

Trace fossil preservation and the early evolution of animals

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Abstract

The trace fossil record is an important element in discussions of the timing of appearance of bilaterian animals. A conservative approach does not extend this record beyond about 560–555 Ma. Crucial to the utility of trace fossils in detecting early benthic activity is the preservational potential of traces made close to the sediment–water interface. Our studies on the earliest Cambrian sediments suggest that shallow tiers were preserved to a greater extent than typical for most of the Phanerozoic. This can be attributed both directly and indirectly to the low levels of sediment mixing. The low levels of sediment mixing meant that thin event beds were preserved. The shallow depth of sediment mixing also meant that muddy sediments were firm close to the sediment–water interface, increasing the likelihood of recording shallow tier trace fossils in muddy sediments.

Preservation of surficial trace fossils in this type of setting remains problematic but the above factors suggest that also these can be expected to have left a reasonable record. Overall, the trace fossil record can be expected to provide a sound record of the onset of bilaterian benthic activity. The lack of convincing trace fossils significantly before the Cambrian supports models of late appearance of macroscopic benthic bilaterians.

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1. Introduction

The appearance and subsequent diversification of bilaterian animals are topics of current controversy (e.g., Wray et al., 1996; Fortey et al., 1996, 1997;

Knoll and Carroll, 1999; Budd and Jensen, 2000, in press; Conway Morris, 1998, 2000; Collins and Valentine, 2001; Erwin and Davidson, 2002). There are three principal sources of evidence: body fossils, trace fossils (trails, tracks, and burrows of animal activity recorded in the sedimentary record), and molecular data in the form of divergence times calculated by means of the molecular “clock” theory. A literal reading of the body fossil record suggests that the diversification of bilaterian animals did not

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significantly precede the Neoproterozoic–Cambrian boundary (ca. 545 Ma). This is in line with a conservative evaluation of the trace fossil record; the oldest certain traces likely to have been made by bilaterians have been dated at 555.3 Ma (Martin et al., 2000). Even taking into consideration uncertainties in the precise correlation of trace fossil-bearing Neoproterozoic strata, this date is likely close to the age of the oldest trace fossils. On the other hand, there are reports of bilaterian trace fossils (Seilacher et al., 1998), as well as molecular clock data (Wray et al., 1996), which suggest that diversification of bilaterian groups may have commenced more than 1000 Ma. There is, however, a considerable spread in the results from molecular clock studies, with some coming close (Ayala et al., 1998), or even very close (Peterson and Takacs, 2002), to the pattern seen from body fossils. Furthermore, the reports of deep Proterozoic trace fossils are doubtful, as briefly discussed below. The trace fossil record is of particular interest in that it should, compared to the body fossil record, be less prone to taphonomic biases towards animals with mineralized hard parts. Several authors have made a case for bilaterians being primitively benthic, arguing that many of the morphological features of bilaterians could only have evolved in a moderately large animal with a benthic lifestyle (e.g., Valentine, 1994; Budd and Jensen, 2000; Collins and Valentine, 2001). This is by no means universally received: others favor an extended history of small meiofaunal or planktic larva-like bilaterians (e.g., Davidson et al., 1995; Fortey et al., 1996, 1997). Nevertheless, if a benthic cradle is accepted, trace fossils should give a useful estimate to the timing of appearance of moderately large mobile bilaterian animals.

Trace fossils, however, do come with their own set of problems. Distinguishing simple trace fossils from sedimentary structures of inorganic origin is far from trivial. Furthermore, trace fossils have their own set of taphonomic limitations. With respect to early bilaterian trace fossils, it is particularly important to recall that in most modern marine settings, traces made on or near the sediment surface have a low preservational potential (e.g., Seilacher, 1978).

The purpose of this paper, therefore, is to discuss trace fossil preservation, with particular reference to the preservational potential of surface and near-surface trace fossils in the Proterozoic and earliest Cambrian.

