Priapulid worms: Pioneer horizontal burrowers at the Precambrian-Cambrian boundary

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ABSTRACT

The major evolutionary events that characterize the Precambrian–Cambrian transition are accompanied by profound ecological changes in the composition of benthic communities, the nature of the substrate, and the occupation of marine ecospace. The increased animal activity on and within the substrate is attested to by numerous trace fossils, such as the cosmopolitan *Treptichnus pedum* whose first appearance is used as the global stratotype section and point (GSSP) to mark the base of the Cambrian. In spite of its major importance in biostratigraphy, the maker of *Treptichnus* trace fossils, and more generally of treptichnids, has long remained an enigma. Treptichnids were subhorizontal burrow systems produced in the subsurface and had a worldwide distribution throughout the Cambrian. Here we show, by using experimental ichnology, that the treptichnid burrow systems were most probably produced by priapulid worms or by worms that used the same locomotory mechanisms as the Recent priapulids (e.g., *Priapulus*). Their typical three-dimensional morphology with repeated arcuate probing branches suggests that their function was related to the feeding strategy of the worm such as predation or scavenging upon small epibenthic or endobenthic invertebrates. This interpretation is strongly supported by the preserved gut contents of Cambrian priapulids from the Burgess Shale Lagerstätte that contain effectively a variety of small epibenthic prey. The antiquity of treptichnids would designate priapulids as one of the earliest infaunal colonizers of the substrate that possibly interacted with epibenthic communities, thus playing a leading role (1) in the construction of the early marine food chain, and (2) as important subhorizontal bioturbators in the early stages of the "Cambrian Substrate Revolution."

INTRODUCTION

The Precambrian–Cambrian transition is marked by the rise of animal communities that built up a new type of complex and interactive marine ecosystem (Butterfield, 1997, 2001; Vannier and Chen, 2005; Caron and Jackson, 2008; Hu et al., 2007; Dunne et al., 2008) with no equivalent in the preceding Ediacaran period (Narbonne, 2005). This ecological event is accompanied by drastic changes at the water-sediment interface. Relatively firm seafloors dominated by microbial mats were replaced by softer and more fluid substrates increasingly colonized by bioturbators ("Cambrian Substrate Revolution"; see Seilacher and Pflüger, 1994; Droser et al., 1999; Bottjer et al., 2000; Dornbos et al., 2005; Bottjer and Clapham, 2006). In the Early Cambrian, tracks and burrows became more diverse and penetrated deeper into the sediment, indicating the subvertical and oblique exploration of the sediment by more complex bilaterians. Rich assemblages of such trace fossils occur in the Early Cambrian of many regions such as Sweden (Jensen, 1997), Greenland (Bryant and Pickerill, 1990), Namibia (Geyer and Uchman, 1995), and South China (Zhu, 1997), with more than 60 ichnogenera described to date (Jensen et al., 2006). Among them are the treptichnids

characterized by subhorizontal segmented burrow systems exemplified by *Treptichnus pedum* that is internationally recognized as the marker of the Precambrian-Cambrian boundary (Narbonne et al., 1987; Brasier et al., 1994). *Treptichnus* is actually no longer limited to the Phanerozoic and extends back into the late Ediacaran (e.g., Gehling et al., 2001, for global stratotype section and point [GSSP] in Newfoundland; Jensen et al., 2000, for Namibia). Despite their global occurrence and major stratigraphical importance (Table DR1 in the GSA Data Repository[1]), the identity of the treptichnid makers has so far never been elucidated, although the worm hypothesis is generally favored (Dzik, 2005, 2007). Priapulids (Huang et al., 2004a), with some sipunculans as a much rarer component (Huang et al., 2004b), seem to dominate the Cambrian worm fauna at least in dysaerobic settings such as those of the Chengjiang (Hou et al., 2004) and the Burgess Shale (Briggs et al., 1994; Caron and Jackson,

2008) Lagerstätten. Experimental ichnology with Recent priapulids collected in Sweden is used here for testing the worm hypothesis and to elucidate the animal activity responsible for treptichnid burrow systems.

