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RAPID COMMUNICATION

Early Cambrian priapulid worms buried with their lined burrows

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Abstract

Five specimens of the priapulid *Maotianshania cylindrica* preserved inside their lined burrows were described from the Lower Cambrian Chengjiang deposits near Kunming, southern China. The exceptional preservation suggests that this worm made a dwelling tube by lining within the uppermost sediment layers. This seems to be unique among priapulids in comparison with the Cambrian *Selkirkia* and *Paraselkirkia*, as well as some modern priapulid larvae and loriciferans. Taphonomic evidence indicates that the burrow-and-worm specimens are not buried *in situ* but were moved by storm, tsunami, or turbidity generated currents that are thought to have brought sedimentary material intermittently.

Keywords: priapulids, lined burrow, behaviour, taphonomy, early Cambrian.

1. Introduction

Priapulids are a group of burrowing marine worms belonging to the cycloneuralian clade (Nicholas, 2001; Nielsen, 2001). Only 18 extant priapulid species are known, and most of them inhabit cold water and dysoxic muds. However, the priapulids underwent a remarkable evolutionary radiation and flourished during the Cambrian explosion (Aguinaldo *et al.* 1997; Conway Morris, 1998). In both the Burgess Shale (Conway Morris, 1977; Whittington, 1985; Briggs, Ervin & Collier, 1994) and the Chengjiang faunas (Chen *et al*. 1996; Hou *et al*. 2004), priapulids constitute an important portion of the shallow marine mud-dwellers, accounting for no less than 20 species in these two occurrences alone. Among modern priapulids, some large-bodied species are considered to be carnivores, some small ones probably are sediment feeders, and a few may be suspension-feeding carnivores (Ruppert, Fox & Barnes, 2003, p. 772). Based on morphological and functional analyses and comparisons with extant representatives, some Cambrian priapulids have also been regarded as sediment feeders or as possible carnivores (Bruton, 2001; Huang, Vannier & Chen, 2004). Recently, some priapulids were suggested to adopt an epifaunal mode of life (Zhang & Pratt, 1996; Han, Zhang & Liu, 2004; Ivantsov & Wrona, 2004; Hu, 2005), but this is not conclusive. We still lack a thorough understanding of the mode of life of the Cambrian priapulid worms, as well as of the associated taphonomy and palaeoecology. In previous studies, the soft-bodied worms are almost exclusively reported as isolated specimens separated from their probable dwelling places, although the significance of soft-bodied organisms associated with their traces has been emphasized, for instance, by Conway Morris & Robison (1986). As an exceptional instance, here we report on priapulids preserved in lined burrows, which provide convincing evidence that some of the early Cambrian worms, if not all, did live in burrows.

It has been suggested that the Chengjiang fauna was transported and aggregated by either turbidity currents (Seilacher, 1991), which do not necessarily imply destruction of soft-bodied organisms (Allison, 1986; Allison & Brett, 1995), or by storm flows (Zhu, Zhang & Li, 2001). The fact that, on the whole, the animals are complete in the Chengjiang fauna indicates that the disruptive forces were limited. In our case, the worms are complete, but most of the delicate tubes have been ripped off. Here, therefore, we are close to the limit of what can be preserved during transport. Note that it is of course possible that the transport distance was quite short, and a short transport distance has been suggested for *Microdictyon* and its supposed host *Eldonia* which have been buried together (Chen & Zhou, 1997).

2. Material and preservation

The mudstone of the Lower Cambrian Yu'anshan Formation at Mafang village near Haikou, a small town about 50 km south of Kunming in Yunnan Province, southern China (Fig. 1), has yielded many trilobite exoskeletons that were assigned to *Eoredlichia intermedia* (Lu, 1940) and *Yunnanocephalus yunnanensis* (Mansuy, 1912) – the typical representatives of the second trilobite zone within the Lower Cambrian Qiongzhusian Stage (Zhang, 2003). More significantly, it also yielded large numbers of soft-bodied fossils (Luo *et al*. 1997), including many excellently preserved priapulid worms. According to a recent summary (Hou *et al*. 2004), this fossil assemblage is about 525 million years old, and falls within the Lower Cambrian Atdabanian Stage.

