

Spiral-shaped graphoglyptids from an Early Permian intertidal flat

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ABSTRACT

Spiral-shaped foraging trace fossils, assigned to the graphoglyptid cf. *Spirorhaphe azteca*, are reported from an Early Permian intertidal flat in the Robledo Mountains of southern New Mexico, USA. Remarkably similar spiral-shaped structures are produced in modern intertidal flats by the paraonid polychaete *Paraonis fulgens*, and function as traps to capture mobile microorganisms migrating in the sediment in response to tides. We envisage a similar function for the Early Permian trace fossils. Previous studies have suggested that the lack of *P. fulgens*-type traces from ancient intertidal deposits indicates that such behavior only evolved geologically recently in such settings. However, this report demonstrates that such specialized foraging behavior was present in intertidal settings by at least the Early Permian. Graphoglyptids are typical of deep-marine settings, and characteristic of the *Nereites* ichnofacies. This represents their first undoubted occurrence in intertidal facies in the geological record. We postulate that the occurrence of graphoglyptids in deep-marine and intertidal settings is related to the predictability of resources. The scarcity of intertidal graphoglyptids in the geological record is most likely a preservational effect.

Keywords: behavior, ichnofacies, preservation, resource utilization, trace fossils.

INTRODUCTION

Trace fossils represent direct evidence of the activities of animals and have wide-ranging utility. Their geological application in fine-scale discrimination of depositional settings, through the identification of ichnofacies, is well documented (e.g., Seilacher, 1964, 1967; Buatois and Mángano, 1995; Genise et al., 2000; Pemberton et al., 2001); although, in terms of analyzing animal behavior and its evolution, they are an underutilized resource (e.g., Raup and Seilacher, 1969; Seilacher, 1977a, 1977b; Jensen, 2003). Trace fossils are generally preserved in situ, often in settings devoid of body fossils, so they can be used to extend the stratigraphic, geographic, and paleoenvironmental ranges of various animals, particularly those with low fossilization potentials.

The graphoglyptids are a group of geometrically complex trace fossils, including spirals (*Spirorhaphe*), continuous meanders (*Cosmorhaphe*), branched meanders (*Belorhaphe*), radiating forms (*Glockrichnus*), and irregular and regular nets (*Paleodictyon*). They are typical of deep-marine settings and characteristic of the *Nereites* ichnofacies (Seilacher, 1964, 1967). Their patterns, with systematic gaps and branching, are considered too complicated to represent simple deposit feeding and are incompatible with optimal grazing strategies (Seilacher, 1977a). Instead, they are interpreted as traps, by analogy with the burrows of the extant intertidal paraonid polychaete *Paraonis fulgens*, or as 'farming' traces (Röder, 1971; Seilacher, 1977a, 1977b). Here, for the first time, we report examples of spiral-shaped graphoglyptids from an ancient intertidal deposit of Early Permian age in New Mexico, USA.

SEDIMENTOLOGY AND PALEOENVIRONMENT

The Early Permian Robledo Mountains Formation of the Hueco Group crops out in Doña Ana County, southern New Mexico, and

comprises a complex intercalation of siliciclastic redbeds (tidal flat), limestones, and calcareous shales (shallow-marine shelf). The material described here was recovered from New Mexico Museum of Natural History and Science (NMMNH) locality 2851, the strata of which have been interpreted as the foresets of a small shelf delta (Lucas et al., 1995; Braddy, 1998; for an expanded description of the depositional setting see GSA Data Repository Appendix A¹). The majority of associated trace fossils belong to *Tonganoxichnus* and *Stiaria*, and represent the walking, jumping, and feeding activity of monuran insects (Mángano et al., 1997; Minter and Braddy, 2006). They are incredibly abundant on some surfaces, and probably formed during brief periods of activity on newly exposed surfaces between high tides. Tetrapod trackways are relatively rare in comparison to other trace fossil localities within the Robledo Mountains and probably reflect the proximity of locality 2851 to the paleoshoreline.