METHODS

Priapulid worms form a very small phylum with only 18 living species. *Priapulus* and *Halicryptus* are the only two macrobenthic genera, the other representatives of the group being mainly meiobenthic. Cambrian priapulids (Fig. DR1) display a remarkable variety of shapes, external ornament, and body ratios. They best resemble Recent macrobenthic priapulids such as *Priapulus* and *Halicryptus* in key aspects of their functional anatomy, especially those related to feeding (eversible toothed pharynx) and locomotion (eversible and contractile proboscis). With its slender shape, *Priapulus* is the most suitable experimental model for our comparative study with early priapulids. *Priapulus caudatus* (Priapulida; Van der Land, 1970) was dredged from muddy, poorly oxygenated sediments (bottom depth ~30 m, salinity ~32‰) of the Gullmarfjord near Lysekil (~120 km north of Göteborg) and the Kosterfjord near Strömstad, Sweden. *Halicryptus spinulosus* (Priapulida) was obtained from brackish muds (salinity ~10‰) in the vicinity of the Askö island, 80 km south of Stockholm. Experimental ichnology was performed by using trays filled with a thin (~10 mm) layer of decanted mud from the original localities and seawater. This experimental device was designed in order to constrain the movement of the worms within a single horizontal plane and to make it observable. The behavior of worms was recorded with a Sony HDR-HC7E digital video camera and a Nikon D-200 camera. The morphology of tracks produced in experiments (general outline, number, morphology, and orientation of segments) was analyzed and compared with that of well-preserved treptichnid burrow systems, mainly those of *Treptichnus pedum*, *Treptichnus rectangularis*, and *Treptichnus bifurcus* from the Cambrian of Poland (Wiśniówka Duża, Holy Cross Mountains, Poland, ~75 specimens; Orłowski and Żylińska, 1996), Greenland (Bryant and Pickerill, 1990), Sweden (Jensen, 1997), and China (Meichucun, Yunnan Province; Zhu, 1997). Recent specimens used in experiments

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[1]GSA Data Repository item 2010196, Figure DR1 (morphological diversity of Cambrian and Recent priapulid worms), Figure DR2 (*Ottoia prolifica* from the Burgess Shale), Tables DR1–DR4, and Video DR1 (locomotory behavior and trace making of *Priapulus caudatus*), is available online at www.geosociety.org/pubs/ft2010.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

were eventually fixed with 10% formalin and preserved in 70% ethanol for dissections and observations in stereomicroscopy and scanning electron microscopy (SEM), especially the anatomical features (muscles, trunk, proboscis) involved in locomotion and trace making.

LOCOMOTION IN RECENT PRIAPULID WORMS

Locomotion in *Priapulus caudatus* is performed through the combined action of circular, longitudinal, and retractor muscles (Storch, 1991) that act by turns following a repeated cycle (Hammond, 1970; Elder and Hunter, 1980). Our experiments show that this cycle is characterized by four successive events: (1) peristaltic contraction of the trunk that propagates rapidly forward to eventually reach the proboscis, (2) invagination, (3) powerful eversion, and (4) club-shaped inflation of the proboscis (Fig. 1A; Video DR1). The cuticular spines (>20 scalid rows, Fig. 1C) that line the proboscis clearly act as a major terminal anchoring feature. It is only after the spiny proboscis swells up and anchors to the sediment (Fig. 1A, images 5 and 6) that the rest of the body can be pulled forward. The same locomotory mechanism is used by *P. caudatus* to move horizontally on the surface of sediment and to dig deeper into the mud (Vannier, 2007). Smaller priapulids such as *Halicryptus spinulosus* show identical behavior (J. Vannier, 2008, personal commun.). *P. caudatus* changes its

direction at almost every cycle (Fig. 1B). The anterior part of the worm generally strongly rotates clockwise (CW) or counterclockwise (CCW), then turns back slightly while the eversion of the proboscis starts. Such repeated directional changes imprint lobate markings along the main axis of the worm track (Fig. 1C) and give the general outline of the track its typical segmented pattern (Fig. 1D) that does not occur in other worms (e.g., sipunculans; I. Calandra and J. Vannier, 2008, personal commun.). The 18 horizontal tracks obtained in our experiments (Table DR2) generally show a composite outline with straight (successive very low-angle rotations), curved, and looped (series of CW or CCW rotations at higher angle) sections.

