BIOGENIC SEDIMENTARY STRUCTURES

Synonyms

Trace fossils

Ichnofossils

Definition

Biogenic sedimentary structures are evidence of organism–substrate interactions preserved in rocks and sediments. Their study is "paleoichnology" (from the Greek *palaios* = old, ancient and *ichnos* = a trace, a track), whereas similar studies in modern sediments are referred to as "neoichnology". Markings that do not reflect the behavior of organisms (e.g., marks made by the shells of dead mollusks passively transported on the sea floor by waves and/or currents) are excluded from the trace fossils. Nor do biogenic sedimentary structures include body fossils (direct remains, such as shells, bones, teeth, etc.) or molds of organism bodies.

Introduction

Organisms that have adopted endobenthic or epibenthic modes of life produce biogenic sedimentary structures by "disturbing" the substrate. The number of biogenic sedimentary structures is vast and various authors have proposed subdividing them into component groups to better define their significance (Frey, 1971 and 1973; Frey and Pemberton, 1984; Pemberton *et al*., 1992; Bromley, 1996, among others). Four major categories of structures produced by the activities of organisms are generally accepted:

- Bioturbation structures: which reflect the disruption by organisms of biogenic and physical stratification features or sediment fabrics, and include tracks, trails, burrows, and similar structures.
- Biostratification structures: which consist of stratification features imparted by organism activities, and include certain stromatolites, biogenic graded bedding, byssal mats, and similar evidence.
- Biodepositional structures: which reflect the production or concentration of sediments, and includes coprolites, fecal pellets, pseudofeces, and fecal castings.
- Bioerosion structures: which are mechanically or biochemically produced by organisms in rigid substrates, and include borings, rasps and scrapes, bites, drill holes, and related traces.

These categories, and others proposed in the literature, are not exhaustive because the divisions among the various categories are vague. For example, plant–arthropod interactions may be revealed by biogenic structures preserved in wood, leaves, and seeds, which are not strictly rigid substrates

comparable to rockgrounds or hardgrounds. Consequently, the appropriate placement of this group in one category or another is unclear. Egg cases are not usually described as trace fossils, but eggs can be preserved within a fossil nest, providing direct evidence of reproductive behavior. In that sense, they fall within the realm of paleoichnology and are often placed under "other evidence of activity".

The conceptual framework

The importance of paleoichnology in traditional fields such as paleontology, paleoecology, sedimentology, and stratigraphy derives from the peculiarities of trace fossils, which reflect both their mode of formation and their taphonomic histories. Unfortunately, the limitations of trace fossil also arise from these basic characteristics (the "ichnological principles" of Bromley & Fursich, 1980; Ekdale *et al*., 1984; Bromley, 1996; Pemberton *et al*., 2001). For example: [1] A long stratigraphic range can limits the use of trace fossils in biostratigraphy. [2] A narrow environmental range may reflect similar responses of tracemakers to a given set of paleoecological parameters, and therefore biogenic sedimentary structures tend to occur preferentially in certain depositional environments. The combination of [1] and [2] greatly facilitates the comparison of rocks of different ages formed in similar depositional settings. [3] The rarity of secondary displacement means that trace fossils are very rarely transported and therefore represent the original environmental position of the tracemakers (i.e., they are *in situ* fossils). This characteristic reveals the strength of ichnofossils in paleoecological reconstruction. [4] Non-preservable soft-bodied trace producers; many biogenic sedimentary structures record the activities of soft-bodied organisms that are usually not preserved because they lack hard parts. This fact highlights once again the difference between trace and body fossils. [5] Occurrences in otherwise nonfossiliferous sediments; this peculiarity is very often the result of diagenetic processes that, on the one hand, enhance the potential preservation of trace fossils and, on the other, may obliterate the tests and shells of body fossils. [6] The same individual or species of organism may produce different structures corresponding to different behavior patterns; this characteristic can produce compound traces, where intergradational forms reflect the transition from one behavior to another. [7] The same individual may produce different biogenic structures, reflecting the same behavior on different substrates; this peculiarity is attributable to variability in the substrate conditions in terms of the degree of consistency, grain size, and stratal position. [8] Conversely, identical (or very similar) structures can be produced by systematically different organisms, where their behavior is similar; this peculiarity makes it impossible to establish a one-to-one relationship between tracemakers and

biogenic structures. [9] A single structure may reflect the activity of two or more organisms, living together or in successive times, within the substrate (the "composite" traces of Pickerill, 1994). Paleoenvironmental research based on these characteristics represents the majority of contemporary ichnological studies and applications.