DESCRIPTION OF THE TRACE FOSSILS

Two specimens (NMMNH P-45651 and NMMNH P-45652) were found exposed on the upper surfaces of bedding planes of purple to red-gray laminated siltstones to fine-grained sandstones. The best-preserved example (NMMNH P-45651; Fig. 1A) is a perfect one-way spiral, consisting of an epichnial groove 0.15–0.3 mm wide that expands outward, with a constant separation of 0.45–0.6 mm from neighboring grooves. At least seven complete whorls can be observed. It extends farther to one side, which may be due to incomplete preservation or being slightly inclined relative to the parting plane, giving a maximum of 19 whorls. Alternatively, it could represent a change from a spiraling to a meandering course. The second specimen (NMMNH P-45652; Fig. 1B) preserves three partial examples clustered together, but there are no complete whorls.

¹GSA Data Repository item 2006230, Appendix A and Appendix B, expanded descriptions of depositional setting and ichnotaxonomic assignments, is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

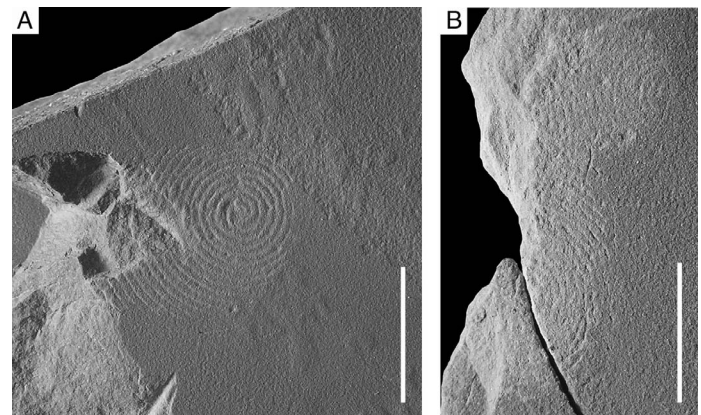


Figure 1. cf. *Spirorhaphe azteca*. A: NMMNH P-45651. B: NMMNH P-45652. Both are preserved in negative epirelief. Scale bars are 10 mm.



Figure 2. Modern spiral-shaped burrows of the paraonid polychaete *Paraonis fulgens* (Willapa Bay, northwestern United States).

The trace fossil credentials of these structures are unquestionable given their regularity and spiral form. Some tool structures such as scratch circles consist of a series of concentric circles (Jensen et al., 2002). Concentric circles and spiral structures can also form in microbial mat grounds due to shrinkage of cohesive material in the troughs of interference ripples, and are common in Precambrian and lower Paleozoic rocks (Pflüger, 1999). These structures have often been confused with trace fossils (manchuriophycus), and spiral shrinkage cracks have recently been referred to a new ichnospecies, *Spirodesmos milanai* (Aceñolaza, 2005). Shrinkage cracks are invariably more irregular than the structures described here.

Several spiral-shaped ichnotaxa are known, including *Spirorhaphe*, *Spirodesmos*, *Spirophycus*, and *Macaronichnus spiralis*. The material described here is most similar to the graphoglyptid *Spirorhaphe azteca*, although whorl width and spacing are more regular, so we refer it to cf. *S. azteca* (for an expanded discussion on the ichnotaxonomic assignment see GSA Data Repository Appendix B; see footnote 1). *Spirorhaphe* and other graphoglyptids represent open burrow systems formed within the substrate, and are commonly preserved in positive relief on the soles of turbidites due to partial exposure by turbidity currents and subsequent casting (Seilacher, 1977a). In contrast, the material from the Robledo Mountains is preserved in negative epirelief, so it is difficult to ascertain whether they were open or backfilled. Examples of modern open spiral burrow systems from deep-marine (Ekdale, 1980) and intertidal areas (Röder, 1971; Risk and Tunnicliffe, 1978) also occur as grooves on the tops of sediment, but their preservation potential after compaction is very low. A faint color difference between the inside of the grooves and the host sediment in the Robledo Mountains material suggests that the burrows were originally mucus lined, and therefore open rather than backfilled. A mucus lining would also increase the chances of survival of an open burrow.