2. Trace fossil preservation—introductory considerations

It is widely thought that surface traces have a low preservational potential in marine settings (e.g., Seilacher, 1978; Hallam, 1975). One contributing factor is that surface sediment is generally rather soupy and therefore prone to reworking by weak currents. In most shallow marine settings, the upper portion of the sediment is extensively mixed, resulting in a diffuse mottled texture and rapid destruction of shallow discrete trace fossils. Preservation of discrete trace fossils generally requires that the trace represents a deep tier, sometimes referred to as elite trace fossils (cf. Bromley, 1996). However, there are situations where relatively shallow-tiered burrows—not necessarily surface traces—are preserved. A particularly important type of trace fossil preservation occurs along an interface, such as a sand sharply overlying mud (Fig. 1A and B) (e.g., Seilacher, 1978). This type of sediment interface generally results from event bedding, such as tempestites. These events generate sharp boundaries of contrasting lithologies that are ideally suited to preserving trace fossils. In addition, some of the loose muddy surface sediments are brought into suspension, which further contributes to a sharp interface and a relatively firm muddy surface. Animals that burrow into the sediment to the mud–sand interface may leave trace fossils that are preserved on the base of the sandstone (Fig. 1A). Much of the descriptive terminology for trace fossil preservation and stratigraphy reflects this relationship (e.g., Seilacher, 1964; Martinsson, 1965); burrows are described with respect to their relationship to a particular sand bed. Providing that the sand layer is thin, this can preserve shallow infaunal traces (Fig. 1B). Open burrows made within the mud may also be exhumed by currents and filled by sand (Fig. 1C). This is particularly characteristic of turbidite settings, but also can occur in storm-influenced settings. In this situation, the upper part of the burrow commonly is eroded, and there often is a tell-tale sign of the trace having been washed out (e.g., Seilacher, 1982). Indeed, trace fossils have been used to measure stratigraphic completeness (Wetzel and Aigner, 1986).

Much of the pattern of trace fossil changes across the Proterozoic–Cambrian boundary is based on discrete trace fossils that were preserved according

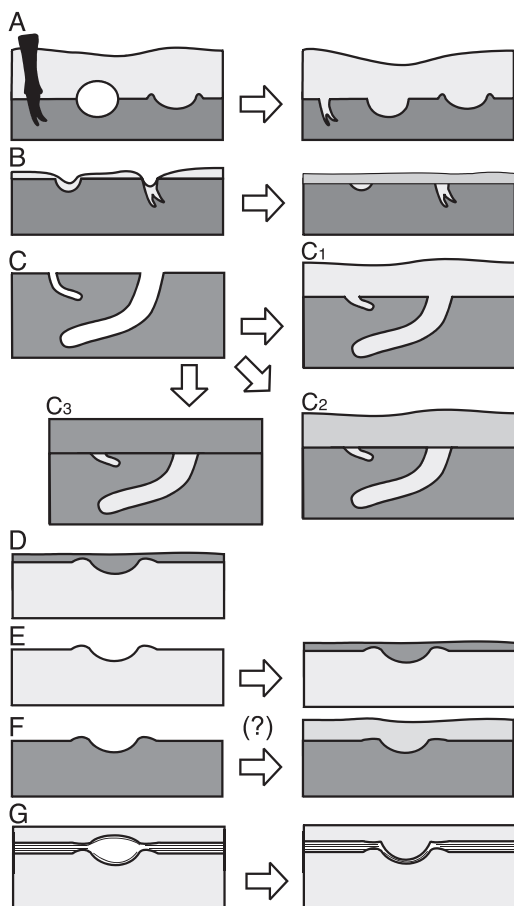


Fig. 1. Selected scenarios for trace fossil preservation with particular emphasis on preservation of shallow tiers in a sub-tidal marine setting. (A) Preservation along a sand–mud interface resulting in instantaneous casting of sand into mud, or collapse of sand into depression in the mud. (B) A thin sand layer may become removed by winnowing leaving sand only where trapped in burrows. These casts may subsequently become attached to the base of new layer of sand. (C) Open burrows constructed in firm mud may be preserved by casting of sand, to which it remains attached (C1). Winnowing and subsequent deposition lead to attached burrows (C2) as in (B). In a setting with sediment bypass, burrows may serve as traps. Depending on subsequent sedimentation, these casts may “float” in muddy sediment (C3) or become attached (C2) (see Droser et al., 2002a for a more exhaustive discourse of this topic). (D) Preservation potential of surface burrows in sand is enhanced if there is a thin blanket of mud at time of burrowing. (E) Preservation potential of surface burrows in sand may also be enhanced blanketing layer of mud introduced shortly after trace formation. (F) The preservation potential of surface burrows in mud is a matter of contention (see text). (G) Preservation of a trace formed by an animal that burrowed along a buried microbial mat. Sand is eventually displaced into the open tunnel.

to the principles outlined above. The preservation of true surface traces remains problematic, as will be discussed below.

