. and Hartline, B.W. (2003). A new vertebrate footprint locality from the Late Triassic Passaic Formation near Birdsboro, Pennsylvania. In *The Great Rift Valleys of Pangea in Eastern North America*, ed. P.M. LeTourneau and P.E. Olsen, New York: Columbia University Press, 264–272.

Tanner, L.H., Lucas, S.G. and Chapman, M.G. (2004). Assessing the record and causes of Late Triassic extinction. *Earth Sciences Reviews*, 65, 103–139.

Tapanila, L. (2005). Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: trace fossil evidence. *Lethaia*, 38, 89–99.

Tapanila, L. (2008). The endolithic guild: an ecological framework for residential cavities in hard substrates. In *Current Developments in Bioerosion*, ed. M. Wisshak and L. Tapanila, Erlangen Earth Conference Series, Berlin: Springer-Verlag, pp. 3–20.

Tapanila, L. and Ekdale, A.A. (2007). Early history of symbiosis in living substrates: Trace-fossil Evidence from the marine record. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 345–355.

Tapanila, L. and Holmer, L.E. (2006). Endosymbiosis in Ordovician–Silurian corals and stromatoporoids: a new lingulid and its trace from eastern Canada. *Journal of Paleontology*, 80, 750–759.

Taylor, A.M. and Gawthorpe, R.L. (1993). Application of sequence stratigraphy and trace fossil analysis to reservoir description: Examples from the Jurassic of the North Sea. In *Petroleum Geology of Northwest Europe*, *Proceedings of the 4th Conference*, ed. J.R. Parker, London: Geological Society, pp. 317–335.

Taylor, A.M. and Goldring, R. (1993). Description and analysis of bioturbation and ichnofabric. *Journal of the Geological Society, London*, 150, 141–148.

Taylor, A.M., Goldring, R. and Gowland, S. (2003). Analysis and application of ichnofabrics. *Earth Science Reviews*, 60, 227–259.

Taylor. A.M. and Pollard, J. (1999). Ichnofabrics in Jurassic strata, North Yorkshire Coast, England. Field Trip Guide Fifth International Ichnofabric Workshop.

Taylor, A.M. and Skinner, J.D. (2000). Associative feeding between aardwolves (*Proteles cristatus*) and aardvarks (*Orycteropus afer*). *Mammal Review*, 30, 141–143.

Taylor, J.H. (1964). Some aspects of diagenesis. *Advancement in Science*, 18, 417–436.

Taylor, P.D. and Wilson, M.A. (2003). Palaeoecology and evolution of marine hard substrate communities. *Earth Science Reviews*, 62, 1–103.

Tchoumatchenco, P. and Uchman, A. (2001). The oldest deep-sea *Ophiomorpha* and *Scolicia* and associated trace fossils from the Upper Jurassic–Lower Cretaceous deep-water turbidite deposits of SW Bulgaria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 169, 85–99.

Tedesco, L.P. and Wanless, H.R. (1991). Generation of sedimentary fabrics and facies by repetitive excavation and storm infilling of burrow networks, Holocene of South Florida and Caicos Platform, B.W.I. *Palaios*, 6, 326–343.

Terwindt, J.H.J. (1988). Palaeo-tidal reconstructions of inshore tidal depositional environments. *In Tide-influenced Sedimentary Environments*, ed. P.L. de Boer, A van Gelder and S.D. Nio, Dordrecht: D. Reidel Publishing Company, pp. 233–263.

Tevis, L. and Newell, I.M. (1962). Studies on the biology and seasonal cycle of the giant red velvet mite, *Dinothrombium pandorae*. (Acari, Trombidiidae). *Ecology*, 43, 497–505.

Thayer, C.W. (1979). Biological bulldozers and the evolution of marine benthic communities. *Science*, 203, 458–461.

Thayer, C.W. (1983). Sediment–mediated biological disturbance and the evolution of marine benthos. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M.J.S. Tevesz and P.L. McCall, New York: Plenum Press, pp. 479–625.

Thomas, M.A. and Anderson, J.A. (1994). Sea-level controls on the architecture of the Trinity/Sabine incised-Valley System, Texas continental shelf. In *Incised-Valley Systems: Origin and sedimentary sequence*, ed. R.W. Dalrymple, R. Boyd and B.A. Zaitlin, *Society for Sedimentary Geology Special Publication*, 51, 63–82.

Thomas, R.G., Smith, D.G., Wood, J.M., Visser, J., Caverley-Range, E.A. and Koster, E.H. (1987). Inclined heterolithic stratification: Terminology, description, interpretation and significance. *Sedimentary Geology*, 53, 123–179.

Thomas, R.D.K. (1986). Taphonomy: ecology's loss is sedimentology's gain. *Palaios*, 1, 206.

Thomason, J.R. and Voorhies, M.R. (1990). Grasslands and grazers. In *Palaeobiology, a Synthesis*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Scientific Publications, pp. 84–87.

Thorne, B.L., Grimaldi, D.A. and Krishna, K. (2000). Early fossil history of the termites. In *Termites: Evolution, Sociality, Symbioses, Ecology*, ed. T. Abe, D.E. Bignell and M. Higashi, Dordrecht: Kluwer Academic, pp. 77–93.

Thulborn, R.A. (1990). *Dinosaur Traces*. London: Chapman & Hall.

Thum, A.B. and Griffiths, C.L. (1977). Ecology of the meiofauna from a subtidal biogenous ripple system. *Proceedings of the 3rd International Meiofauna Conference Hamburg*, abstract.

Ting, H.H., Huang, C.Y. and Wu, L.C. (1991). Paleoenvironments of the Late Neogene sequences along the Nantzuhsien River, southern Taiwan. *Petroleum Geology of Taiwan*, 26, 121–149.

Titschak, J., Bromley, R.G. and Freiwald, A. (2005). Plio-Pleistocene cliff-bound, wedge-shaped, warm-temperate carbonate deposits from Rhodes (Greece): sedimentology and facies. *Sedimentary Geology*, 180, 29–56.

Tognoli, F.M.W. and Netto, R. (2003). Ichnofabric patterns of the Paleozoic estuarine deposits from the Rio Bonito-Palermo succession, eastern of the Paraná Basin, Brazil. In *Icnología: Hacia una convergencia entre Geología y Biología*, ed. L.A. Buatois and M.G. Mángano, *Asociación Argentina de Paleontología Publicación Especial*, 9, 141–155.