RESULTS: PRIAPULID ORIGIN OF TREPTICHNID BURROWS

Our comparative study reveals remarkable similarities between the horizontal tracks made by Recent priapulids in laboratory conditions and the Cambrian treptichnid burrow systems. (1) Both display the same segmented pattern resulting from constant directional changes of the trace-maker and have a comparable diversity of outline with alternating straight, curved, and often looped sections. (2) Measurements in eight excellently preserved subhorizontal burrow systems of *Treptichnus pedum* (Table DR3) indicate that the average angle between two succeeding segments varies from ~20° to 40°. These values are very close to

those obtained by measuring the rotation angle of *P. caudatus* (~30°; Table DR2). (3) The lateral lobate imprints that characterize the locomotory behavior of *Priapulus* (Fig. 1C; Video DR1) show strong similarities with treptichnids such as *Treptichnus pedum* (Fig. 2A, segments 1–7). (4) The cuticular ornament of the proboscis of *Priapulus* imprints regularly spaced striated markings in mud that closely resemble the striae present along the segments of *Treptichnus rectangularis* (Fig. 2C) and *Trichophycus venosus* (Jensen, 1997). These four lines of evidence strongly suggest that the producers of treptichnids were most probably priapulids or were worms with a locomotory behavior closely similar to that of Recent priapulids, i.e., characterized by repeated peristaltic cycles, proboscis action, and constant reorientations of the worm. Supporting fossil evidence from exceptional fossil sites indicate that Cambrian priapulid worms (Conway Morris, 1977; Dzik, 2005) indeed had morphologies compatible with such locomotory mechanisms (e.g., slender, cylindrical shape, eversible proboscis lined with cuticular spines; Fig. DR1). Their ability to penetrate the sediment at least subhorizontally is confirmed by specimens preserved in situ within their burrow (Zhang et al., 2006, for *Maotianshania* from the Chengjiang biota; J. Vannier, 2008, personal commun., for *Ottoia* from the Burgess Shale biota). However, these inhabited burrows consist of very short cylindrical sections that rarely exceed the length of the worm, making comparisons with treptichnids difficult. The lack of longer and well-preserved segmented burrow systems in these two Lagerstätten may reflect the natural behavior of the worms that might have effectively lived in short individual burrows with a locomotory behavior different from that of the treptichnid makers. Or, more likely, most activity traces were obliterated due to environmental factors (e.g., topmost water-saturated layer soft and remobilized by turbidity-generated currents, compaction of mud).

DISCUSSION: FUNCTION OF TREPTICHNID BURROWING AND IMPLICATIONS

If we admit that treptichnid burrows were indeed produced by priapulids or priapulid-like worms, there remains the question of their function as possible resting, locomotory, or feeding traces. Their three-dimensional architecture within the sediment provides some clues. By contrast with experimental priapulid tracks, treptichnid burrow systems were made in the subsurface within a profile where oxygen concentration was sufficient for the trace-maker to live and move through the sediment. Their three-dimensional, hypichnial preservation results from the partial erosion/exhumation
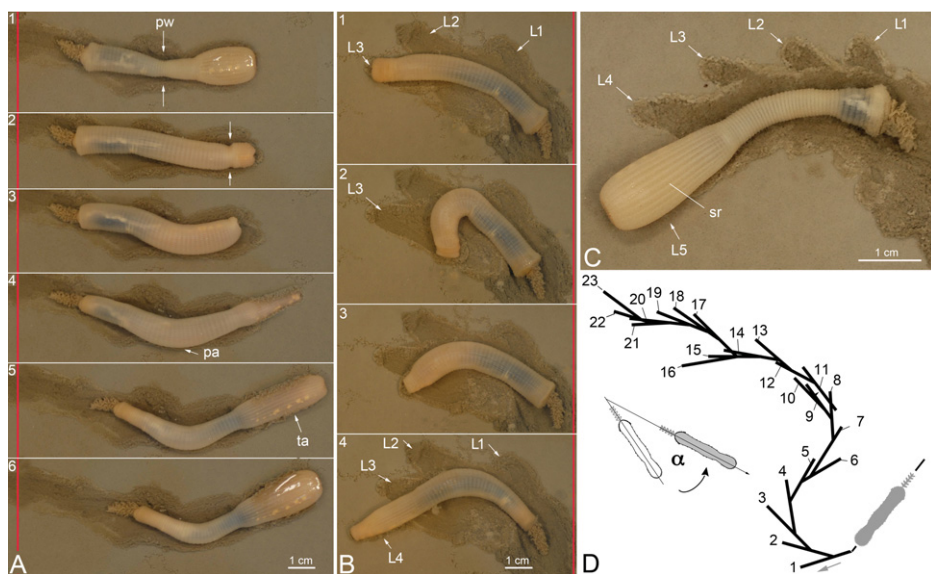