3. The record of Neoproterozoic and Cambrian trace fossils

3.1. Characteristics of Lower Cambrian trace fossils in muddy sediments

The greatest diversity of Cambrian trace fossils has been documented from shelf settings that have a heterolithic bedding characterized by moderately thin, generally centimeter-scale, often sharp-based sand and siltstone beds, separated by layers dominated by mudrock. We have previously demonstrated that firmground conditions relatively close to the sediment–water interface were widespread in these types of settings in the Early Cambrian (Droser et al., 2002a,b). This was based on the examination of over 10 Cambrian units on four continents.

Of the units that we examined, the Lower Cambrian formations exhibited a number of shared ichnological and sedimentological characteristics. These characteristics include the following:

1. Preservation of shallow tiers and scarcity of deep tiers: Earliest Cambrian sediments preserve a range of trace fossils that represent shallow tiers. The geometry and style of preservation of these trace fossils suggest that they formed less than a few centimeters below the sediment–water surface (Droser et al., 2002a,b). These trace fossils include *Treptichnus pedum* and other treptichnids, as well as *Gyrolithes*, all of which are common in Lower Cambrian shallow marine terrigenous rocks.
2. Quality of preservation: Even though treptichnids were constructed close to the sediment–water interface, they have sharp walls, and in certain cases, they preserve delicate surface ornamentation. There is no sign of actively reinforced burrow margins. The extent of compaction of the burrows is also relatively minor. Several other trace fossils of shallow emplacement show sharp preservation of detail. This includes the vertical spiral burrow *Gyrolithes* and shallow *Rusophycus*.

This quality of preservation is ubiquitous in the Lower Cambrian units examined.

3. Styles of preservation: In most shallow marine settings, burrows preserved on the base of sandstone beds are created by animals that burrow through the sand to the interface with the underlying finer-grained sediment (e.g., [Seilacher, 1970](#)). In Lower Cambrian strata, particularly, but also commonly in Middle and Upper Cambrian strata, a fundamentally different style of preservation appears to be particularly common. Cambrian sand-filled burrows are generally preserved in one of two manners. The burrow may be cast by a source bed to which it remains attached, or the burrow may be cast by a sand source which bypasses that environment and thus the cast is attached to the base of a different bed, or may even be preserved as a sand-filled burrow completely surrounded by muddy sediment ([Fig. 1C](#)) ([Droser et al., 2002a](#)). This is a common style of preservation of treptichnids, *Gyrolithes*-type burrows, and *Palaeophycus/Planolites*-type burrows, and was found to be the most common style of preservation in all of the Lower Cambrian units examined. This type of preservation requires that the burrows be open and, given the preservation of shallow tier trace fossils in this manner, that the muddy sediment be rather resistant to erosion.
4. Sedimentary structures: These units contain sedimentary structures that must have been formed close to the sediment–water interface. This includes *Kullingia*-type scratch circles, which form when a tethered organism is rotated by currents to imprint delicate concentric grooves ([Jensen et al., 2002](#)). These structures formed in mud or fine sands, and were cast by a coarser material.
5. Lack of homogenized sediment: Some animals that burrow do not leave well-defined, discrete trace fossils. Instead, the record produced is one of some degree of homogenization. That is, primary sedimentary structures are not preserved and the final texture is one of a mottled appearance (e.g., [Bromley, 1996](#)). This is direct evidence of a mixed layer. In sedimentary rocks of the earliest Cambrian, there is virtually no evidence of such homogenization, with rare isolated examples less

than 1 cm in thickness of homogenized sediment ([Droser et al., 2002a,b](#)).