Naming biogenic sedimentary structures

The use a formal taxonomy by ichnologists must accommodate the many difficulties that arise from both the historical background and the intrinsic nature of ichnofossils. In the early years of paleoichnology, a large number of invertebrate trace fossils were named and described as the remains of algae or other organisms (Age of Fucoids by Osgood, 1975). However, based on the priority law, many of these names result as taxonomically valid, including such celebrities as *Cruziana*, *Zoophycos*, and *Chondrites* erected as algae and *Nereites* as worms.

The 1964 edition of the International Code of Zoological Nomenclature (ICZN) ruled that trace fossil names erected after 1930 were to be accompanied by a statement on the identification of the tracemakers. Because fulfilling that requirement is essentially impossible, all post-1930 trace fossil names (= ichnotaxa) became formally unavailable, whereas the pre-1930 taxa retained their valid names but were treated on the same basis as body fossils. This is considered the beginning of the Dark Age of Ichnotaxonomy (Bromley, 1996). Thanks to the long-lasting and determined activities of ichnologists and exhaustive scientific debate, ichnofossils have finally been bounded by the ICZN in 1985. The 4th edition of the ICZN (1999) includes in the "work of animals" all trace fossils. This means that animal, protistan, plant, and fungal trace fossils are considered in exactly the same way as zoological taxa in terms of the availability and validity of their names. However, they are called "ichnotaxa" ("ichnogenera" and "ichnospecies") to distinguish them clearly from true biotaxa. The significant departures with respect to body fossils (see also the previous section) further complicate trace fossil taxonomy. For example, according to the ICZN, only fossil specimens should be named, which prevents ichnologists erecting ichnotaxa based on recent biogenic structures that might be assigned very often to their producers on a case-by-case basis. Under these circumstances, some authors prefer to name the tracemaker associated with the recent structure, whereas others opt to use the prefix "incipient" before the ichnotaxon (e.g., incipient *Thalassinoides*) (Bromley & Fursich, 1980).

A separate code for naming trace fossils, as proposed by Sarjeant and Kennedy (1973), might be a possible alternative to circumvent the aforementioned difficulties but this proposal has never gained legal standing.

Classification of trace fossils

Although the recent ICZN explicitly encompasses ichnofamilies, there is no true ichnotaxonomic superstructure above the rank of ichnogenus, and trace fossils can be grouped together in several ways. Traditionally, the most important classifications include preservational, phylogenetic, and behavioral schemes, although virtually all classifications are to some extent genetic because they presuppose that the structures were produced biogenically.

The preservational aspect takes into account two main facets: 1) the physiochemical processes of preservation and alteration; and 2) the toponomy (or stratinomy). The former facet falls within the realm of diagenesis, which is of paramount importance in trace fossil preservation; nevertheless, no classification based on diagenetic features is yet available. The latter focuses on the description and classification of biogenic structures in terms of their mode of preservation and occurrence.

Toponomic schemes have been devised by various authors (Simpson, 1957; Seilacher, 1964; Martinsson, 1970, among others) and most of these attempt to relate the position of a trace fossil to the main casting medium. The schemes of Martinsson (1970) and Seilacher (1964) have a lot in common and have gained the greatest acceptance.

Phylogenetic classification attempts to establish a correspondence between a trace fossil and the potential producer, a fascinating target but very difficult to reach. This is because ichnofossils usually reflect an animal behavior, and reflect their anatomy or morphology to a much smaller extent. As stated in a previous section, a single taxon may construct different biogenic structures and conversely, identical (or very similar) structures may be made by different taxa. It is sometimes possible to match tracemaker and trace fossil, but we must approach this problem with caution, bearing in mind that generalizations should be avoided and each occurrence of a given ichnofossil must be treated on an individual basis.

Above all, trace fossils are good indicators of the behavior of animals, and it is therefore unsurprising that ethological classification has been extremely successful. The original scheme proposed by Seilacher (1953), based on five categories, has been progressively modified and enlarged by various authors, among them Frey (1973), Ekdale *et al*. (1984), Ekdale (1985), and Bromley (1996). Frey and Pemberton (1985) suggested that categories be restricted in number and that new proposals are only justified if they are well founded on new behaviors. Today, a dozen categories are generally accepted (Fig. 1), although it must be emphasized that the overlap among groupings is unavoidable, reflecting the intergradation inherent in Nature.