Törnqvist, T.E., Kidder, T.R., Autin, W.J., van der Borg, K., de Jong, A.F.M., Klerks, C.J.W., Snijders, E.M.A., Storms, J.E.A., van Dam, R.L. and Wiemann, M.C. (1996). A revised chronology for Mississippi River subdeltas. *Science*, 273, 1693–1696.

Tomkin, N.S., McIlroy, D., Meyer, R. and Moore-Turpin, A. (2010). Bioturbation influence of reservoir quality: A case study from the Cretaceous Ben Nevis Formation, Jeanne'dArc Basin, offshore Newfoundland, Canada. *Bulletin of the American Association of Petroleum Geologists*, 94, 1059–1078.

Trewin, N.H. (2000). The ichnogenus *Undichna*, with examples from the Permian of the Falkland Islands. *Palaeontology*, 43, 979–997.

Trewin, N.H. and McNamara, K.J. (1995). Arthropods invade the land: Trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 85, 177–210.

Trueman, E.R. (1966). Bivalve molluscs: fluid dynamics of burrowing. *Science*, 152, 523–525.

Trueman, E.R., (1967). The dynamics of burrowing in *Ensis* (Bivalvia). *Proceedings of the Royal Society of London B*, 166, 459–476.

Trueman, E.R. (1968a). Burrowing habit and the early evolution of body cavities. *Nature*, 218, 96–98.

Trueman, E.R. (1968b). The burrowing activities of bivalves. *Symposia of the Zoological Society of London*, 22, 176–186.

Trueman, E.R. (1971). The control of burrowing and the migratory behaviour of *Donax denticulatus* (Bivalvia: Tellinacea). *Journal of Zoology, London*, 165, 453–469.

Trueman, E.R. (1975). *The Locomotion of Soft-Bodied Animals*. New York: Elsevier.

Trueman, E.R. and Ansell, A.D. (1969). The mechanism of burrowing into soft substrates by marine animals. *Oceanography and Marine Biology Annual Review*, 7, 315–366.

Trueman, E.R., Brand, A.R. and Davis, P. (1966). The dynamics of burrowing of some common littoral bivalves. *Journal of Experimental Biology*, 44, 469–492.

Tufail, A., Meadows, P.S. and McLaughlin, P. (1989). Meso- and microscale heterogeneity in benthic community structure and the sedimentary environment on an intertidal muddy-sand beach. *Scientia Marina*, 53, 2–3.

Tunis, G. and Uchman, A. (1996a). Trace fossils and facies changes in Cretaceous-Eocene flysch deposits of the Julian Prealps (Italy and Slovenia): Consequences of regional and world-wide changes. *Ichnos*, 4, 169–190.

Tunis, G. and Uchman, A. (1996b). Ichnology of Eocene flysch deposits of the Istria Peninsula, Croatia and Slovenia. *Ichnos*, 5, 1–22.

Turek, V. (1989). Fish and amphibian trace fossils from Westphalian Sediments of Bohemia. *Palaeontology*, 32, 623–634.

Turner, B.R. (1978). Trace fossils from the Upper Triassic fluviatile Molteno Formation of the Karoo (Gondwana) Supergroup, Lesotho. *Journal of Paleontology*, 52, 959–963.

Turner, B.R., Stanistreet, I.G. and Whateley, M.K.G. (1981). Trace fossil and palaeoenvironments in the Ecca Group of the Nongoma Graben, northern Zululand, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 36, 113–123.

Turner, J.S. (2000). *The Extended Organism. The Physiology of Animal-Built Structures*, Cambridge, MA: Harvard University Press.

Turner, J.S. (2003). Trace Fossils and extended organisms: a physiological perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 15–31.

Turner, J.S. (2004). Extended phenotypes and extended organisms. *Biology and Philosophy*, 19, 327–352.

Tuttle R.H. (1987). Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1,G-2/3 and A. In *Laetoli: A Pliocene Site in Northern Tanzania*, ed. M.D. Leakey and J.M. Harris, Oxford, UK: Clarendon Press, pp. 503–523.

Tuttle, R.H. (1996). The Laetoli hominid G footprints. Where do they stand today? *Kaupia*, 6, 97–102.

Tuttle, R.H. (2008). Footprint clues in hominid evolution and forensics: lessons and limitations. *Ichnos*, 15, 158–165.

Tuttle, R.H., Webb, D., Weidi, E. and Baksh, M. (1990). Further progress on the Laetoli trails. *Journal of Archeological Science*, 17, 347–362.

Twitchett, R.J. (1999). Palaeoenvironments and the faunal recovery after the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 154, 27–37.

Twitchett, R.J. and Barras, C.G. (2004). Trace fossils in the aftermath of mass extinction events. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 397–418.

Twitchett, R.J. and Wignall, P.B. (1996). Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 124, 137–151.

Tyson, R.V. and Pearson, T.H. (1991). Modern and ancient continental shelf anoxia: An overview. In *Modern and Ancient Continental Shelf Anoxia*, ed. R.V. Tyson and T.H. Pearson, *Geological Society Special Publication*, 58, 1–24.

Uchman, A. (1991a). "Shallow water" trace fossils in Paleogene flysch in the southern part of the Magura nappe, Polish Outer Carpathians. *Annales Societatis Geologorum Poloniae*, 61, 61–75.

Uchman, A. (1991b). Trace fossils from stress environments in Cretaceous–Palaeogene of Polish Outer Carpathians. *Annales Societatis Geologorum Poloniae*, 61, 207–220.

Uchman, A. (1991c). Diverse tiering patterns in Paleogene flysch trace fossils of the magura nappe, Carpathian Mountains, Poland. *Ichnos*, 1, 287–292.

Uchman, A. (1992). An opportunistic trace-fossil assemblage from the flysch of the Inoceramian beds (Campanian-Paleocene), Bystrica zone of the Magura Nappe, Carpathians, Poland. *Cretaceous Research*, 13, 539–547.

Uchman, A. (1995). Taxonomy and paleoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria*, 15, 1–115.

Uchman, A. (1998). Taxonomy and ethology of flysch trace fossils; revision of the Marian Książkiewicz Collection and studies of complementary material. *Annales Societatis Geologorum Ploniae*, 68, 105–218.

Uchman, A. (1999). Ichnology of the Rhenodanubian Flysch (Lower Cretaceous-Eocene) in Austria and Germany. *Beringeria*, 25, 67–173.

Uchman, A. (2001). Eocene flysch trace fossils from the Hecho Group of the Pyrenees, northern Spain. *Beringeria*, 28, 3–41.

Uchman, A. (2003). Trends in diversity, frequency and complexity of graphoglyptid trace fossils: Evolutionary and palaeoenvironmental aspects. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 192, 123–142.