Our material contains hundreds of priapulid worms found on closely associated bedding surfaces in mudstone. Such concentrations have been presumed to result from sorting during transport before the burial. Of these priapulids, five specimens assigned to *Maotianshania cylindrica* are peculiar in each being buried within its dwelling tube (Fig. 2). This is a rare aspect, not found previously in the Chengjiang biota.

During the process of fossilization, both the worms and their tubes were strongly compressed. The worms are distinctly coloured and have a characteristic surface pattern, which makes it easy to identify them. The dwelling tubes may

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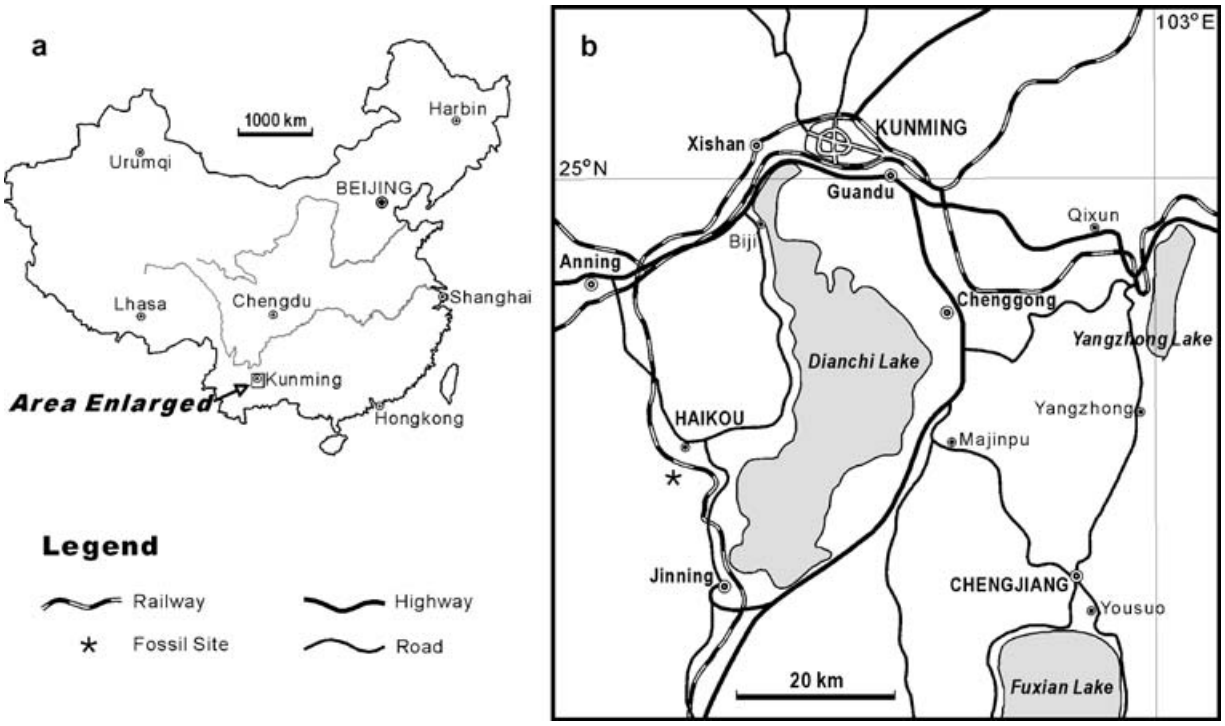


Figure 1. Location map. Asterisk in (b) indicates the early Cambrian fossil site at Mafang village near Haikou, Kunming, southern China.

consist in part of sediment. However, they have a reddish tint and/or a smooth surface and some relief, which makes them distinguishable from the surrounding sediment. The hue is, therefore, presumably caused by an organic content. Also, the border of the tube is locally preserved as a fine vertical ridge (Fig. 2c, f–h), which marks its original outline.