INTERPRETATION

A variety of modern animals is known to produce spiral traces, including polychaetes (Röder, 1971; Clifton and Thompson, 1978; Risk and Tunnicliffe, 1978; Pemberton et al., 2001) and hemichordates (Bourne and Heezen, 1965; Smith et al., 2005). Photographs of the deep-sea floor have documented hemichordates producing spiral and meandering fecal trails, which are relatively large (Bourne and Heezen, 1965; Smith et al., 2005), and are similar to ichnotaxa such as *Spirodesmos* and *Nereites irregularis* (= *Helminthoida labyrinthica*). The ophelid polychaetes *Euzonus mucronata* and *Ophelia limacina* produce spiral traces in modern high-energy upper shoreface and foreshore settings (Clifton and Thompson, 1978; Pemberton et al., 2001). These

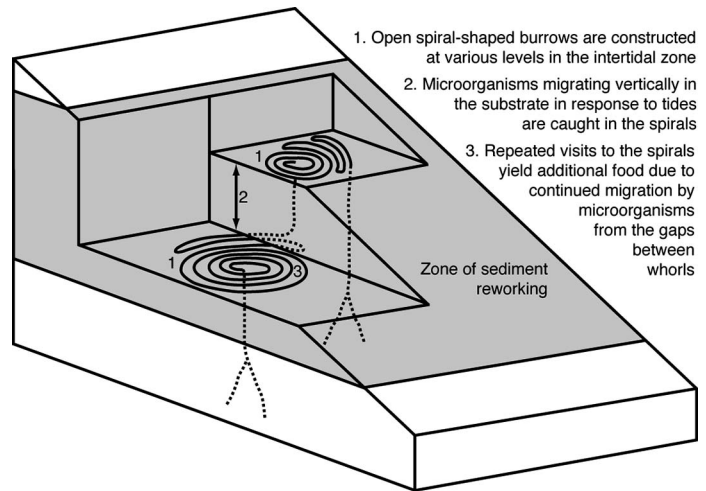


Figure 3. Functional model of burrows of *Paraonis fulgens*, and spiral-shaped graphoglyptids from Robledo Mountains Formation (adapted from Röder, 1971).

traces are actively backfilled and represent deposit feeding whereby sand is ingested to exploit epigranular organic detritus and bacteria. They are quite different from the material described here, but have been proposed as a model to interpret *Macaronichnus* (Clifton and Thompson, 1978; Pemberton et al., 2001).

The paraonid polychaete *Paraonis fulgens* inhabits modern intertidal flats and produces spiral burrows within the sediment (Fig. 2). The whorls of these burrows range from 0.2 to 0.75 mm wide and are separated by 1.5–5 mm (Röder, 1971; Risk and Tunnicliffe, 1978), which is remarkably similar to the material from the Robledo Mountains (Fig. 1). A detailed study by Röder (1971), summarized by Bromley (1990, p. 90–93), revealed that *P. fulgens* produces an open, mucus-lined burrow system with horizontal spirals in the upper oxic zone of the sediment, connected by vertical and oblique shafts that extend down into the lower anoxic zone. Röder (1971) suggested that *P. fulgens* fed selectively upon diatoms on the basis of its gut contents, and by virtue of being too small to be a deposit feeder. He interpreted the spiral burrows as traps to capture mobile microorganisms such as diatoms as they migrate vertically within the sediment in response to tides (Fig. 3).