Uchman, A., (2004a). Phanerozoic history of deep-sea trace fossils. In *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, ed. D. McIlroy, *Geological Society Special Publication*, 228, 125–139.

Uchman, A. (2004b). Deep-sea trace fossils controlled by palaeo-oxygenation and deposition: an example from the Lower Cretaceous dark flysch deposits of the Silesian Unit, Carpathians, Poland. In *Trace Fossils in Evolutionary Palaeoecology*, ed. B.D. Webby, M.G. Mángano and L.A. Buatois, *Fossils & Strata*, 51, 39–57.

Uchman, A. (2007). Deep-Sea Ichnology: Development of Major Concepts. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 248–267.

Uchman A. (2008a). Stop 11, Słopnice, Ropianka Formation (Senonian-Palaeocene) and variegated shale (Eocene). In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch, The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 136–138.

Uchman, A. (2008b). Stop 8, Zbludza, Beloveza Formation (Eocene) and Bystriaca Formation (Eocene): Outer fan ichnology and sequential colonization of turbidites. In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 124–130.

Uchman, A. (2009). The *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies: Characteristics and constraints. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 276, 107–119.

Uchman, A. and Álvaro J.J. (2000). Non-marine invertebrate trace fossils from the Tertiary Calatayud-Teruel Basin, NE Spain. *Revista Española de Paleontología*, 15, 203–218.

Uchman, A. and Cieszkowski, M. (2008a). Stop 2, Rzyki – Siliceous marl and the lowermost part of the Godula Beds: ichnology of the calcareous turbidites. In *The Second International Congress on Ichnology, Cracow, Ichnological Sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, ed. G. Pieńkowski and A. Uchman, The Pre-congress and post-congress field trip Guidebook, Polish Geological Institute, 104–109.

Uchman, A. and Cieszkowski, M. (2008b). Stop 5, Szczawa, Glebieniec, upper part of the Ropianka Formation (Palaeocene): *Nereites* ichnosubfacies of the *Nereites* ichnofacies and ichnological evidences of turbiditic sedimentation in shales. In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 115–118.

Uchman, A. and Cieszkowski, M. (2008c). Stop 4, Szczawa-Centrum, Grybów beds (Early Oligocene) and sub-Cergowa beds (early Oligocene): *Diplocraterion* in deep-sea sediments. In *The Second International Congress on Ichnology, Cracow, Ichnological sites of Poland: The Holy Cross Mountains and the Carpathian Flysch*, *The Pre-congress and Post-congress Field Trip Guidebook*, ed. G. Pieńkowski and A. Uchman, Warsaw: Polish Geological Institute, pp. 110–114.

Uchman, A. and Demircan, H. (1999). Trace fossils of Miocene deep-sea fan fringe deposits from the Cingöz Formation, southern Turkey. *Annales Societatis Geologorum Poloniae*, 69, 125–153.

Uchman, A. and Pervesler, P. (2006). Surface Lebensspuren produced by amphipods and isopods (Crustaceans) from the Isonzo delta tidal flat, Italy. *Palaios*, 21, 384–390.

Uchman, A., Bubniak, I. and Bubniak, A. (2000). The *Glossifungites* ichnofacies in the area of its nomenclatural archetype, Lviv, Ukraine. *Ichnos*, 7, 183–195.

Uchman, A., Demircan, H., Toker, V., Derman, S., Sevim, S. and Szulc, J. (2002). Relative sea level changes recorded in borings from a Miocene rocky of the Mut Basin, southern Turkey. *Annales Societatis Geologorum Poloniae*, 72, 263–270.

Uchman, A., Janbu, N.E. and Nemec, W. (2004a). Trace fossils in the Cretaceous-Eocene flysch of the Sinop-Boyabat Basin, central Pontides, Turkey. *Annales Societatis Geologorum Poloniae*, 74, 197–235.

Uchman, A., Pika-Biolzi, M. and Hochuli, P.A. (2004b). Oligocene trace fossils from temporary fluvial plain ponds: An example from the Freshwater Molasse of Switzerland. *Eclogae Geologicae Helvetia*, 97, 133–148.

Uchman, A., Nemec, W., Ilgar, A. and Messina, C. (2007). Lacustrine trace fossils and environmental conditions in the Early Miocene Ermenek Basin, southern Turkey. *Annales Societatis Geologorum Poloniae*, 77, 123–139.

Uchman, A., Kazakauskas, V. and Gaigalas, A. (2009). Trace fossils from Late Pleistocene varved lacustrine sediments in eastern Lithuania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272, 199–211.

Unwin, D.M. and Corbet, S.A. (1991). *Insects, Plants and Microclimate*. Slough, UK: Richmond Publishing Company Ltd.

Vader, W.J.M. (1964). A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. *Netherlands Journal of Sea Research*, 2, 189–222.

Vail, P.R., Mitchum, R.M. Jr. and Thompson, S. III. (1977). Seismic stratigraphy and global changes of sea level, part 3: relative changes of sea level from coastal onlap. In *Seismic Stratigraphy: Applications to Hydrocarbon Exploration*, ed. C.E. Payton, *American Association of Petroleum Geologists Memoir*, 26, 63–81.

Valentine, J.W. (2004). *On the Origin of Phyla*. Chicago, IL: Chicago University Press.

Vannier, J. and Chen, J.-Y. (2005). Early Cambrian food chain: New evidence from fossil aggregates in the Maotianshan Shale Biota, SW China. *Palaios*, 20, 3–26.

Vannier, J., Calandra, I., Gaillard, C. and Żylińska, A. (2010). Priapulid worms: pioneer horizontal burrowers at Precambrian-Cambrian boundary. *Geology*, 38(8), 711–714.

Van Loon, A.J. (2008). The nature of *Mawsonites* (Ediacara fauna). *Gondwana Research*, 14, 175–182.

Van Wagoner, J.C., Mitchum, R.M., Campion, K.M. and Rahmanian, V.D. (1990). Siliciclastic sequences, stratigraphy in well logs, cores, and outcrops. *American Association of Petroleum Geologists, Methods in Exploration Series*, 7, 1–55.

Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebre, B., el Hariri, K. and Briggs, D.E.G. (2010). Ordovician faunas of Burgess Shale type. *Nature*, 465, 215–218.

Varricchio, D.J., Martin, A.J. and Katsura, Y. (2007). First trace and body fossil evidence of a burrowing, denning dinosaur. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1361–1368.