3.2. Why are muddy substrates firm in the Cambrian?

The characteristics described above suggest that sediment just beneath the sediment–water interface is firm enough to maintain delicate features formed close to the sediment–water interface and to withstand the erosion of currents in subtidal shallow marine settings.

The most likely explanation for firm muddy sediments close to the sediment–water interface is the limited extent of sediment mixing. Animal infaunal activity is known to have dramatic effects on sediment surface topology, as well as on biogeochemical processes in the sediment (e.g., [Ziebis et al., 1998](#)). Bioturbation clearly also has an effect on the physical properties of sediments, but these effects are rather complex, and differ as a consequence of sediment type and type of infaunal activity (e.g., [Lee and Swartz, 1980](#); [Meadows and Tait, 1989](#)). It appears, however, that in muddy sediments, the effect of bioturbation is to reduce surface–sediment shear strength, primarily by causing an increased water content and irregular surface topology, which makes these sediments increasingly prone to resuspension by weak currents (see [Droser et al., 2002b](#) for discussion).

3.3. Microbial mats and Neoproterozoic trace fossils

The Neoproterozoic trace fossil record is dominated by essentially horizontal unbranched traces (e.g., [Gehling, 1999](#); [Seilacher, 1999](#); [Jensen, in press](#)). It has been suggested that the orientation of these trace fossils was controlled by exploitation of microbial mats buried by a thin veneer of sand ([Seilacher and Pflüger, 1994](#); [Seilacher, 1999](#); [Gehling, 1999](#)). Indeed, the trace fossils are often preserved along the interface of two sandstone beds with no evidence of a muddy parting; here the interface was sand/microbial mat rather than sand/mud ([Fig. 1G](#)). There is convincing (and growing) indirect evidence for these Proterozoic microbial mats, which were spread to a greater extent than commonly seen in normal marine settings ([Gehling, 1999](#)). The microbial mats would have lowered sand erodability (e.g., [Paterson, 1994](#)), and also created taphonomic

conditions favorable to the preservation of the non-mineralized Ediacaran biota (Gehling, 1999). These microbial mats may have been an important influence on early bilaterians (Seilacher, 1999; Bottjer et al., 2000); adaptations to matground conditions may be seen also in some Cambrian trace fossils (Hagadorn and Bottjer, 1999).

4. Preservation of surface (superficial) traces

Based on the criteria discussed above, there is good evidence that Neoproterozoic–Cambrian burrows formed within the sediment—even at very shallow depths—would have had a reasonable chance of entering the stratigraphic record.

The preservational potential of true surface traces in a marine setting is, however, more problematic. It should be noted that there is no absolute definition for what constitutes a surface trace. There is a gradation from surface movement in which no sediment is displaced to that in which the animal is partly submerged but remains in more or less continuous contact with the sediment–water interface. This depends not only on the animal's activity, but also the nature of the sediment, especially water content, grain size, and within-bed heterogeneity, all of which are of great importance for the quality of preservation as well as the resulting trace morphology (e.g., Gräf, 1956; Knox and Miller, 1985). In subaerially exposed sediments, the depth of the trace increases with water

content (e.g., Gräf, 1956). The effect will be less pronounced in subaqueous settings but nevertheless be a factor.

The surface traces discussed here all involve various degrees of sediment displacement. A possible alternative mode of surface trace formation is of interest. Collins et al. (2000) studied experimentally produced mucociliary creeping trails of animals, such as ceriantharian anemones and flatworms, and compared these with certain Neoproterozoic trace fossils. The movement of these animals above a soft substrate resulted in sediment trapped in the mucus film. It would, however, appear that relatively little sediment was actually trapped by the mucus, and that most of the relief was provided by mucus. It is therefore questionable how resistant such a trace would be to sediment loading. Mucus containing little sediments also would be prone to disruption by gentle currents. Most of the Neoproterozoic ichnotaxa with which Collins et al. (2000) compared their experimental traces clearly owe their preservation and morphology to displacement/excavation of sediment to a much greater degree than can be envisaged for such mucus creeping trails. Further experiments on the preservation potential of mucus trails would be of great interest.