Ichnofacies model

According to the concept proposed by Seilacher (1964, 1967), ichnofacies are trace fossil assemblages that recur through long intervals of time and are typical of a given set of environmental conditions (Frey & Pemberton, 1985). Ichnofacies are named after a characteristic ichnogenus, and may be recognized even if the namesake form is absent. The classic marine ichnofacies, those named for *Nereites*, *Zoophycos*, *Cruziana*, and *Skolithos* by Seilacher (1967), were originally based on the fact that many of the parameters controlling the distributions of the tracemakers tend to change progressively with increasing depth. Because these bathymetrical relationships are potentially very valuable for paleoenvironmental reconstruction, the ichnofacies sequence has long been regarded as a relative paleobathymeter. Today, it is well known that ichnofacies are essential for the reconstruction of depositional settings, but paleobathymetry constitutes only one aspect because the distribution of tracemakers is controlled by a number of interrelated ecological/sedimentological parameters, including the sedimentation rate, substrate grain size, salinity, oxygen level, turbidity, light, temperature, and water energy (Pemberton *et al*., 1992). Because these parameters may occur at specific water depths or not, it should not be surprising to find nearshore assemblages in offshore sediments, and *vice versa*. For example, the *Skolithos* ichnofacies, which is typical of nearshore settings, may occur in offshore tempestites or deep-marine turbidites, and the *Cruziana* ichnofacies, which is typical of lower shoreface to offshore deposits, may also be present in shallower settings, such as intertidal flats on tide-influenced shorelines (Miller III, 2007).

In recent decades, ichnologists have proposed many new ichnofacies from continental and marine environments, some of which are considered well founded, some are retained as mutually equivalent, and still others are considered invalid categories (see Buatois & Mangano, 2011, for a detailed discussion). In a recent paper, Knaust and Bromley (2012) recognized 14 formally defined ichnofacies among those that conform to Seilacher's paradigm. Five of them encompass the marine to marginal-marine softground substrates: *Psilonichnus*, *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites*. Three are regarded as substrate-controlled (omission) ichnofacies and are very useful for delineating surfaces, with sequence-stratigraphic implications: *Glossifungites*, *Trypanites*, and *Teredolites*. Six ichnofacies encompass the continental realm: *Scoyenia*, *Mermia*, *Coprinisphaera*, *Termitichnus*, *Celliforma*, and *Octopodichnus–Entradichnus*.

Ichnology and estuarine systems

The term "estuary" has been applied in a number of ways that are appropriate to their contexts, but most ichnologists agree with the definition of Dalrymple *et al*. (1992). According to these authors, an estuary is "the seaward portion of a drowned valley system which receives sediments 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 the tidal facies at its head to the seaward limit of the coastal facies at its head." All these environments are characterized by rapid perturbations and typically by salinity changes, but also other ecological controls may generate stressful conditions that strongly affect the benthic biota. Ichnology has provided a powerful tool with which to identify these depositional settings by recognizing anomalous ichnofaunas (typical of marginal-marine brackish conditions), which display less variety and a lower abundance of forms than are found in fully marine environments (Buatois & Mangano, 2011). Dalrymple *et al*. (1992) classified estuaries into two main groups: wave-dominated and tide-dominated estuaries. In the former, there is a well-structured spatial distribution of energy and three main zones are recognized: 1) the bay-head delta, a high-energy inner zone dominated by river processes; 2) the central basin, characterized by the mixing of marine energy and fluvial currents; 3) the estuary mouth, dominated by marine processes.

Bay-head deltas are strongly stressful environments with unbioturbated or sparsely bioturbated deposits showing very low ichnodiversity, which is dominated by the dwelling structures of suspension feeders. In terms of ichnofacies, this zone mainly contains the *Skolithos* ichnofacies, followed by an impoverished *Cruziana* ichnofacis. Central basin settings show a combination of stress agents (brackish water, water turbidity, and oxygen depletion) associated with a low degree of bioturbation, although bioturbation may be moderate in some beds. The ichnofauna reflects the dominance of unspecialized deposit feeders and is characterized by the depauperate *Cruziana* ichnofacies, with minor contributions from the *Skolithos* ichnofacies. Although the estuary-mouth complex is highly variable, in terms of both trace concentrations and depositional settings, the bioturbation intensity and ichnodiversity generally range from moderate to intense (higher than in the previous zones), reflecting near-normal marine salinities; mixed depauperate *Cruziana* and *Skolithos* ichnofacies are present. In summary, trace fossil distributions along wave-dominated estuaries are mainly controlled by the salinity gradient, varying from the brackish waters of the inner zone to the near-open-marine salinity of the outer estuary.