Verde, M. and Martínez, S. (2004). A new ichnogenus for crustacean trace fossils from the Upper Miocene Camacho Formation of Uruguay. *Palaeontology*, 47, 39–49.

Verde, M., Ubilla, M., Jimenez, J.J. and Genise, J.F. (2007). A new earthworm trace fossil from paleosols; aestivation chambers from the late Pleistocene Sopas Formation of Uruguay. *Palaeogeography, Paleoclimatology, Palaeoecology*, 243, 339–347.

Vermeij, G.J. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, 3, 245–258.

Vermeij, G.J. (1987). *Evolution and Escalation. An Ecological History of Life*. Princeton, NJ: Princeton University Press.

Vernberg, W.B. (1983). Responses to estuarine stress. In *Estuaries and Enclosed Seas. Ecosystems of the World 26*, ed. B.H. Ketchum, New York: Elsevier Scientific, pp. 43–60.

Vidal, G., Jensen, S. and Palacios, T. (1994). Neoproterozoic (Vendian) ichnofossils from Lower Alcudian strata in central Spain. *Geological Magazine*, 131, 169–179.

Viohl, G. (1990). *Taphonomy; Taphonomy of Fossil-lagerstatten; Solnhofen Lithographic Limestones*. Oxford, UK: Blackwell Scientific Publications.

Virtasalo, J.J., Kotilainen, A.T. and Gingras, M.K. (2006). Trace fossils as indicators of environmental change in Holocene sediments of the Archipelago Sea, northern Baltic Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240, 453–467.

Vizcaíno, S.F. and De Iuliis, G. (2003). Evidence for advanced carnivory in fossil armadillos (Mammalia: Xenarthra: Dasypodidae). *Paleobiology*, 29, 123–138.

Vizcaíno, S.F. and Fariña, R.A. (1999). On the flight capabilities and distribution of the giant Miocene bird *Argentavis magnificens* (Teratornithidae). *Lethaia*, 32, 271–278.

Vizcaíno, S.F., Fariña, R.A. and Janis, C. (2001). *Biomechanics and Paleobiology of Vertebrates. Acta Paleontologica Polonica, Special Issue*, 46.

Vogel, K. and Marincovich, L. Jr. (2004). Paleobathymetric implications of microborings in Tertiary strata of Alaska, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 206, 1–20.

Vogel, K., Bundschuh, M., Glaub, I., Hofmann, K., Radtke, G. and Schmidt, H. (1995). Hard substrate ichnocoenoses and their relationships to light intensity and marine bathymetry. *Neues Jahrbuch fuer Geologie und Palaeontologie, Abhandlungen*, 195, 49–61.

Vogel, K., Balog, S., Bundusch, M., Gektidis, M., Glaub, I., Krutschinna, J. and Radtke, G. (1999). Bathymetrical studies in fossil reefs, with microendoliths as paleoecological indicators. *Profil*, 16, 181–191.

Vogel, K., Gektids, M., Golubic, S., Kiene, W. and Radtke, G. (2000). Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: Implications for paleoecological reconstructions. *Lethaia*, 33, 190–204.

Voigt, E. (1959). Die ökologische Bedeuyung der Hartgründe ("Hardgrounds") in der oberen Kreide. *Paläontologische Zeitschrift*, 33, 129–147.

Voigt, E. (1974). Über die Bedeutung der Hartgründe ("Hardgrounds") für die Evertebratenfauna der Maastrichter Tuffkreide. *Natuurhistorisch Maandblad*, 63, 32–39.

Voigt, S. and Hoppe, D. (2010). Mass occurrence of penetrative trace fossils in Triassic lake deposits (Kyrgyzstan, Central Asia). *Ichnos*, 17, 1–11.

Voigt, S., Berman, D.S. and Henrici, A.C. (2007). First well-established track–trackmaker association of Paleozoic tetrapods based on *Ichniotherium* trackways and diadectid skeletons from the Lower Permian of Germany. *Journal of Vertebrate Paleontology*, 27, 553–570.

Voorhies, M.R. (1975). Vertebrate burrows. In *The Study of Trace Fossils. A Synthesis of Principles, Problems, and Procedures in Ichnology*, ed. R.W. Frey, New York: Springer–Verlag, pp. 325–350.

Vossler, S.M. and Pemberton, S.G. (1988a). Superabundant *Chondrites*: a response to storm buried organic material? *Lethaia*, 21, 94

Vossler, S.M. and Pemberton, S.G. (1988b). *Skolithos* in the Upper Cretaceous Cardium Formation: an ichnofossil example of opportunistic ecology. *Lethaia*, 21, 351–362.

Vossler, S.M. and Pemberton, S.G. (1989). Ichnology and plaeoecology of offshore deposits in the Cardium Formation (Turonian, Alberta, Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 74, 217–239.

Wada, M., Kinoshita, K. and Kogure, K. (2004). Mud shrimp burrows as traps of tidal-flat organic matters. In *Proceedings of the Symposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublitoral Sediments: From Individual Behavior to their Role as Ecosystem Engineers*, ed. A. Tamaki, Nagasaki, Japan: Nagasaki University, pp. 101–106.

Waisfeld, B.G., Sánchez, T.M. and Carrera, M.G. (1999). Biodiversification patterns in the Early Ordovician of Argentina. *Palaios*, 14, 198–214.

Waisfeld, B.G., Sánchez, T.M., Benedetto, J.L. and Carrera, M.G. (2003). Early Ordovician (Arenig) faunal assemblages from western Argentina: biodiversification trends in different geodynamic and palaeogeographic settings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 196, 343–373.

Waldron, J.W.F. (1992). The Goldenville-Halifax transition, Mahone Bay, Nova Scotia: Relative sea-level rise in the Maguma source terrane. *Canadian Journal of Earth Sciences*, 29, 1091–1105.

Walker, E.F. (1985). Arthropod ichnofauna of the Old Red Sandstone at Dunure and Montrose, Scotland. *Transactions Royal Society of Edinburgh: Earth Sciences*, 76, 287–297.

Walker, K.R. and Bambach, R.K. (1974). Feeding by benthic invertebrates: classification and terminology for paleoecological analysis. *Lethaia*, 7, 67–78.

Walker, R.G. (1978). Deep-water sandstone facies and ancient submarine fans: models for exploration for stratigraphic traps. *American Association of Petroleum Geologists, Bulletin*, 62, 932–966.

Walker, R.G. (1984). General Introduction: Facies, Facies Sequences and Facies Models. In *Facies Models*, ed. R.G. Walker, *Geoscience Canada Reprint Series*, 1–9.