4.1. Surface traces in mud

The surfaces of muddy sediments are highly unlikely sources for finding the earliest bilaterian benthic epistratal activity (Fig. 1F). A muddy sub-

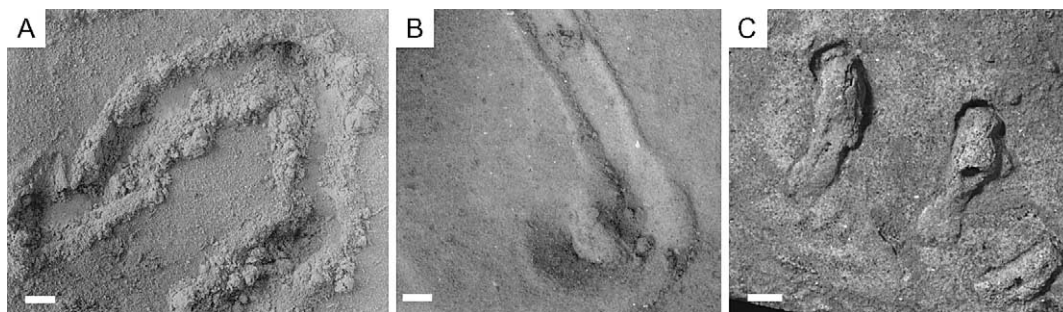


Fig. 2. Trace made by the gastropod *Hinia reticulata* in experiments using natural sediments in marine tanks. Scale bars are 10 mm. (A) Surface trace from crawling over a muddy surface resulting in poorly defined levees. (B) Surface traces made in sand. Surficial movement resulted in a smooth flat base and narrow distinct lateral levees. Near lower margin of picture, the animal has dug deeper into the sediment and was by this stage seen only from its “snorkel.” (C) Experimentally produced undertraces (following the protocol of Jensen and Atkinson, 2001, with a sand layer about 3 cm thick) resulting from the behavior seen in the deeper portion of the trace in (B). The flat surface corresponds to the base of a storm bed, with the gastropod traces forming pronounced raised ridges. Note that the pronounced depression surrounding the traces formed as mud moved up into the sand.

strate with high water content will have low potential of recording the traces as well as a low potential of preservation (Fig. 2A). A completely firm muddy substrate, on the other hand, will not record any such surficial movement in the first place. A possible exception is sediments that largely consist of silt, which will be discussed in Section 4.2.

4.2. Surface traces in sand and silt

Traces formed close to the sediment–water interface in mobile sand clearly have negligible preservational potential. Movement over sheets of sand and silt that had been deposited by storms offshore, could, however, provide a more favorable scenario because these are unlikely to be rapidly reworked by additional currents. A likely range of traces that may form in this setting was provided by experiments with the netted dog whelk *Hinia reticulata*. This animal exhibited a range of behaviors from “ice skating” on top of the sediment to burrowing slightly beneath the sediment with a “snorkel,” providing contact with the sediment–water interface (Fig. 2). In these experiments, movement on the surface resulted in lateral levees of displaced sand (Fig. 2B). By and large, this type of trace represents involuntary sediment displacement. Upon digging deeper in the sediment, a pronounced V-shaped furrow formed. At this stage, the animal impinged across a mud–sand interface and produced what would amount to interface trace fossils if preserved at the base of sandstone (Fig. 2C).

Surficial sand traces would be even more likely to be preserved if the sand was covered by a thin blanket

of muddy sediment at the time of trace formation (Fig. 1D), or became covered with muddy sediment shortly afterwards. In a sense, the mud serves to “protect” the trace (Fig. 1E). Neoproterozoic trace fossils that can be assigned to *Archaeonassa* appear to represent movement over sandy substrates, and may be analogous to the situation of the creeping gastropods (Fig. 3). While these traces show displacement of sediment to various depths, they clearly were made by a producer that kept in contact with sediment–water interface.