Tide-dominated estuaries are characterized by a less pronounced distribution of energy along the estuarine valley because of the migration of intertidal run-off channels. Nevertheless, the following zones are recognized: 1) the upper estuary, a fluvio-estuarine transition zone characterized by freshwater conditions; 2) the middle estuary, meandering to straight tidal channels, tidal flats, and salt marshes; 3) the lower estuary, comprising the outer zone with elongate subtidal sandbars, channels, and tidal flats (Fig. 2).

Arthropods are the dominant tracemakers in the typical freshwater/terrestrial biotas of upper estuaries and their activities are recorded in tidal rhythmites, which display a mixture of the elements of continental depauperate *Scoyenia* and *Mermia* ichnofacies. Further towards the sea, the middle estuary commonly shows brackish-water conditions, to different degrees in a number of settings: tidal flat deposits are dissected by a network of meandering tidal channels and creeks that migrate across the intertidal zone, producing lateral accretions in point bars (Dalrymple, 1992); the substrate-controlled *Glossifungites* ichnofacies may occur, corresponding to coplanar surfaces (incision during a sea-level fall and subsequent transgressive erosion), whereas mixed impoverished *Cruziana* and *Skolithos* ichnofacies record the activities of opportunistic communities that developed under stressed conditions (brackish waters) in transgressive sediments overlying coplanar surfaces. The outer zone of the estuary displays fully or almost fully marine conditions, and the possible trace assemblages reflect the activities of organisms that include deposit feeders, predators, and suspension feeders in intertidal to subtidal settings. However, high energy and rapidly migrating bedforms generally tend to preclude the establishment of a mobile epifaunal and/or shallow infaunal biota (Buatois and Mangano, 2003).

Summary

Trace fossils can be retained as both paleontological and sedimentological entities because they represent not only the morphology and ethology of the tracemakers, but also the physical characteristics of the substrate on which the tracemakers lived. In this sense, biogenic sedimentary structures can make meaningful contributions to numerous research fields in the earth sciences, with an integrated approach that articulates ichnological information with other sources of data. A good example of this way of proceeding is the reconstruction of ancient depositional settings, which notably takes advantage of the integration of both sedimentological/stratigraphic and ichnological data. In marginal marine environments (including estuaries), trace fossil assemblages play a major role in the distinction of open-marine, brackish-water, and freshwater/terrestrial deposits.

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Cross-references
Estuarine Geomorphology
Estuarine Sedimentary Facies
Intertidal Zone
River-dominated Estuaries
Sandflats
Tidal Environments
Wave and Tide-Dominated Estuaries

Captions of figures
Fig. 1 – List of acceptable ethological classes according to De Gibert et al. (2004) (modified).
Fig. 2 – Reconstruction of a tide-dominated estuary from Santa Rosita Formation (cambriano, Argentina) (from Buatois and Mangano, 2003, modified).

ETHOLOGIC CLASS	AUTHOR/S	BEHAVIOR	INVALID CLASSES INCLUDED
REPICHNIA	Seilacher 1953	direct locomotion	natichnia, cursichnia, volichnia (Muller 1962)
PASCICNIA	Seilacher 1953	locomotion + feeding	
FODINICHNIA	Seilacher 1953	dwelling + feeling	
DOMICHNIA	Seilacher 1953	dwelling	
CUBICHNIA	Seilacher 1953	temporary immobility	
FUGICHNIA	Seilacher 1953	sudden escape	taphichnia, (Pemberton et al. 1992)
AGRICHNIA	Simpson 1975	dwelling + trapping/gardening	'chemichnia' (Bromley 1996)
PRAEDICHNIA	Ekdale et al. 1984	predation	Mordichnia (Muller 1962)
AEDIFICICHNIA	Bown & Rattcliffe 1988	construction above substrate	
EQUILIBRICHNIA	Bromley 1990	gradual adjustment	
CALICHNIA	Genise & Bown 1994	breeding	
FIXICHNIA	De Gibert et al. 2004	anchoring	