



The first record of a possible complete 'priapulid' from the lower Cambrian (Series 2) of Estonia

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Abstract: The *Yunnanpriapulid*? sp. can be divided into three distinct parts: an anterior introvert, a slightly constricted elongated neck, and a slightly bulbous elongated posterior trunk. The fossil is preserved as a three-dimensional cast in the fine-grained sandstone and is oriented parallel to the bedding plane. Rapid burial helped protect the organism from scavengers and decay and provided the opportunity for fossilization via pyritization. The preservation of the specimen on a bedding plane resulted from the post-mortem transportation of the dead animal, likely due to a storm event. The priapulid likely hunted other worms for food. The similarity of the Estonian specimen to the Chinese species suggests that there may have been some faunal exchange between the remote continents of Baltica and South China in the early Cambrian.

Keywords:

- lower Cambrian;
- exceptional preservation;
- priapulid worms;
- sandstones;
- Baltica

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Résumé : Le premier signalement d'un possible 'priapulien' du Cambrien inférieur (Série 2) d'Estonie.- Le *Yunnanpriapulid*? sp. peut être divisé en trois parties distinctes : un introvert antérieur, un cou allongé légèrement rétréci et un tronc postérieur allongé légèrement bulbeux. Le fossile est préservé sous forme de moulage tridimensionnel dans un grès fin. Il est orienté parallèlement au plan de stratification. Un enfouissement rapide a contribué à protéger l'organisme des charognards et de la décomposition, permettant ainsi une fossilisation par pyritisation. La préservation du spécimen sur un plan de stratification résulte d'un transport post-mortem du cadavre, probablement à l'occasion d'un événement de type tempête. Le priapulien chassait probablement d'autres vers pour se nourrir. La similitude du spécimen estonien avec les espèces chinoises suggère qu'il pourrait avoir existé un échange faunique entre les continents éloignés de la Baltica et de la Chine du Sud au Cambrien inférieur.

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**Mots-clefs :**

- Cambrien inférieur ;
- préservation exceptionnelle ;
- vers priapulien ;
- grès ;
- Baltica

1. Introduction

Priapulid worms today consist of a small group of cycloneuralians, with approximately 20 species (SCHMIDT-RHAESA, 2013). Most of them are small and live within the sediment (SHIRLEY & STORCH, 1999). While the geological record of priapulids is somewhat limited due to low preservation potential. The archaeopriapulids (CONWAY MORRIS, 1977), some of which may be part of the early evolutionary lineage of modern priapulids, are notably diverse in lower and middle Cambrian Lagerstätten (PEEL, 2017). Most Cambrian worms are scalidophorans that closely resemble modern priapulids. Their fossils are not rare and they occur in various localities in China (even in the 535 Ma-old-Kuanchuanpu Formation) (WANG *et al.*, 2021, 2023).

A variety of skeletal fossils have been identified in the lowermost Cambrian of Estonia, including *Sabellidites cambriensis* YANICHEVSKY, *Sabellidites* sp., *Platysolenites antiquissimus* EICHWALD, *P. lontova* ÕPIK, *Spirosolenites spiralis* (POSTI), *Yanichevskyites petropolitanus* (YANICHEVSKY), *Aldanella kunda* (ÕPIK), as well as pyritized casts of hyolithids and "hyolithelminthes", chitinous horn-like sclerites, fragments of brachiopods, and agglutinated tubes of *Onuphionella agglutinata* KIRJANOV (MENS & PIRRUS, 1977, 1997; MENS, 2003). The upper part of the lower Cambrian also contains trilobites, *Volborthella*, and *Mickwitzia* (MEIDLA, 2017). There are *Treptichnus pedom* burrows in the lower Cambrian of Estonia (PALIJ *et al.*, 1979). These burrow systems are likely to have been made by priapulid-like worms (see KESEDIS *et al.*, 2019; VANNIER *et al.*, 2010).

The aim of the paper is to: 1) describe a priapulid-like scalidophoran from the lower Cambrian of Baltica, and 2) discuss its ecology and paleobiogeography.

2. Geological background

During the early Cambrian, Baltica was positioned in the southern hemisphere, between 60 and 30 degrees, in a cold-temperate zone (LINDSTRÖM, 1972; COCKS & TORSVIK, 2005). The area that is now Estonia was submerged under a shallow epicontinental sea. The Cambrian Baltic Basin is known for its terrigenous sedimentation. The lowermost part of the trilobite-bearing Cambrian on the East European Platform, deposited during the Liivi evolutionary stage in the East Baltic region (MENS & PIRRUS, 1997), is defined as the Dominopol' Stage (Series 2) (MEIDLA, 2017).