5. Trace fossil producers

As is the case for the majority of Phanerozoic trace fossils, it is difficult to assign producers to Neoproterozoic trace fossils. Stem group molluscs and priapulids are likely candidates for some of the early trace fossils (Valentine, 1994), but specific evidence is lacking. The flat central area in specimens of *Archaeonassa* certainly would be in agreement with a mollusc-type producer. Priapulids (sensu lato) may have been responsible for some of the earliest penetrative burrows. Unfortunately, little is known of the types of burrows constructed by Recent priapulids (Powilleit et al., 1994). Typical arthropod-type trace fossils are not known from the Neoproterozoic, and bilobed forms with characteristic scratch patterns (*Rusophycus*) first appear somewhat above the currently defined base of the Cambrian (e.g., Narbonne et al., 1987). When discussing arthropod-type trace fossils, it should be kept in mind



Fig. 3. Neoproterozoic trace fossils representing movement close to the sediment–water interface in fine sand. (A) *Archaeonassa* sp. from the UstPinega Formation, Winter Coast of the White Sea, north-west Russia (SM 27518). Scale bar is 10 mm. (B) Several morphologic varieties of *Archaeonassa* sp. in the Ediacara Member, Flinders Ranges, South Australia, reflecting depth of animal movement within the sediment (specimen in collection of J.G. Gehling, Adelaide). Scale bar is 10 mm.

that preservation of such features that would identify a trace as produced by an arthropod is under strong taphonomic control (Fig. 4). Furthermore, the earliest arthropods may not have had the equipment with which typical arthropod-type trace fossils are identified. For example, Budd (1996) derived arthropods from lobopodians with the development of lateral lobes, and segmentation, occurring prior to the development of sclerotized limbs.

Although most Neoproterozoic traces can be reasonably assumed to have been produced by bilaterian animals, it is worth considering alternatives. There are burrowing cnidarians, but these generally form simply vertical burrows. Simple vertical plugs such as *Bergaueria* generally are interpreted as formed by actinians or even by pennatulacean hold-fasts (Alpert, 1973; Seilacher-Drexler and Seilacher, 1999). More complex, short, branching, cnidarian-made burrows have been described (e.g., Bradley, 1981; Jensen, 1992), which could be confused with bilaterian traces. Collins et al. (2000) observed surface creeping in cerianthid cnidarians, which trapped sediment in a mucus string or lateral levees. As discussed above, the preservational potential of this type of mucus-bound surface trace is unclear.

Protists rarely figure in the discussion of producers of trace fossils. Numerous observations, however, suggest that foraminiferans are likely producers of trace fossils. Buchanan and Hedley (1960) showed that *Astrorhiza limicola* will create a trace identical to *Archaeonassa* by the leading edge of the test pushing a wave of sand that disperses to the sides as two ridges. Severin et al. (1982) observed that burrowing of the

benthic foraminiferan *Quinqueloculina impressa* produced vertical traces thought to represent escape, and a horizontal and vertical maze-like system. The ability to burrow apparently is present also in forms with a mostly planktic habit. Hilbrecht and Thierstein (1996) observed foraminifera burrow and produce pits by removing sediment with rhizopodia. Hilbrecht and Thierstein (1996) suggested that there was evidence for active lining of the burrow. These lined burrows would potentially preserve as small dimples.

The above discussion suggests that producers other than bilaterians must be considered for simple trace fossils, and perhaps also for short-branched forms. That some of the nonbilaterian trace makers discussed above represent groups that on phylogenetic grounds are unlikely to have been present in the Neoproterozoic is besides the point. Nevertheless, the relatively gradual increase in diversity and complexity of trace fossils at the Neoproterozoic–Cambrian boundary suggests that it reflects bilaterian radiation. The biology of a number of Ediacaran organisms has long been debated. The lack of evidence of mobility has been one important factor for nonmetazoan interpretations of the Ediacaran fossils. Recent finds of associations of Ediacarans with trace fossils appear to provide evidence of mobility and thus support for metazoan affinities. In the White Sea area of northern Russia, Ivantsov and Malakhovskaya (2002) found series of imprints of *Dickinsonia* preserved in positive relief on the base of a sandstone slab, terminated by a *Dickinsonia* preserved in negative relief, with the latter being the common mode of preservation for this organism. This suggests that the *Dickinsonia* had made repeated depressions in the microbial mat that remained open until filled by the smothering sand (Ivantsov and Malakhovskaya, 2002). Although these traces bear little resemblance to the traditional terminal Proterozoic trace fossils, this should rekindle interest in Ediacarans as trace makers (cf. Gehling, 1991; Seilacher, 1997).