Walker, R.G. and Plint, A.G. (1992). Wave- and storm-dominated shallow marine systems. In *Facies Models, response to sea level change*, ed. R.G. Walker and N.P. James, St John's, NL: Geological Association of Canada, pp. 219–238.

Walker, S.E. and Behrens-Yamada, S.B. (1993). Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. *Palaeontology*, 36, 735–741.

Walker, S.E. and Miller, W. (1992). Organism–substrate relations: toward a logical terminology. *Palaios*, 7, 236–238.

Walker, S.E., Holland, S.M. and Gardiner, L. (2003). *Coenobichnus currani* (new ichnogenus and ichnospecies): fossil trackway of a land hermit crab, early Holocene, San Salvador, Bahamas. *Journal of Paleontology*, 77, 576–582.

Walter, H. (1983). Zur taxonomie, okologie und biostratigraphie der ichnia limnisch–terrestrischer arthropoden des mitteleuropaischen Jungpalaozoikums. *Freiberger Forschungssheft C*, 382, 146–193.

Walter, H. (1985). Zur ichnologie des Pleistozans von Liebegast. *Freiberger Forschungssheft* C, 400, 101–116.

Walter, H. and Suhr, P. (1998). Lebesspuren aus kaltzeitlichen Bändersedimenten des Quartärs. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden*, 43/44, 311–328.

Walter, M.R., Elphinstone, R. and Heys, G.R. (1989). Proterozoic and Early Cambrian trace fossils from the Amadeus and Georgina Basins, central Australia. *Alcheringa*, 13, 209–256.

Wang, M., Qi, Y.A., Yang, W.T. and Zhou, F. (2009). Stop 4: *Skolithos* and *Beaconites* ichnofabrics in fluvial deposits from the Middle Triassic Youfangzhuang Formation, Nanshan Foreest Park, Jiyuan city, Henan. *The Tenth International Ichnofabric Workshop, Program and Abstracts with Field Trip Guidebook*, p. 107–118.

Wang, Y., Zhu, D.K. and Wu, X.G. (2002). Tidal flats and associated muddy coast of China. In *Muddy Coasts of the World: Process, Deposits and Function*, ed. T. Healy, Y. Wang and J.A. Healy, Amsterdam: Elsevier, pp. 319–345.

Wang, Y., Lin, J.-P., Zhao Y.-L. and Orr, P.J. (2009). Palaeoecology of the trace fossil *Gordia* and its interaction with nonmineralizing taxa from the early Middle Cambrian Kaili Biota, Guizhou province, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 277, 141–148.

Ward, J.V., Tockner, K. and Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: cotones and connectivity. *Regulated Rivers: Research and Management*, 15, 125–139.

Ward, J.V., Tockner, K., Arscott, D.B. and Claret, C. (2002). Riverine landscape diversity. *Freshwater Biology*, 47, 517–539.

Warren, J.W. and Wakefield, N.A. (1972). Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature*, 238, 469–470.

Warman, C.G., O' Hare, T.J. and Naylor, E. (1991). Vertical swimming in wave-induced currents as a control mechanism of intertidal migration by a sand-beach isopod. *Marine Biology*, 111, 49–50.

Warme, J.E. (1977). Carbonate borers: their role in reef ecology and preservation. In *Reefs and Related Carbonates: Ecology and Sedimentology*, ed. S.H. Frost, M.P. Weiss and J.B. Saunders, *American Association of Petroleum Geologists Studies in Geology*, 4, 261–279.

Watanabe, Y., Martini, J.E.J. and Ohmoto, H. (2000). Geochemical evidence for terrestrial ecosystems 2.6 billion years ago. *Nature*, 408, 574–578.

Webb, S., Cupper, M.L. and Robins, R. (2005). Pleistocene human footprints from the Willandra lakes, southeastern Australia. *Journal of Human Evolution*, 50, 405–413.

Webby, B.D. (1983). Lower Ordovician arthropod trace fossils from western New South Wales. *Proceedings of the Linnean Society of New South Wales*, 107, 59–74.

Weber, B. and Braddy, S.J. (2004). A marginal marine ichnofauna from the Blaiklock Glacier Group (?Lower Ordovician) of the Shackleton Range, Antarctica. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 94, 1–20.

Weimer, R.J., Howard, J.D. and Lindsay, D.R. (1981). Tidal flats and associated tidal channels. In *Sandstone Depositional Environments*, ed. P.A. Scholle and D. Spearing, *American Association of Petroleum Geologists Memoir*, 31, 191–246.

Wellman, C.H., Osterloff, P.L. and Mohluddin, U. (2003). Fragments of the earliest land plants. *Nature*, 425, 282–285.

Werner, F. and Wetzel, A. (1982). Interpretation of biogenic structures in oceanic sediments. *Bulletin de l'Institute de Géologie du Bassin d'Aquitaine*, 31, 275–288.

West, D.J. and Hasiotis, S.T. (2007). Trace fossils in an archaeological context: Examples from bison skeletons, Texas, USA. In *Trace Fossils: Concepts, Problems, Prospects*, ed. W. Miller III, Amsterdam: Elsevier, pp. 428–441.

West, R.R. and Ward, E.L. (1990). *Asteriacites lumbricalis* and a protasterid ophiuroid. In *Evolutionary Paleobiology of Behavior and Coevolution*, ed. A.J. Boucot, Amsterdam: Elsevier, pp. 321–327.

Westaway, R., Guillou, H., Yurtmen, S., Beck, A., Bridgeland, D., Demir, T., Scaillet, S. and Rowbotham, G. (2006). Late Cenozoic uplift of Western Turkey: Improved dating of the Kula Quaternary volcanic filed and numerical modeling of the Gediz River terrace staircase. *Global and Planetary Change*, 51, 131–171.

Wetzel, A. (1981). Ökologische und stratigraphische Bedeutung biogener Gefüge in quartären Sedimenten am NW-afrikanischen Kontinentalrand. *"Meteor" Forschungs-Ergebnisse C*, 34, 1–47.

Wetzel, A. (1983). Biogenic structures in modern slope to deep-sea sediments in the Sulu Sea Basin (Philippines). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 42, 285–304.

Wetzel, A. (1984). Bioturbation in deep-sea fine-grained sediments, influence of sediment texture, turbidite frequency and rates of environmental change. In *Fine-grained Sediments: Deep Water Processes and Facies*, ed. D.A.V. Stow and D.J.W. Piper, *Geological Society Special Publication*, 15, 595–608.

Wetzel, A. (1991). Ecological interpretation of deep-sea trace fossil communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 85, 47–69.