There are, however, contradictory views regarding the feeding ecology of *P. fulgens* and other paraonids. Gaston et al. (1992) found that the gut contents of *P. fulgens* and *P. pygoenigmatica* contained a large proportion of detritus; *P. fulgens* had ingested more diatoms, but this was suggested to be a function of habitat differences rather than selective feeding. However, Levin et al. (1999), using ^{13}C -labeled diatoms, concluded that paraonids on the continental slope fed selectively upon diatoms. The size of an animal affects its feeding ecology; deposit feeding involves ingesting relatively large amounts of low-quality material, so it must be processed at high rates, and places constraints on their minimum size (Jumars et al., 1990; Penry and Jumars, 1990). Röder (1971) reported that *P. fulgens* can reach lengths of 22–30 mm and 0.4 mm in diameter, equating to body volumes of 2.76–3.77 mm³, at the lower end of values for intertidal and shallow subtidal deposit-feeding polychaetes (Penry and Jumars, 1990). Smaller individuals of *P. fulgens* may therefore feed selectively, whereas larger individuals can be deposit feeders. This is borne out by studies documenting that smaller species of deposit feeders tend to be more selective (Self and Jumars, 1988), and that there are ontogenetic changes in feeding strategies of polychaetes with deposit-feeding adults (Hentschel, 1998).

The spiral parts of the burrow system of *P. fulgens* are relatively short-lived because they occur within the zone of sediment reworking,

although *P. fulgens* passes through them several times (Röder, 1971). Such behavior, coupled with the consistent areas of unexploited sediment between whorls, is difficult to reconcile with a deposit feeder, and must have some selective advantage. Röder's (1971) trap model provides an explanation whereby the gaps between the whorls function as an area from which new diatoms can move into the trap and repeated visits yield additional food (Fig. 3). Röder (1971) and Seilacher (1977a, 1977b) proposed that the burrows of *P. fulgens* can be used as a model to interpret the function of graphoglyptids, and can be distinguished from *Nereites irregularis*-type trace fossils, which can be more readily explained as deposit-feeding traces. The narrow whorls of the material described here indicate a small producer that was unlikely to be a deposit feeder, and the depositional setting is consistent with the habitat of *P. fulgens*. We therefore envisage a similar function for these trace fossils (Fig. 3).

IMPLICATIONS

Graphoglyptids are characteristic of the *Nereites* ichnofacies (Seilacher, 1964, 1967) and previous models suggest that they, along with other typical deep-marine trace fossils, originated in shallow-marine settings in the late Precambrian and Early Cambrian, and subsequently 'retreated' to deep-marine settings around the Cambrian-Ordovician boundary (e.g., Crimes and Fedonkin, 1994). Reports of spiral-shaped graphoglyptids are almost invariably from deep-marine turbidite facies, ranging from the Ordovician to Tertiary of Europe and the Americas (see Uchman, 2004), although Gierlowski-Kordesch and Ernst (1987) mentioned a possible shallow-marine occurrence from the Cretaceous of Africa. Modern counterparts are found in intertidal settings in the form of the burrows of *Paraonis fulgens*, but this report documents their first undoubted occurrence from shallow marine settings in the geological record after the Early Ordovician.

The distribution of trace fossils is not controlled by depth, but rather by a number of environmental factors that tend to covary with depth (Frey et al., 1990), although preservation also plays a role (Bromley and Asgaard, 1991). Deep-marine and intertidal settings are markedly different in terms of substrate and hydraulic energy, but both are similar in terms of resource predictability, and this may explain the occurrence of graphoglyptids in both settings. Valentine (1971) postulated that selection pressures in settings with low but predictable levels of resources favor specialized and efficient populations, whereas selection pressures in settings with plentiful but unpredictable levels of resources favor generalized and inefficient populations. Deep-marine settings are regarded as resource poor, but predictable (Sanders and Hessler, 1969), which explains the presence of graphoglyptids and efficient deposit-feeding traces. Resources are more plentiful in intertidal settings, but they are also predictable due to tides. In such settings, Valentine's (1971) model predicts a combination of specialized, efficient animals and unspecialized, inefficient animals. This explains the presence of spiral-shaped graphoglyptids and opportunistic arthropod feeding traces in the intertidal deposits from the Robledo Mountains. The lack of *P. fulgens*-type traces in ancient intertidal deposits led Risk and Tunnicliffe (1978) to conclude that the construction of traps only evolved geologically recently as a foraging strategy in such settings. However, this report demonstrates that such foraging behaviors were present in intertidal settings by at least the Early Permian. Such foraging behavior is remarkably specialized in comparison to other marginal-marine and nonmarine foraging trace fossils such as *Mermia*, which generally represent "scribbling" grazing patterns (e.g., Buatois and Mángano, 1995), and probably reflect the result of different selection pressures, depending on the levels and predictability of resources.