Figure 1. Locomotory mechanism of Recent priapulid worms exemplified by *Priapulus caudatus* from Sweden. A: Successive phases of the locomotory cycle: peristaltic wave through trunk (1, 2), proboscis invagination (3), eversion (4, 5), and inflation (6). B: Directional change of the worm: proboscis inverted (1), counterclockwise rotation (2), clockwise rotation (3), proboscis eversion (4). C: Lobate markings imprinted by the worm in sediment along the track axis. D: Track outline showing 23 directional changes (α = angle between two successive cycles). L1–L5—lobate markings; pa—penetration anchor; pw—peristaltic wave (contraction); sr—longitudinal scalid rows (anchoring features); ta—terminal anchor (rows of spines along proboscis). The red lines are landmarks. See "Methods" for details of experimental device.
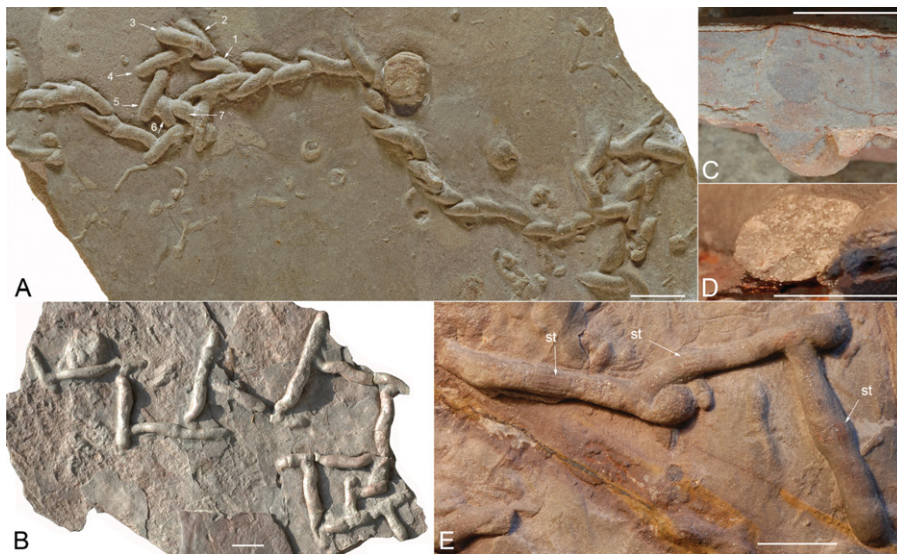
Figure 2. Treptichnid subhorizontal burrow systems from the Cambrian. A: *Treptichnus pedum* from the Lower Cambrian Mickwitzia Sandstone, Sweden (SGU 8598; see Jensen, 1997), general view of slab. 1–7—curved section with seven succeeding segments. B–E: *Treptichnus rectangularis* from the Furongian (upper Cambrian) of the Holy Cross Mountains, Poland (see Orłowski and Żylińska, 1996), general view (MUZWG ZI/29/3136), details of striated segments (MUZWG ZI/29/3184), and transverse sections through segments. st—striae. Scale bars are 1 cm in A–D, 5 mm in E. SGU denotes Swedish Geological Survey, Uppsala, Sweden; MUZWG denotes Museum of the Faculty of Geology, University of Warsaw, Poland.