The dark stain associated with the lobopodian Hallucigenia was regarded as a relic of body fluids and organic matter (Ramsköld, 1992), and the reddish colour seen associated with the exoskeletons and soft parts with cuticular surface of the trilobite *Eoredlichia* was assumed to result from the staining by body fluids (Shu *et al*. 1995). However, during the taphonomic process, the original tissue composition has been thoroughly altered. As shown by Gabbot *et al*. (2004), preservation occurred through original framboidal pyritization and degradation of the organic carbon film. In these ways, thin films (or layers) of the carcass are preserved. Some convexity is preserved because of sediment in some guts and between body parts. None the less, the reason for specific colours in the fossils remains unknown. The same holds true for the lined tubes, which are remarkably different from the matrix in their colour.

3. Description

Exceptional preservation can provide significant insights into the taphonomic processes affecting the Cambrian priapulids and their dwelling tubes.

It is not entirely clear whether the structures described were made as isolated tubes or whether they consist of enforcing lining applied to the wall of a burrow. We have chosen to use the words lined burrow and burrow lining because it emphasizes the distinction from tube-like structures produced by other priapulids, such as *Selkirkia* and *Paraselkirkia*. The structure can be considered as a dwelling tube even if a dwelling tube with burrow lining is defined as being used by semi-sessile, suspension-feeding animals (Frey, 1973).

One of the complete worms enclosed in a tube measures about 40 mm (Figs 2a, 3a). The posterior portion of its trunk is curved, twisted, and even bent forward within the burrow lining (Fig. 2b), but unfortunately the anterior end of the worm is poorly preserved (Fig. 2c). The burrow lining is open at one end, closed at the other. The average diameter of the tube is only slightly larger than the worm's trunk and it is unlikely that the worm was able to turn around, particularly in the narrow middle portion (Fig. 2a, d). Near the closed end it is bulb-shaped and perhaps wide enough for the worm to have turned around. This end is observed in two specimens (Figs 2e, h, 3b, e), which both have lost the open end. Another lined burrow is fairly wide at the closed end but tapering at the other (Fig. 2g; Fig. 3d). The burrow lining may have more than one opening (Fig. 2c).

4. Do worm and burrow lining belong together?

The basic structure of the burrow lining is comparable to that of some extant marine burrowers. For instance some extant enteropneusts are known to live in burrows that are lined with mucus, and the tube may be branched and provided with funnel-like openings (Hyman, 1959). The branching upward that is seen in one specimen makes it resemble the trace fossils *Altichnus* and *Polycladichnus* of later times (e.g. Schlirf, Uchman & Kümmel, 2001). It seems apparent that many unrelated types of benthic animal take shelter in tubes, which they make by lining the walls of burrows. For this reason, it is conceivable that the priapulid may have 'borrowed' the burrow – but see below.