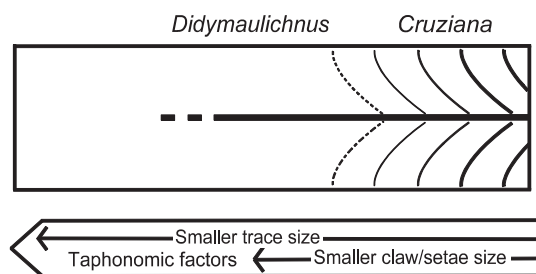


Fig. 4. Schematic drawing to illustrate preservational control on trace fossil morphology. The morphology of a trace produced by an animal with paired appendages will depend on the animals size as well as sediment properties. Loss of distinct scratches yields a smooth bilobed trace (e.g., *Didymaulichnus*). Further loss of preservational detail renders the trace essentially smooth.

6. How far back does the trace fossil record extend?

The low levels of bioturbation in the Cambrian, and even more so in the Proterozoic, mean that these were times in which the preservation of shallow tier

trace fossils in marine settings would have been particularly favorable. The most obvious consequence is the reduced destruction of thin event beds (e.g., Sepkoski, 1982). As discussed above, the low levels of sediment mixing would have led to a more rapid dewatering of muddy sediments with resulting firm sediments close to the sediment–water interface. The early development of infaunal activity should therefore be readily observable in burrows preserved by sediment filling open mud burrows, where an animal burrowed through a sand–mud interface, and probably also from surficial traces. The widespread microbial mats also would have been beneficial to the preservation of shallow tier trace fossils. In either case, the trace fossil record should be relatively sensitive to the onset of infaunal activity in storm-influenced settings.

There are several reasons why particular care should be taken in examining Proterozoic sedimentary structures of suspected biogenic origin. The Neoproterozoic contains a range of sedimentary structures of problematic origin. For many of these structures, such as *Arumberia*, opinions are divided about whether their origin is biogenic or physical, or a combination of the two. In our opinion, *Arumberia* is an obvious physical sedimentary structure, as outlined by McIlroy and Walter (1997). This conundrum probably can be explained by unusual preservational conditions. High cohesiveness of the sediment may explain preservation of these aberrant sedimentary structures; the physical processes causing these structures were not necessarily unusual but the preservational conditions were. Additionally, in the absence of bioturbation, the sedimentological record would be dominated by physical sedimentary structures. The common presence of microbial mats also would have led to unusual preservational conditions (e.g., Seilacher, 1997; Gehling, 1999). It therefore may not be an exaggeration to consider much of the Proterozoic as being a sedimentary structure preservation Lagerstätte. It follows that it is a dubious approach to favor a biogenic origin of a problematic structure merely because there is no obvious explanation for it as an inorganic sedimentary structure.

The distinction between a trace fossil and a pseudofossil is far from trivial (see discussion in Ekdale et al., 1984, pp. 29–36). Particularly in the Neoproterozoic, there is the additional problem of confounding trace fossils with metaphytes. It is

impossible to find definitive criteria that will give the true origin of a sedimentary structure but some of the features to look for include the following:

- Gradual tapering in dimensions, where this is not stratinomically controlled, argues against a trace fossil origin.
- Angular terminations may be expected from breakage of an organism with a modular growth, but not from a trace fossil.
- Displacement of sediment. Active displacement of sediment, such as levees and cross-cutting of other sedimentary structures, is a strong indicator of a trace fossil, although care must be taken with compactional deformation.
- Mensicate fill, if accompanied by fecal pellets or sorting yielding different properties to different parts of the trace, suggests a trace fossil origin.
- Carbonized remains strongly suggest a body fossil origin.

There have been numerous reports of pre-Neoproterozoic trace fossils, but upon critical evaluation, these traces turn out to be misidentified inorganic structures or metaphytes, or to have been misdated (e.g., Hofmann, 1992; Fedonkin and Runnegar, 1992). Nevertheless, there has been a steady flow of new reports, of which Table 1 presents a partial listing.