Wetzel, A. (1992). The New Zealand *Zoophycos* revisited: morphology, ethology, and paleoecology; some notes for clarification. *Ichnos*, 2, 91–92.

Wetzel, A. (1999). Tilting marks: a wave-produced tool mark resembling a trace fossil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 145, 251–254.

Wetzel, A. (2002). Modern *Nereites* in the South China Sea: ecological association with redox conditions in the sediment. *Palaios*, 17, 507–515.

Wetzel, A. (2003). *International Ichnofabric Workshop Field Guide*, Basel, Switzerland.

Wetzel, A. (2008). Recent bioturbation in the Deep South China Sea: a uniformitarian ichnologic approach. *Palaios*, 23, 601–615

Wetzel, A. (2009). The preservation potential of ash layers in the deep-sea: the example of the 1991-Pinatubo ash in the South China Sea. *Sedimentology*, 56, 1992–2009.

Wetzel, A. (2010). Deep-sea ichnology: observations in modern sediments to interpret fossil counterparts. *Acta Geologica Polonica*, 60, 125–138.

Wetzel, A. and Aigner, T. (1986). Stratigraphic completeness: Tiered trace fossils provide a measuring stick. *Geology*, 14, 234–237.

Wetzel, A. and Balson, P. (1992). Sedimentology of fine-grained turbidites inferred from continuously recorded physical properties data. *Marine Geology*, 104, 165–178.

Wetzel, A. and Uchman, A. (1997). Ichnology of deep-sea fan overbank deposits of the Ganei Slates (Eocene, Switzerland): A classical flysch trace fossil locality studied first by Oswald Heer. *Ichnos*, 5, 139–162.

Wetzel, A. and Uchman, A. (1998a). Deep-sea benthic food content recorded by ichnofabrics: A conceptual model based on observations from Paleogene Flysch, Carpathians, Poland. *Palaios*, 13, 533–546.

Wetzel, A. and Uchman, A. (1998b). Biogenic sedimentary structures in mudstones: an overview. In *Shales and Mudstones* I, eds. J. Schieber, W. Zimmerle and P. Sethi, E. Schweizeirbart'sche, Stuttgart: Verlagbuchhandlung, p. 351–369.

Wetzel A. and Uchman, A. (2001). Sequential colonization of muddy turbidites in the Eocene Beloveza Formation, Carpathians, Poland. *Paleogeography, Paleoclimatology, Paleoecology*, 168, 171–186.

Wetzel, A. and Werner, F. (1981). Morphology and ecological significance of *Zoophycos* in deep-sea sediments off NW Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 32, 185–212.

Wetzel, A., Blechschmidt, I., Uchman, A. and Matter, A. (2007). A highly diverse ichnofauna in Late Triassic deep-sea fan deposits of Oman. *Palaios*, 22, 567–576.

Wetzel, A., Werner, F., and Stow, D.A.V. (2008). Bioturbation and biogenic sedimentary structures in contourites. In *Contourites*, ed. M. Rebesco and A. Camerlenghi, Developments in Sedimentology, Elsevier, 60, 183–202.

Wetzel, A., Tjallingii, R. and Stattegger, K. (2010). *Gyrolithes* in Holocene estuarine incised-valley fill deposits, offshore southern Vietnam. *Palaios*, 25, 239–246.

Wheatcroft, R.A. (1989). Comment on "Characteristic trace-fossil associations in oxygen-poor sedimentary environments". *Geology*, 17, 674.

Wheatcroft, R.A. (1990). Preservation potential of sedimentary event layers. *Geology*, 18, 843–845.

Whicker, A.D. and Detling, J.K. (1988). Ecological consequences of prairie dog disturbances. *Bioscience*, 38, 778–785.

Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213–251.

White, D.S. and Miller, M.F. (2008). Benthic invertebrate activity in lakes: Linking present and historical bioturbation patterns. *Aquatic Biology*, 2, 269–277.

Whitford, W.G. (2002). *Ecology of Desert Systems*. London: Academic Press.

Whitford, W.G. and Kay, F.R. (1999). Biopedoturbation by mammals in deserts: a review. *Journal of Arid Environments*, 41, 203–230.

Whittington, H.B. (1992). *Fossils Illustrated, Volume 2, Trilobites*. Woodbridge, UK: The Boydell Press.

Wiggins, G.B. and Wichard, W. (1989). Phylogeny and pupation in Trichoptera, with proposals on the origin and higher classification of the order. *Journal of the North American Benthological Society*, 8, 260–276.

Wightman, D.M., Pemberton, S.G. and Singh, C. (1987). Depositional modelling of the Upper Mannville (Lower Cretaceous), east-central Alberta: Implications for the recognition of brackish water deposits. In *Reservoir Sedimentology*, ed. R.W. Tillman and K.J. Weber, *Society for Sedimentary Geology Special Publication*, 40, 189–220.

Wignall, P.B. (1991). Dysaerobic trace fossils and ichnofabrics in the Upper Jurassic Kimmeridge Clay of southern England. *Palaios*, 6, 264–270.

Wignall, P.B. (1993). Distinguishing between oxygen and substrate control in fossil benthic assemblages. *Journal of the Geological Society of London*, 150, 193–196.

Wignall, P.B. (2001). End Permian mass extinction. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 226–229.

Wilf, P., Labandeira, C.C., Kress, W.J., Staines, C.L., Windsor, D.M., Allen, A.L. and Johnson, K.R. (2000). Timing the radiations of leaf beetles: Hispines on gingers from latest Cretaceous to Recent. *Science*, 289, 291–294.

Wilf, P., Labandeira, C.C., Johnson, K.R., Coley, P.D. and Cutter, A.D. (2001). Insect herbivory, plant defense and Early Cenozoic climate change. *Proceedings of the National Academy of Sciences, USA*, 98, 6221–6226.

Willey, P., Watson, P.J., Crothers, G. and Stolen, J. (2009). Holocene human footprints in North America. *Ichnos*, 16, 70–75.

Wills, L.J. and Sarjeant, W.A.S. (1970). Fossil vertebrate and invertebrate tracks from boreholes through the Bunter series (Triassic) of Worcestershire. *Mercian Geology*, 3, 399–414.

Williams, M., Siveter, D.J. and Peel, J.S. (1996). *Isoxys* (Arthropoda) from the Early Cambrian Sirius Passet Lagerstätte, North Greenland. *Journal of Paleontology*, 70, 947–954.

Willis, B.J. (2005). Tide-influenced river delta deposits. In *River Deltas: Concepts, Models, and Examples*, ed. L. Giosan and J.P. Bhattacharya, *Society for Sedimentary Geology Special Publication*, 83, 87–129.