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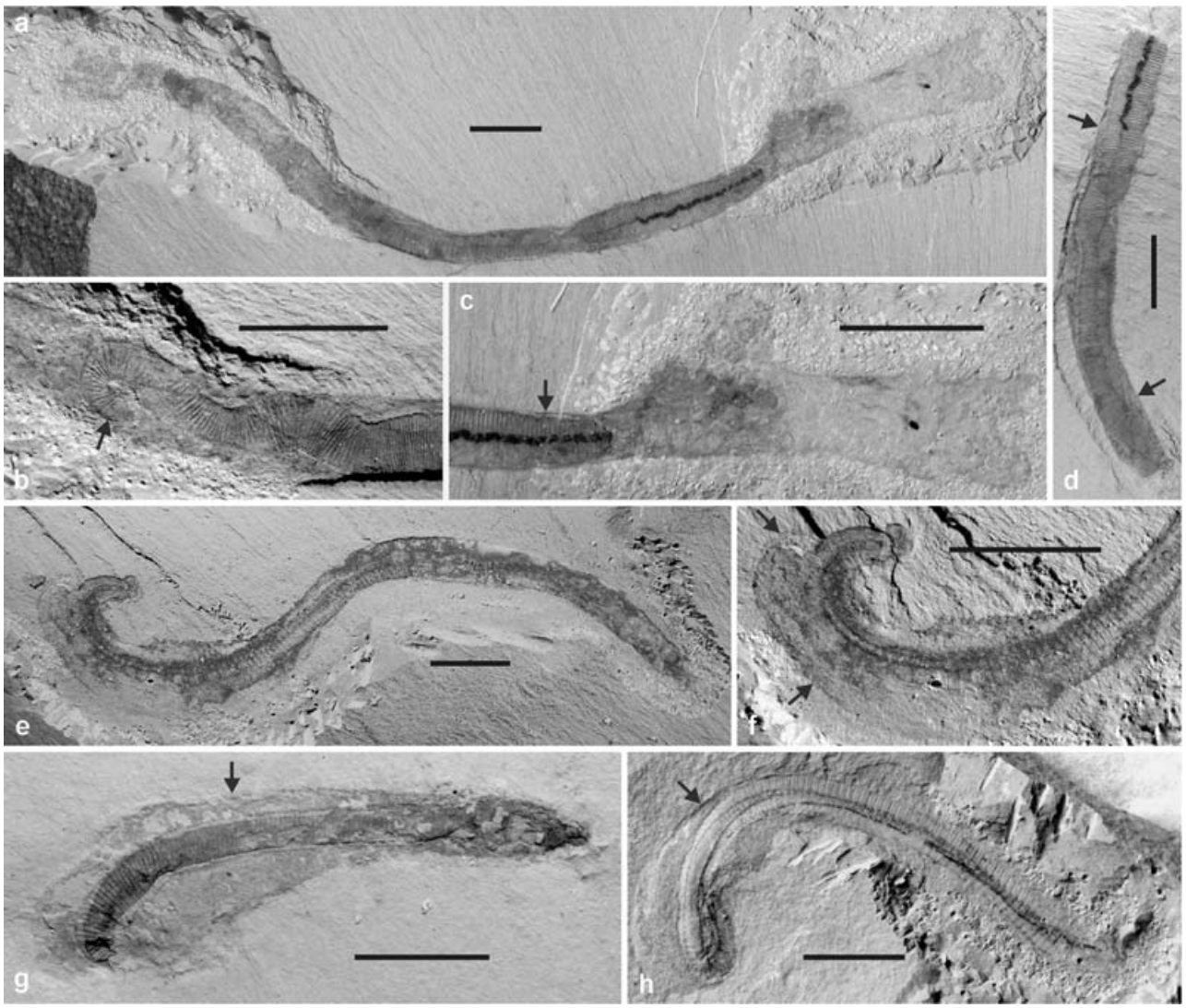


Figure 2. The early Cambrian priapulid *Maotianshania cylindrica* Sun & Hou, 1987. (a) A complete worm (YKLP 10197) preserved in its lined burrow. (b) Enlargement of the posterior part of (a) showing the strongly curved tail (arrows). (c) Enlargement of the anterior part of (a) showing the tube wall (arrow) and the introvert extending through a hole in the wall. (d) The middle portion of the trunk (YKLP 10198) with the partially preserved lined burrow (arrow). (e) A complete worm with the posterior portion of the lined burrow preserved – the anterior portion was ripped off before deposition (YKLP 10377). (f) Details of rear portion of (e) showing the tube wall (arrows). (g) A complete worm within a broad but partially preserved lined burrow (YKLP 10605). (h) A worm lacking anterior portion preserved within the posterior portion of the lined burrow (YKLP 10606), arrow indicating the burrow tube wall. Scale bars, 5 mm.