Table 1

A selection of recent reports of purported trace fossils 600 Ma and other with brief evaluations

<i>Neonereites uniserialis</i> , ca. 600 Ma, Scotland, Brasier and McIlroy (1998), dubiofossil (also Brasier and Shields, 2000)
<i>Lockeia</i> sp., ca. 600 Ma, Mexico, McMenamin (1996), undiagnostic, probably pseudofossil
<i>Palaeophycus tubularis</i> , ca. 600 Ma, Mexico, McMenamin (1996), undiagnostic, probably pseudofossil
<i>Cochlichnus anguineus</i> , Riphean, India, Kulkarni and Borkar (1996b), pseudofossil, shrinkage cracks (Chakrabarti, 2001)
<i>Vermiforma antiqua</i> gen. et sp. nov., 620 Ma, USA, Cloud et al. (1976), pseudofossil (Seilacher et al., 2000)
Metazoan burrows, ca. 1.6 Ga, India, Seilacher et al. (1998), dubiofossil, shrinkage cracks?
Grazing traces, Mesoprot., USA, Breyer et al. (1995), dubiofossil
<i>Changchengia dahongyuensis</i> igen. et isp. nov., Mesoprot., P.R. China, Gao et al. (1993), pseudofossil
<i>Dahongyuichnus dahongyuensis</i> igen. et isp. nov., Mesoprot., P.R. China, Gao et al. (1993), pseudofossil
Trace-like fossils, Mesoprot., western Australia, Rasmussen et al. (2002a,b), dubiofossil

Below we will briefly consider some of the reports of trace fossil older than 600 Ma.

Breyer et al. (1995) reported grazing traces more than 1 Ga old. However, the evidence for a continuous meander is unconvincing. Possibly this structure has an origin similar to that of the pseudofossil *Arumberia* (cf. Bekker, 1980; Fig. 2). Kulkarni and Borkar (1996a) reported the vertical trace fossil *Skolithos linearis* from Riphean beds, which appears similar to Phanerozoic examples. This needs further study. In addition to the possibility that these are water escape pipes, more information on age constraint on this report would be welcome.

Perhaps the most widely known recent report of ancient trace fossils is that of Seilacher et al. (1998) from India. Now known to be close to 1.6 Ga in age (Rasmussen et al., 2002a), these were described as trace fossils of triploblastic animals. The irregular crinkly development is unlike that of trace fossils and better explained by the release of tensile strength in a compacting sediment. Similarly, the presence of numerous pointed terminations is better explained by an origin as shrinkage cracks. It should also be noted these structures occur together with a range of other sedimentary structures (e.g., Sarkar et al., 1996).

Another noteworthy recent report is of more than 1.5 Ga hair pin-like ridges on the base of sandstone beds in Western Australia (Rasmussen et al., 2002b). A major concern with these purported traces is in reconciling the preservation on the base of sandstone beds with the proposed mode of preservation as casts of surface traces consisting of mucus and displaced sediment (Budd and Jensen, in press).

7. Conclusions

1. Cambrian (particularly earliest Cambrian) muddy sediments in shelfal settings were firm close to the sediment–water interface to a much higher degree than what is typical of the Phanerozoic. The most likely interpretation for this is the low level and intensity of bioturbation of surface sediments.
2. Firm sediments and low levels of disruptive bioturbation increased the likelihood of preservation of trace fossils made close to the sediment–

water interface as well as sedimentary structures. There also should have been an increased likelihood in the preservation of superficial trace fossils. Proterozoic sediments therefore should have been particularly sensitive in recording the onset of infaunal activity.

3. Despite reports to the contrary, there is no widely accepted trace fossil record from sediments older than about 560–555 Ma.
4. The above conclusions place serious constraints on the time of appearance of bilaterian animals. For example, assuming that key bilaterian features could only have been acquired in moderately large benthic animals, the absence of an ancient trace fossil record suggests that the Cambrian “explosions” are a reality in terms of the relatively rapid appearance and diversification of macroscopic bilaterians.

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