Wilson, D.P. (1954). The attractive factor in the settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biological Association of the United Kingdom*, 33, 361–380.

Wilson, D.P. (1955). The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny. *Journal of the Marine Biology Association of the United Kingdom*, 34, 513–543.

Wilson, J.B. (1982). Shelly faunas associated with temperate offshore tidal deposits. In *Offshore tidal sands*, ed. A.H Stride, London: Chapman & Hall, pp. 126–171.

Wilson, J.B. (1986). Faunas of tidal current and wave-dominated continental shelves and their use in the recognition of storm deposits. In *Shelf Sands and Sandstones*, ed. R.J. Knight and J.R. McLean, *Memoir of the Canadian Society of Petroleum Geology*, 11, 313–326.

Wilson, J.L. (1975). *Carbonate Facies in Geologic History*. Heidelberg: Springer-Verlag.

Wilson, M.A. (2007). Macroborings and the evolution of bioerosion. In *Trace Fossils: Concepts, Problems, Prospects*, *ed*. W. Miller III, Amsterdam: Elsevier, pp. 356–367.

Wilson, M. A. and Palmer, T. J. (1998). The earliest *Gastrochaenolites* (Early Pennsylvanian, Arkansas, U.S.A.): an Upper Paleozoic bivalve boring? *Journal of Paleontology*, 72, 769–772.

Wilson, M.A. and Palmer, T.J. (2001). The Ordovician bioerosion revolution. *Geological Society of America Abstracts with Programs* A, 33, 248.

Wilson, M.A. and Palmer, T.J. (2006). Patterns and processes in the Ordovician bioerosion revolution. *Ichnos*, 13, 109–112.

Wilson, M.A., Allen, C. and White, B. (1998). Paleontological evidence of a brief global sea-level event during the last interglacial. *Lethaia*, 31, 241–250.

Wing, S.L., Hasiotis, S.T. and Bown, T.M. (1995). First ichnofossils of flank-buttressed trees (late Eocene), Fayum Depression, Egypt. *Ichnos*, 3, 281–286.

Wisshak, M. (2006). High-Latitude Bioerosion. *The Kosterfjord Experiment. Lecture Notes in Earth Sciences*, 109, 1–202.

Wisshak, M. and Neumann, C. (2006). A symbiotic association of a boring polychaete and an echinoid from the Late Cretaceous of Germany. *Acta Palaeontologica Polonica*, 51, 589–597.

Wisshak, M. and Porter, D. (2006). The new ichnogenus *Flagrichnus*: a paleoenvironmental indicator for cold-water settings? *Ichnos*, 13, 135–145.

Wisshak, M. and Rüggeberg, A. (2006). Colonisation and bioerosion of experimental substrates by benthic foraminifera from euphotic to aphotic depths (Kosterfjord, SW-Sweden). *Facies*, 52, 1–17.

Wisshak, M., Volohonsky, E. and Blomeier, D. (2004). Acanthodian fish trace fossils from the early Devonian of Spitsbergen. *Acta Palaentologica Polonica*, 49, 629–634.

Wisshak, M., Gektids, M., Freiwald, A. and Lundalv, T. (2005). Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study. *Facies*, 51, 93–117.

Wolcott, T.G. (1973). Physiological ecology and intertidal zonation in limpets (Acmaea): A critical look at "limiting factors". *Biological Bulletin, Marine National Laboratory, Woods Hole*, 145, 389–422.

Wolf, T. (1960). The hadal community: an introduction. *Deep-Sea Research*, 6, 95–124.

Wolfe, J.A. and Russell, D.A. (2001). Impact of K-T boundary events on terrestrial life. In *Palaeobiology II*, ed. D.E.G. Briggs and P.R. Crowther, Oxford, UK: Blackwell Science, pp. 232–234.

Wolff, W.J. (1973). The estuary as a habitat. An analysis of data on the soft-bottom macro-fauna of the estuarine area of the rivers Rhine, Meuses, and Scheldt. *Zoologische Verhandlungen Leiden*, 126, 1–242.

Wolff, W.J. (1983). Estuarine benthos. In *Estuaries and Enclosed Seas, Ecosystems of the World 26*, ed. B.H. Ketchum, Amsterdam: Elsevier, pp. 151–182.

Woolfe, K.J. (1990). Trace fossils as paleoenvironmental indicators in the Taylor Group (Devonian) of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 80, 301–310.

Wooton, R.J. (1988). The historical ecology of aquatic insects: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62, 477–492.

Wright, L.D. (1977). Sediment transport and deposition at river mouths: a synthesis. *Geological Society of America, Bulletin*, 88, 857–868.

Wright, J.P. and Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience*, 56, 203–209.

Wu, X. (1982). Storm-generated depositional types and associated trace fossils in Lower Carboniferous shallow-marine carbonates of Three Cliffs Bay and Ogmore-by-sea, South Wales.

Palaeogeography, Palaeoclimatology, Palaeoecology, 39, 187–202.

Yang, B.C., Dalrymple, R.W. and Chun, S.S. (2005). Sedimentation on a wave-dominated, open-coast tidal flat, south-western Korea: a summer tidal flat–winter shoreface. *Sedimentology*, 52, 235–252.

Yang, B., Dalrymple, R.W. and Chun, S. (2006). The significance of hummocky cross-stratification (HCS) wavelengths: evidence from an open-coast tidal flat, South Korea. *Journal of Sedimentary Research*, 76, 2–8.

Yang, B.C., Dalrymple, R.W., Chun, S.S., Johnson, M.F. and Lee, H.J. (2008a). Tidally modulated storm sedimentation on open-coast tidal flats, southwestern coast of Korea: distinguishing tidal-flat from shoreface storm deposits. In *Recent Advances in Modelsof Siliciclastic Shallow-Marine Stratigraphy*, ed. G.J. Hampson, R.J. Steel, P.B. Burgess and R.W. Dalrymple, *SEPM Special Publication*, 90, 161–176.

Yang, B.C., Gingras, M.K., Pemberton, S.G. and Dalrymple, R.W. (2008b). Wave-generated tidal bundles as an indicator of wave-dominated tidal flats. *Geology*, 36, 39–42.

Yang, S.L., Li, H., Ysebaert, T., Bouma, T.J., Zhang, W.X., Wang, Y.Y., Li, P., Li, M. and Ding, P.X. (2008b). Spatial and temporal variations in sediment grain size in tidal wetlands, Yangtze Delta: on the role of physical and biotic controls. *Estuarine, Coastal and Shelf Science*, 77, 657–671.