In Estonia, the Dominopol' Stage is represented by three consecutive formations: Sõru, Lükati, and Tiskre, which are easily distinguished based on lithological and palaeontological evidence. The Dominopol' strata are distributed in

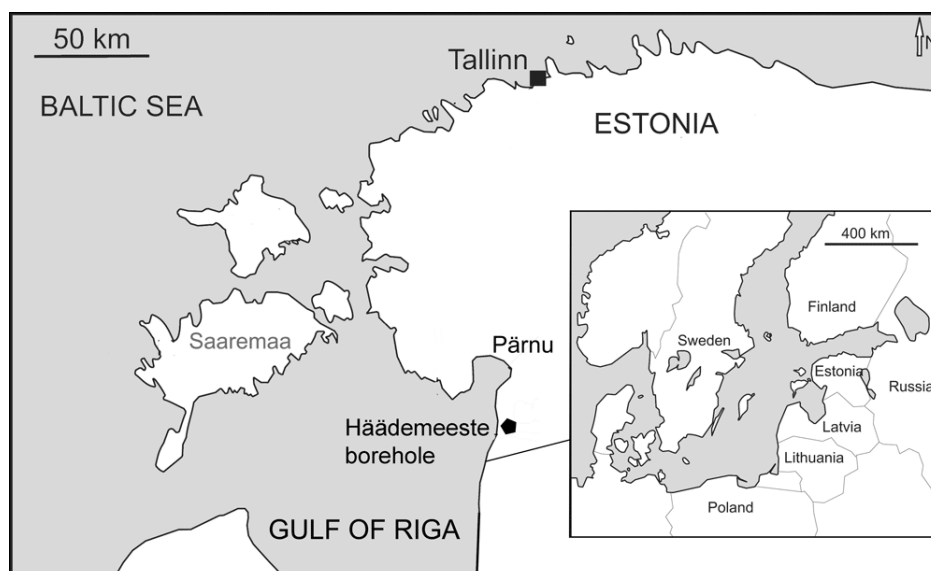
the West Estonian Archipelago islands (except Ruhnu) and in the western, northern, and central parts of mainland Estonia. Only the upper part of the stage (Lükati and Tiskre formations) is exposed along the North Estonian Klint, stretching from the Pakri Peninsula in the west to the Narva River in the east. Key localities include Türisalu, Rannamõisa, Kakumägi, Lükati, Saviranna, Kunda, and Utria. The maximum thickness of the stage (76.6 m) has been recorded in the Kalana borehole, where all three formations are present (MENS & PIRRUS, 1997). The Dominopol' Stage corresponds to the Cambrian Series 2 (JANKAUSKAS & LENDZION, 1994; MENS & PIRRUS, 1997).

The stage consists mainly of siliciclastics, primarily sandstones. The lower boundary of the stage is distinct both lithologically and in terms of faunal composition, and in some locations, it is marked by conglomerate lenses (MENS & PIRRUS, 1997).

Fossils in the lower part of the stage (Sõru Formation) are scarce, represented mostly by trace fossils, rare tests of agglutinated foraminifers, and a few acritarchs. The latter include leiosphaerides and rare *Globosphaeridium* cf. *cerinum* (VOLK.), *Asteridium pallidum* (VOLK.), *Loposphaeridium tentativum* (VOLK.), and *Tasmanites bobrowskae* WAZ. (MENS & PIRRUS, 1997). This part of the stage corresponds to the *Rusophycus parallelum* Zone (MENS & PIRRUS, 1997).

The middle part of the stage (Lükati Formation) is well characterized palaeontologically. Typical species include *Volborthella tenuis* SCHM., *V. conica* SCHINDEWOLF, *Schmidtellus mickwitzi* (SCHM.), *Mickwitzia monilifera* (LINNARS.), torellidids, hyolithids, agglutinated foraminifers (*Luekatiella estonica* ZHIGULINA, 1999), and, in the west, *Platysolenites antiquissimus* EICHWALD in the basal beds. The acritarch assemblage in this part of the stage is abundant and diverse, with baltisphaerids being dominant (MENS & PIRRUS, 1997). The middle and upper parts of the stage correspond to the *Schmidtellus mickwitzi* Zone (MENS & PIRRUS, 1997).