What we see from the specimens illustrated here must be a burrow lining, which was probably reinforced with mucus or something similar by the worm. The direct evidence is (1) the colour is darker than the surrounding sediment and may indicate the original presence of organic matter, and (2) the topographically raised edges of the structure indicate the presence of a somewhat durable wall. Our conclusion that the specimens were transported also necessitates the existence of a durable structure.

There are no faecal pellets identified in any part of the tube. Perhaps the faecal material was there but was totally altered during the taphonomic process, leaving nothing to be determined. On the other hand, the assumed tube dweller may have left its excretions outside of the tube.

It should be noted that, in every case where it can be confirmed, the worm has its tail end toward the closed end of the burrow lining. In contrast, a temporary occupant would more likely have had its anterior end towards the closed end. Chatterton, Collins & Ludvigsen, (2003) described the occasional occurrence of small trilobite and agnostid arthropods in the tube of the Burgess Shale priapulid *Selkirkia columbia*. Some 80 % of them do not contain the producers of the tube. The intruding arthropods consistently have the anterior end facing the narrow end of the *Selkirkia* tube, which is in contrast to the *Maotianshania* specimens. This would obviously be the wrong orientation for a priapulid searching for food. The authors speculate that the arthropods may have entered the empty tube on purpose, 'most likely to feed (scavenge on remnants of the dead priapulid worm?) or hide' (Chatterton, Collins & Ludvigsen, 2003, p. 158).

Maotianshania is not known to occur in any other burrows or tubes, nor do we know of any case in which this type of

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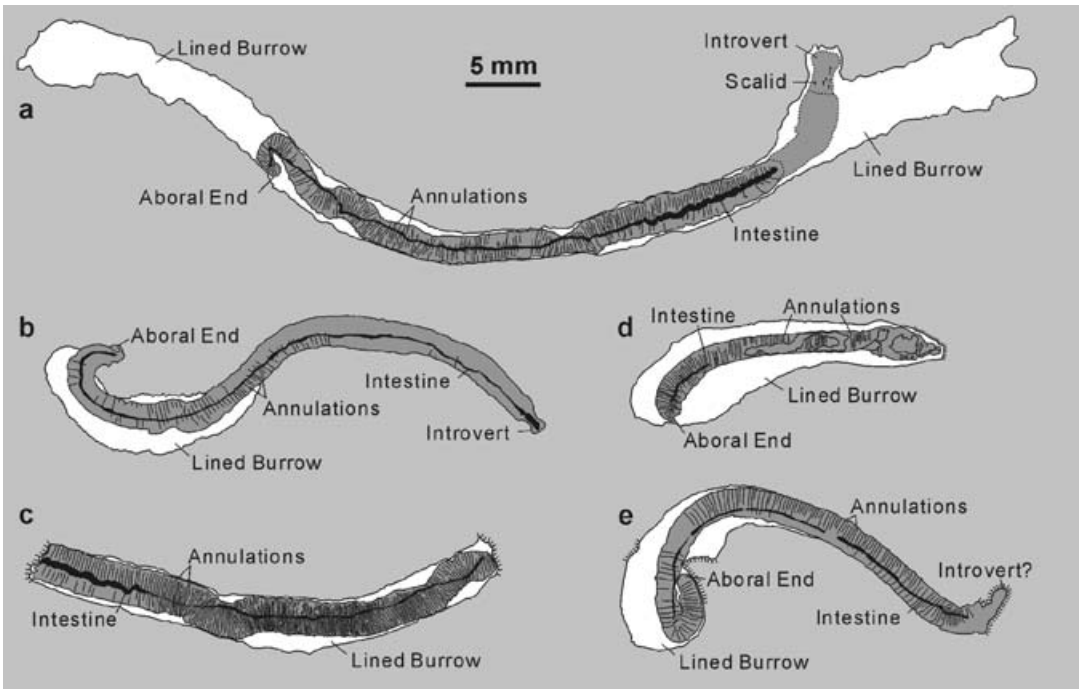


Figure 3. Camera lucida drawings of the priapulid *Maotianshania cylindrica* preserved within the lined burrow. (a–e) Based on specimens of YKLP 10197, 10377, 10198, 10605, 10606 respectively.

lined burrow contains animal remains. Although all this is indirect evidence, it is consistent with the conclusion that *Maotianshania* was the maker of these dwellings.