of their tubular structure by bottom currents or storms prior to their casting by redeposited sediment (mainly sand). Some treptichnid burrow systems such as those of *T. rectangularis* and *T. bifurcus* spread horizontally within a single plane (Fig. 2). The typical bulbous end of their segments clearly results from the directional change of the worm within the sediment (see behavioral analogue in Recent priapulids, Fig. 1). However, more frequently, the distal part of the tubular segments of treptichnids curves up toward the top of the bedding sequence (Geyer and Uchman, 1995; Bryant and Pickerill, 1990), for example in the worldwide-distributed *Treptichnus pedum* (Figs. 2B and 2C). Such features strongly suggest that this particular type of treptichnid burrow system developed within the uppermost layer of bottom sediment and formed repeated probing branches toward the water-sediment interface (Fig. 3). The assumed probing is interpreted here as resulting from the feeding behavior of the worm such as predation or scavenging upon small epibenthic invertebrates or detritus at the water-sediment interface. Evidence from priapulid body fossils does support our interpretation. The gut of Middle Cambrian priapulid worms from the Burgess Shale (e.g., *Ottoia prolifica*; Fig. DR2; Conway Morris, 1977) often contain the identifiable remains of diverse epibenthic animals such as hyoliths, tiny arthropods, and brachiopods. Similarly, the guts of Recent priapulids also contain a variety of epifaunal and infaunal prey such as polychaetes, oligochaetes, and
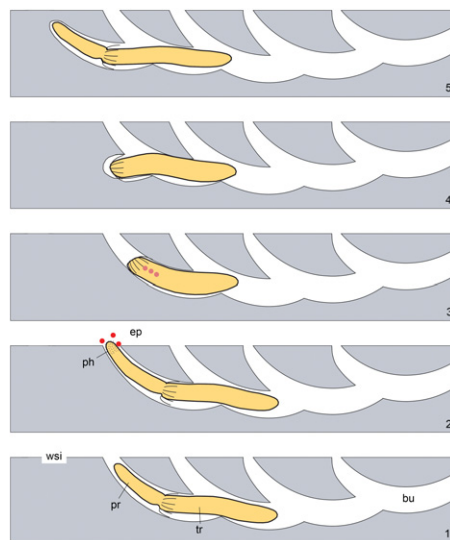

Figure 3. Treptichnids interpreted as priapulid burrow systems with a possible feeding function (predation/scavenging of small epibenthic invertebrates [red dots]). Model based on the morphology of *Treptichnus pedum* (see text). Individual segmented burrows open up at water-sediment interface. bu—burrow; ep—epibenthic prey; ph—pharynx; pr—proboscis; tr—trunk; wsi—water-sediment interface.

crustaceans (Ankar and Sigvaldadottir, 1981; Trott, 1998), indicating a comparable feeding type. The morphological diversity of treptichnid burrows suggests that their producers used different strategies to exploit their infaunal

niches (e.g., subsurface scanning in *T. rectangularis* versus open probing in *T. pedum*). A final conundrum to be noted is that present-day priapulid worms such as *Priapulus*, by contrast with the Cambrian treptichnid makers, do not generally produce well-defined subhorizontal burrow systems. They dig into the mud obliquely and penetrate the sediment by using the same repeated locomotory cycle as that observed on the surface of the mud (J. Vannier, 2008, personal commun., observations through narrow Plexiglas tanks). The preservation of these infaunal burrows actually depends on the consistency and water content of the mud. In watery and fluidized mud, the walls of burrows generally collapse rapidly, whereas their tubular structure is maintained when mud is less soupy. The well-preserved three-dimensional structure of most treptichnids suggests that they were made in relatively consistent mud and possibly consolidated by mucus deposition. Major differences between the Cambrian and the present-day seafloor may also explain the differences between treptichnids and Recent priapulid burrows. The persistence of microbial mats in the late Precambrian–Early Cambrian benthic environments (Bottjer and Clapham, 2006) may have led the pioneer infaunal colonizers such as priapulid worms to exploit the sediment mainly horizontally, whereas the soft muddy sediment where the majority of Recent priapulids live clearly favors a multidirectional exploration. Our treptichnid study highlights the role that priapulid worms may have played in the substrate changes across the Precambrian-Cambrian boundary (Bottjer et al., 2000). The "Cambrian Substrate Revolution" should be seen as a cascade of events possibly triggered by very shallow and subhorizontal burrowers such as priapulids that induced a relatively moderate disturbance of sediments by bioturbation but led to irreversible changes both in the physical properties and in the biological exploitation of the shallow marine substrates.

The abundance of treptichnids and priapulid body fossils both show a very sharp decrease after the Cambrian. Treptichnid burrows occur sporadically in the Ordovician (Table DR1), Devonian, Carboniferous (Buatois and Mángano, 1993), Mesozoic (Häntzschel, 1975), and Eocene (flysch deposits; Uchman et al., 1998). Priapulids are present in the Carboniferous Mazon Creek Lagerstätte (Schram, 1973). A possible scenario to explain this decline is that priapulids may have been replaced by other groups of infaunal predators such as polychaetes that indeed appear in the Ordovician (Conway Morris, 1977). Priapulids survived by adapting to poorly oxygenated muddy (e.g., *Priapulus*, *Halicryptus*) or interstitial environments (meiobenthic taxa) but never recovered their Cambrian dominance.

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