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

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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

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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
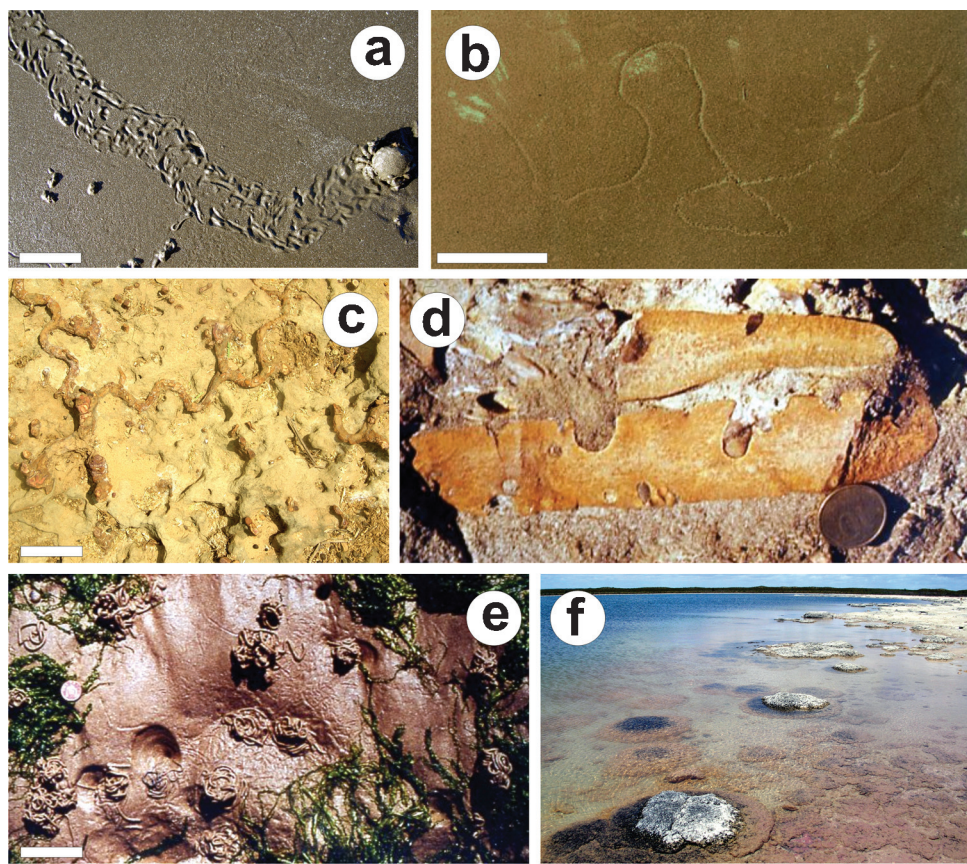
Figure 1.1 Examples of biogenic structures. (a) A trackway produced by a crab (on the right). Tidal flats nearby Estancia Maria Luisa, Tierra del Fuego, Argentina. Scale bar is 5 cm. (b) A trail assigned to the ichnospecies *Gordia marina*. Upper Carboniferous, Guandacol Formation, Río Frío, western 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
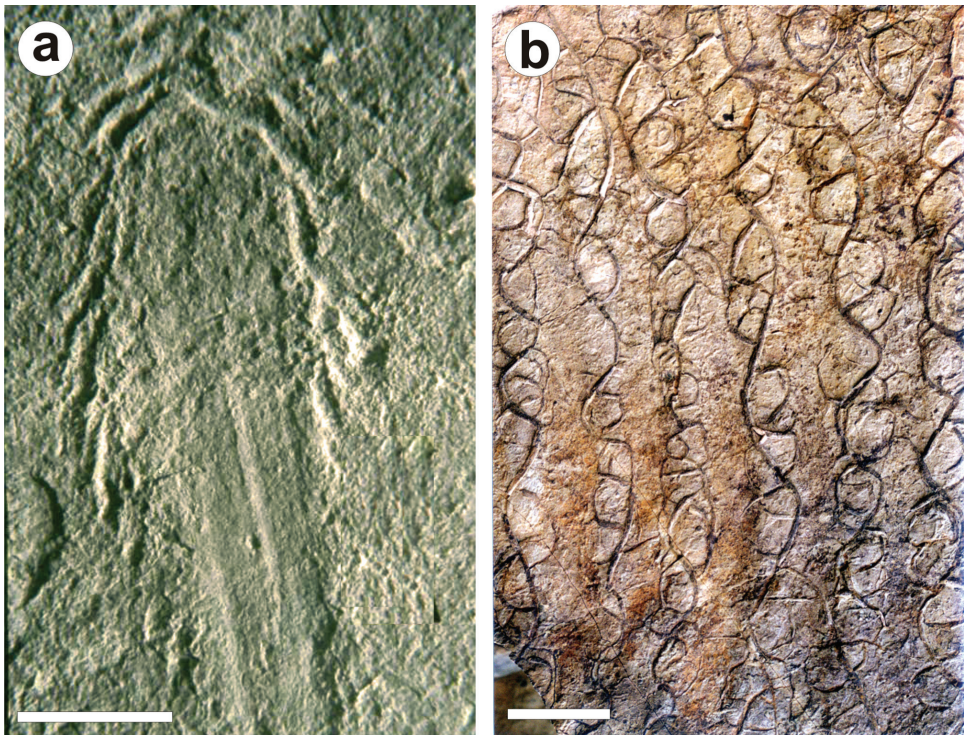
Figure 1.2 Pseudotraces. (a) Inorganic sole mark transitional between groove and chevron mark that superficially may resemble a resting trace. Upper Carboniferous, Agua Colorada Formation, Cantera La Laja, Sierra de Narváez, northwest Argentina. Scale bar is 1 cm. (b) Synaeresis cracks resembling grazing 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 characteristis 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
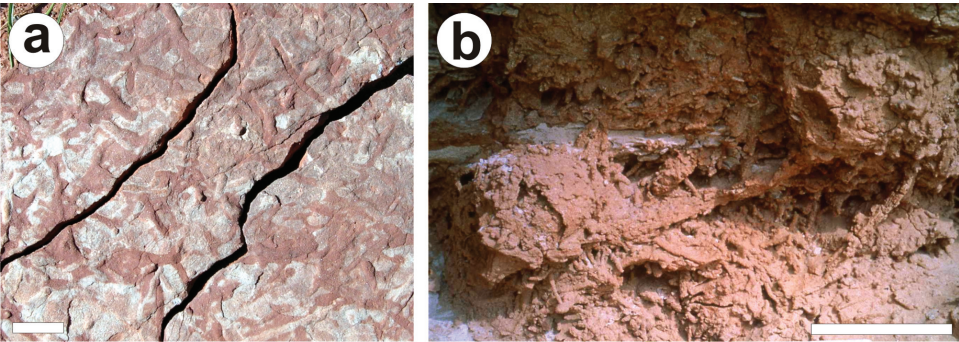