No extant priapulid is known to secrete a burrow lining or dwelling tube, nor are the conical tubes of the Cambrian *Selkirkia* and *Paraselkirkia* any likely dwelling tubes (see below). Secreting a dwelling tube is a common phenomenon among phoronid, pogonophoran and annelid worms. The pogonophorans produce tubes that consist of protein and chitin. The secretion comes from the anterior part of the body. The tubes are usually stiff, but *Riftia pachyptila* produces a flexible tube (knowledge summarized by Ruppert & Barnes, 1994, p. 582).

Pogonophoran tubes often are entirely outside the sediment, and so are many tubes produced by more typical polychaete annelids (such as *Spirorbis*). Others produce a tube or burrow lining within the sediment. The worms can use secretions alone or, at the other extreme, sand grains and other foreign material can dominate the construction. Tubes can be open in both ends (e.g. *Clymenella*) or closed in one end (e.g. *Sabellaria*). Also, some oligochaete annelids make tubes (for instance, *Tubifex*). Secreted products among the non-pogonophoran annelids range from mucus to calcium carbonate. The ability to produce the different kinds of secretion that are used in all separate groups has obviously evolved many times. Priapulids have proved their ability to produce extracellular matter by making a cuticle with three layers of different composition and to change structures during life, while the lorica is produced today only by the larva of one genus (see Ruppert & Barnes, 1994, p. 357). Although there is no detailed description concerning lined tubes of priapulid worms, there is every reason to believe that these meiobethic burrowers (Huang, Vannier & Chen, 2004) could have the potential to use secretions also for lining a burrow, if the life style would motivate it.

5. The burrow lining as a trace fossil

The specimens (burrow lining plus animal) were displaced from were they were made and deposited in a different place because:

(1) All specimens are either parallel or at a low angle to the bedding surface. In a more or less complete specimen, the open end of the burrow lining appears to be flattened in a unique depositional event rather than being vertically compacted during diagenesis (Fig. 2a).
(2) In one specimen with an entire worm the lining is only half as long as the worm (Fig. 2e). Apparently, part of the tube has been ripped off. This may have been caused by mudflow or sediment sliding. Another worm is preserved in a fragmental tube with its tail extending outside the end of the tube (Figs 2e, 3b). This infers that the transport that caused the damage of the tube would have happened before the worm and the tube became finally buried.
(3) The tail end of the same worm extends out through the side of the tube lining (Figs 2e, 3b). This is hardly a natural condition for a worm in its tube, but is most likely due to the damage of the wall during transport.

6. Mode of life and palaeoecology

The exceptional preservation provides an opportunity to understand an unusual aspect of the behaviour and mode of life of the Cambrian priapulid worms.

It should be noted that extant priapulids chiefly live infaunally and some of them may be disturbers of the soft sediment on the sea floor (Valentine, 2004), but none is known to live in a tube or lined burrow. However, in some larvae the trunk is enclosed in a thick cuticular lorica, which