Yang, B., Dalrymple, R.W., Gingras, M.K. and Pemberton, S.G. (2009). Autogenic occurrence of *Glossifungites* ichnofacies: examples from wave-dominated macrotidal flats, southwestern coast of Korea. *Marine Geology*, 260, 1–5.

Yeo, R.K. and Risk, M.J. (1981). The sedimentology, stratigraphy, and preservation of intertidal deposits in the Minas Basin system, Bay of Fundy. *Journal of Sedimentary Petrology*, 51, 245–260.

Yochelson, E.L. and Fedonkin, M.A. (1993). Paleobiology of *Climactichnites*, an enigmatic late Cambrian fossil. *Smithsonian Contributions to Paleobiology*, 74, 1–34.

Yochelson, E.L. and Fedonkin, M.A. (1997). The type specimens (Middle Cambrian) of the trace fossil *Archaeonassa* Fenton and Fenton. *Canadian Journal of Earth Sciences*, 34, 1210–1219.

Yonge, C.M. (1936). Mode of life, feeding, digestion and symbiosis with zooxanthellae in the Tridacnidae. *Scientific Report on the Great Barrier Reef Expedition British Museum*, 1, 283–321.

Yoshida, S., Steel, R.J. and Dalrymple, R.W. (2007). Changes in depostional processes: an ingredient in a new generation of sequence stratigraphic models. *Journal of Sedimentary Research*, 77, 447–460.

Zaitlin, B.A. and Shultz, B.C. (1990). Wave-influenced estuarine sand body, Senlac heavy oil pool, Saskatchewan, Canada. In *Sandstone Petroleum Reservoirs*, ed. J H. Barwis, J.G. McPherson and J.R. Strudlick, New York: Springer-Verlag, pp. 363–387.

Zaitlin, B.A., Dalrymple, R.W. and Boyd, R. (1994). The stratigraphic organization of incised-valley systems associated with relative sea-level changes. In *Incised Valley Systems: Origin and Sedimentary Sequence*, ed. R. Boyd, B.A. Zaitlin and R. Dalrymple, *Society for Sedimentary Geology Special Publication*, 51, 45–60.

Zavala, C., Arcuri, M., Di Meglio, M., Gamero, H. and Contreras, C. (2011). a genetic facies tract for the analysis of sustained hyperpycnal flow deposits. *In Sediment Transfer from Shelf to Deep Water: Revisiting the Delivery System*, ed. R.M. Slatt and C. Zavala, *American Association of Petroleum Geologists Studies in Geology* 61, in press.

Zavala, C.A., Grill, S.C., Martinez, D., Ortiz, H.O. and Gonzalez, R. (1992). Análisis paleoambiental de depósitos cuaternarios. Sitio paleoicnológico Monte Hermoso I, Provincia de Buenos Aires. *3º Jornadas Geológicas Bonaerenses (La Plata), Actas*, 31–37.

Zawiskie, J.M., Collinson, J.W. and Hammer, W.R. (1983). Trace fossils of the Permian-Triassic Takrouna Formation, Northern Victoria Land, Antartica. In *Antartic Earth Science*, ed. J.R. Oliver, P.R. James and J.B. Jago, Canberra, Australia: Australian Academy of Science, pp. 215–220.

Zhang, D.D. and Li, S.H. (2002). Optical dating of Tibetan human hand- and footprints: an implication for the palaeoenvironment of the last glaciation of the Tibetan Plateau. *Geophysical Research Letters*, 29, 1072–1074.

Zhang, G., Buatois, L.A., Mángano, M.G. and Aceñolaza, F.G. (1998). Sedimentary facies and environmental ichnology of a Permian playa-lake complex in western Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 138, 221–243.

Zhang, J., Li, D., Li, M., Lockley, M.G. and Bai, Z. (2006). Diverse dinosaur-, pterosaur-, bird track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research*, 27, 44–55.

Zhang, X.G., Bergström, J., Bromley, R.G. and Hou, X.G. (2007). Diminutive trace fossils in the Chengjiang Lagerstätte. *Terra Nova*, 19, 407–412.

Zhang Y. and Golubic, S. (1987). Endolithic microfossils (cyanophyta) from early Proterozoic stromatolites, Hebei, China. *Acta Micropaleontologica Sinica*, 4, 1–12.

Zhu, M.-Y., Vannier, J., Van Iten, H., and Zhao, Y.-L. (2004). Direct evidence of predation on trilobites in the middle Cambrian. *Proceedings of the Royal Society B: Biological Sciences*, 271, 277–280.

Zhuravlev, A.Y., Gámez Vintaned, J.A. and Ivantsov, A.Y. (2009). First finds of problematic Ediacaran fossil Gaojiashania in Siberia and its origin. *Geological Magazine*, 146, 775–780.

Zonneveld, J.P. and Pemberton S.G. (2003). Ichnotaxonomy and behavioral implications of Lingulide-derived trace fossils from the Lower and Middle Triassic of western Canada. *Ichnos*, 10, 23–35.

Zonneveld, J.-P., Pemberton, S.G. and Saunders, T.D.A. (2002). Large, robust *Cruziana* from the Middle Triassic of northeastern British Columbia: ethologic, biostratigraphic, and paleobiologic significance. *Palaios*, 17, 435–448.

Zonneveld, J.P., Lavigne, J.M., Bartels, W.S. and Gunnell, G.F. (2006). *Lunulichnus tuberosus* ichnogen. and ichnosp. nov. from the Early Eocene Wasatch Formation, Fossil Butte National Monument, Wyoming: An Arthropod-Constructed Trace Fossil Associated with Alluvial Firmgrounds. *Ichnos*, 13, 87–94.

Zonneveld, J.-P., Beatty, T.W. and Pemberton, S.G. (2007). Lingulide brachiopods and the trace fossil *Lingulichnus* from the Triassic of western Canada: Implications for faunal recovery after the end-Permian mass extinction. *Palaios*, 22, 74–97.

Zonneveld, J.P., Gingras, M.K. and Beatty, T.W. (2010). Diverse ichnofossils assemblages following the P-T mass extinction, Lower Triassic, Alberta and British Columbia, Canada: Evidence for shallow marine refugia on the Northwestern coast of Pangea. *Palaios*, 25, 368–392.

Żylińska, A. (1999). Trace maker of *Cruziana semiplicata* in the Upper Cambrian of the Holy Cross Mts. (Poland). *5th Field Conference of the Cambrian Stage Subdivision Working Group*, *Abstracts of Papers*, 62–63.

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