Figure 1.3 Characteristics of trace fossils. Trace fossils represent evidence of behavior. (a) *Palaeophycus tubularis*, a simple trace fossil produced by worm-like animals or insects Lower Permian, Abo Formation, Jemez Mountains, New Mexico. Scale bar is 1 cm. (b) *Termitichnus qatranii*, a termite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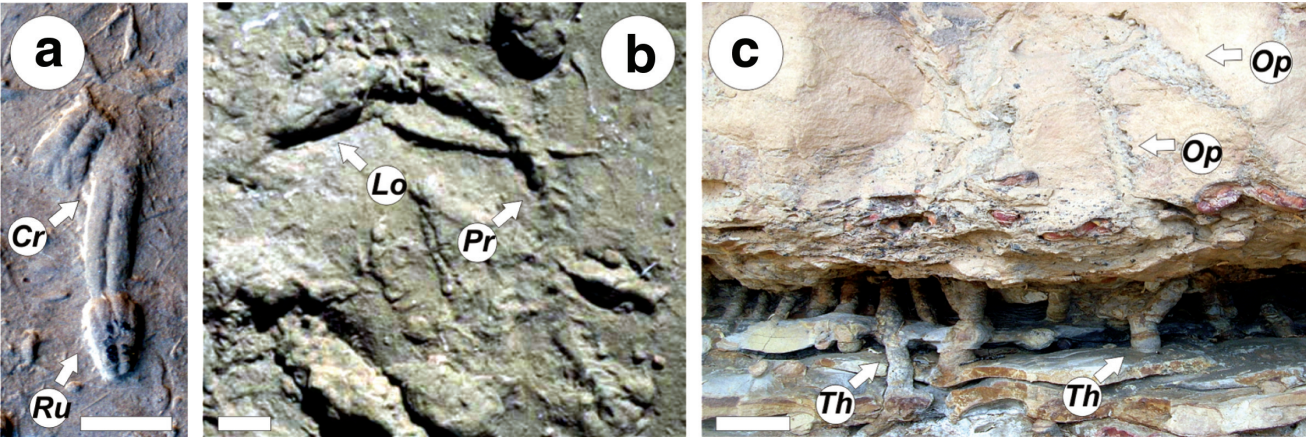

Figure 1.4 Characteristics of trace fossils. The same organism may produce more than one ichnotaxon. (a) Transition between the trilobite locomotion trace *Cruziana* isp. (*Cr*) and the resting trace *Rusophycus* isp. (*Ru*). Upper Carboniferous, Stalnaker Sandstone, roadcut along Kansas Highway 166, 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 nonflying 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
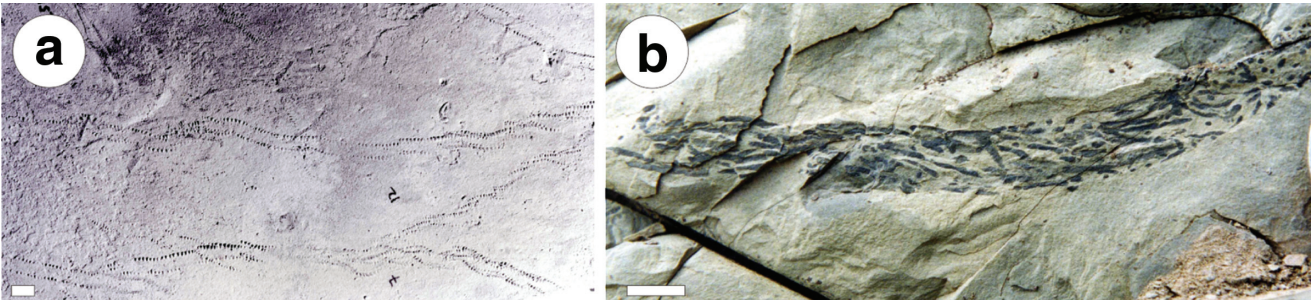
Figure 1.5 Characteristics of trace fossils. (a) The same ichnotaxon may be produced by more than one organism. A wide variety of arthropods, including centipedes, millipedes, onicophorans, and trilobites, are potential producers of *Diplichnites gouldi*. Upper Carboniferous, Tonganoxie Sandstone, Stranger 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.