Graphoglyptids were known from ancient deep-marine facies long before they were discovered in modern deep-marine settings (Ekdale, 1980), although their presence had been predicted (Seilacher, 1977a).

Risk and Tunnicliffe (1978) suggested that intertidal *P. fulgens*-type traces should be found in the geological record if they were originally present because they would have a high preservation potential. This contention is not unreasonable, especially if such traces are linked with microorganisms, which are known to have a role in stabilizing modern intertidal sediments (e.g., Yallop et al., 2000). However, Seilacher (1977b) and Bromley (1990) noted that such intertidal structures would have a low preservation potential because the sediment is frequently reworked. In addition, shallow-marine deposits are commonly intensely bioturbated and, therefore, preservation potential of delicate biogenic structures is typically low. Some tidal flats, particularly those formed close to fluvio-estuarine transitions, host thinly bedded deposits with excellent preservation of the primary sedimentary fabric and associated arthropod trackways and grazing trails (Buatois et al., 1997; Mángano et al., 1997). This is true for the intertidal deposits from the Robledo Mountains, and the absence of associated infaunal bioturbation also helps to explain the preservation of these delicate structures. This suggests that the lack of graphoglyptids in intertidal deposits from the geological record is largely a preservational effect. Bromley and Asgaard (1991) proposed a similar scenario, suggesting that the preturbidite assemblage of the *Nereites* ichnofacies is only preserved when cast by a turbidite because it is obliterated by deeper tier burrowing under normal conditions.

The fossil record of polychaetes, as with many soft-bodied animals, is virtually nonexistent. The oldest known fossil polychaetes are from the Middle Cambrian Burgess Shale, although their affinities are uncertain (Eibye-Jacobsen, 2004), as is their phylogeny (see Bartolomaeus and Purschke, 2005). Rouse and Pleijel (2001) suggested that paraonids dated back to the Cretaceous on the basis of evidence of the trace fossil *Nereites irregularis*; however, this is a deposit-feeding trace, and spiral-shaped graphoglyptids provide a much better ichnological basis for identifying the presence of paraonids. All paraonids probably produce these characteristic spiral burrows (Röder, 1971; Seilacher, 1977b; Rouse and Pleijel, 2001), and their presence in the Robledo Mountains suggests that paraonids were present in intertidal settings by at least the Early Permian. Deep-marine examples extend back to the Ordovician, but are more irregular, and so may have been produced by different animals.

CONCLUSIONS

The occurrence of spiral-shaped graphoglyptid trace fossils in the Early Permian Robledo Mountains Formation of New Mexico demonstrates that they occur in the geological record outside of deep-marine facies after the Early Ordovician. The distribution of trace fossils is not controlled by depth, but rather a number of environmental factors, and we relate the presence of graphoglyptids in deep-marine and intertidal settings to the predictability of resources. The scarcity of intertidal graphoglyptids in the geological record most likely reflects a preservational effect. Remarkably similar spiral-shaped structures are produced in modern intertidal flats by the paraonid polychaete *Paraonis fulgens*, and function as traps to capture mobile microorganisms migrating vertically within the substrate in response to tides. We envisage a similar function for the trace fossils from the Robledo Mountains. Such a foraging strategy is far more specialized than those evidenced by other marginal-marine and nonmarine feeding traces. Previous studies have suggested that the lack of *P. fulgens*-type traces in ancient intertidal sediments indicates that such behavior only evolved relatively recently in such settings. This report documents that such foraging behavior was present in intertidal settings by at least the Early Permian.

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