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will disappear during subsequent development (Ruppert, Fox & Barnes, 2003). The Cambrian priapulid *Corynetis brevis* Luo & Hu, 1999 (Luo *et al*. 1999; Huang, Vannier & Chen, 2004) was inferred to have lived in a vertical burrow and behave as a predator. This conclusion was based mainly on morphology, functional analysis and coexisting fossils (Bruton, 2001). Being preserved always with a curved body, the Burgess Shale priapulid *Ottoia* was suggested to have lived in a U-shaped burrowing tube; the large-sized priapulid *Louisella* was also a burrower (Conway Morris, 1977; Briggs, Ervin & Collier, 1994). However, there remained no direct evidence to verify the association between possible burrow or dwelling tubes and fossil priapulids. The early Cambrian *Paraselkirkia* from the Chengjiang deposits (Hou *et al*. 2004) and the Middle Cambrian *Selkirkia* from the Burgess Shale (Conway Morris, 1977) and Utah (Conway Morris & Robison, 1986) are commonly preserved within a horn-shaped tube with only the introvert protruding from the large opening of the supposed tube. The opposite end has a small opening. It appears possible that the tube was not detached from the worm body, but consisted of trunk cuticle, like the lorica of some extant priapulid larvae (and loriciferans at all stages). This would explain the conical rather than cylindrical shape and the fact that the tube is shorter than the animal, always leaving the everted introvert outside. It is true that we have not observed any separate lorica plates, but it is possible that they are present, or that this construction had not yet evolved.

Because empty *Selkirkia* tubes greatly outnumber those with soft parts, its tube seems fairly tough and has a higher resistance to decay than has the construction of *Maotianshania*. Empty tubes were even used as attachment substrate by brachiopods and sponges (Conway Morris & Whittington, 1985, p. 14 and fig. 25). Accordingly, such a resistant tube with regular shape is most likely to be secreted by the worm to serve as a protective wall for the worm's soft parts. On this ground, the conical and fairly short tube of *Selkirkia* is essentially different from the burrow lining of *Maotianshania* as described here. This is evidence of the diversified modes of life adopted already by the early Cambrian priapulids.

The life in a tube or cylindrical burrow necessitates an ability to move backwards. However, we have no conclusive evidence to demonstrate how the worm moved, particularly as it lived in such a cylindrical tube or lined burrow with a diameter somewhat larger than the body diameter.

Because of an insufficient fossil record of post-Cambrian priapulids, the evolutionary path that led to the modern priapulids from their Cambrian representatives remains obscure. The Cambrian priapulids, both from the Chengjiang and Burgess Shale, either lived in shallow water environments, or as meiobenthic burrowers (Huang, Vannier & Chen, 2004), but most living taxa are in the deep seas (Ruppert, Fox & Barnes, 2003). The distribution associated with a shift of habitat with time may be the result of increased competition from other groups. This competition may also have led to the eradication of clumsy tube-bearers and burrow-liners in favour of more agile animals. It should be noted that the efficient design of the multi-plated, flexible lorica in the larva of the modern priapulid *Halicryptus* is shared by the loriciferans. Some of the Cambrian forms, notably *Selkirkia* and *Maotianshania*, may therefore belong to the stem group not of the Priapulida, but of a larger group Scalidophora including the Priapulida, Loricifera and Kinorhyncha, all derived members of the superphylum Cycloneuralia (cf. Nielsen, 2001).

7. Conclusions

This is the first report of a lined burrow associated with any priapulid, in this case the early Cambrian Maotianshania cylindrica.

The tube of the well-known Cambrian priapulids Paraselkirkia and Selkirkia is most probably an extension of the cuticle, like the lorica of extant loriciferans and some priapulid larvae, and not a burrow lining. If the Paraselkirkia and Selkirkia type tube is homologous with the lorica, it means that these priapulids may belong to the stemgroup of the Scalidophora including the Priapulida, Loricifera and Kinorhyncha, all derived members of the superphylum Cycloneuralia.

The tube-shaped structure enclosing Maotianshania has the character of a burrow lining or dwelling tube. This makes it fundamentally different from the tube of Selkirkia, which has the character of a typical body fossil, and is somewhat comparable to the thick cuticular lorica seen on the trunk of extant loriciferans and some priapulid larvae. The tube of Maotianshania is cylindrical and closed in one end, whereas the tube of Selkirkia is conical and open in both ends. The shape and diameter of the lined borings would fit the size of the enclosed specimens of Maotianshania so that they could use the typical priapulid peristaltic mode of locomotion. Burying of the specimens (burrow lining with worm) was caused by fast sedimentation. They may have suffered short transport, which is most unusual for trace fossils (Bromley, 1996).

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