The upper part of the stage (Tiskre Formation) is well characterized palaeontologically only in its lower part (Kakumägi Member), particularly in the conglomerate lenses, which contain *Mickwitzia monilifera* (LINNARS.), *M. formosa* WIMAN, *M. concentrica* GORJANSKY, *Paterina rara* GORJANSKY, *Sce-nella discinoides* SCHM., *S. tuberculata* SCHM., *Bradoria? estonica* MELNIKOVA, *Konicekion kundaensis* MELNIKOVA, and fragments of trilobites. In the uppermost part (Rannamõisa Member), only occasional, indeterminable fragments of brachiopods and trace fossils are found. Acritarchs have been identified in the Kakumägi Member and, once, in the Rannamõisa Member (Muraste-2 borehole) (MENS & PIRRUS, 1997).



◀ **Figure 1:** Location of Häädemeeste borehole.

3. Material and methods

A fossil of priapulid-like worm from the Domnopol Stage (Häädemeeste 172 borehole, depth 599.4m) (Fig. 1) was cleaned and photographed with a digital camera (Canon EOS 5DSR). The details were photographed using the apochromatic zoom system Leica Z16 APO. The measurements of the specimens were obtained from calibrated high-resolution photographs. The studied specimen (GIT 293-400) is deposited at the Department of Geology, Tallinn University of Technology (GIT).

4. Systematic paleontology

Phylum Priapulida DELAGE et HÉROUARD, 1897
Genus *Yunnanpriapululus* HUANG et al., 2004b
***Yunnanpriapululus?* sp.**

(Figs. 2 - 3)

Description: The animal can be divided into three distinct parts: an anterior introvert, a slightly constricted elongated neck, and a slightly bulbous elongated posterior trunk. The neck and anterior part of the trunk show poorly developed but regular annulation. The annuli are about 0.2 mm thick. The worm is 8.7 mm long. The trunk is 4.7 mm long and 1.2 to 2.0 mm wide, widest at proximal 1/2 of the trunk, and thinnest at the neck. The neck is separated from the trunk via shallow but well-defined constriction. The neck is 3.4 mm long and 1.2 mm to 1.6 mm wide, widest near the introvert. The introvert is short, about 0.8 mm long, and slightly bulbous, about 1.8 mm wide. There is a prominent constriction between the neck and the introvert. Posterior end of the trunk with rudimentary or broken caudal appendage. The caudal appendage is not branched. Some longitudinal structures are visible along the trunk that may correspond to scald rows (Fig. 2.B).

Comparison: The described specimen resembles *Yunnanpriapululus* HUANG et al., 2004b (p. 221, Fig. 4 a-f) in its small size, presence of subspherical introvert, well-defined neck and anterior part of the trunk that shows fine annulations and in-

creases slightly in diameter backward. The described species has only a rudimentary caudal appendage, though it might be broken, which differs from the longer caudal process of *Yunnanpriapululus*. The described specimen also resembles *Eximipriapululus globocaudatus* MA et al., 2014 (Fig. 8 IV-V) by bulbous trunk and broad introvert. It differs by much longer neck region. The body orientation could be reverse with the introvert composing the largest part of the body based on the anatomy of many modern priapulids (MARTÍN-DURÁN et al., 2012), but the location of the caudal appendage is the reason why we oriented the body in that way.

5. Discussion

BODY FOSSIL VERSUS TRACE FOSSIL

KESIDIS et al. (2019) described exceptionally preserved trace and body fossils from sandstones of the lower Cambrian (Stage 4) File Haidar Formation of southern Sweden that can unequivocally be assigned to a scaldiphoran producer. There is a great morphological similarity between priapulid burrows (i.e., trace fossils) and their molds (i.e., body fossils). The major question concerning the described specimen from the lower Cambrian of Estonia is whether it represents a moldic preservation of priapulid or it is a priapulid burrow preserved in positive relief. All previously described priapulid burrows, both Recent and fossil, show a great amount of irregularity in their morphology (see KESIDIS et al., 2019, Figs. 3b-d, 4a-c) as compared to moldic preservation of body fossils (see KESIDIS et al., 2019, Fig. 3a). In this respect, the studied specimen resembles much more the priapulid mold (KESIDIS et al., 2019, Fig. 3a) than burrows (KESIDIS et al., 2019, Figs. 3b-d, 4a-c). Moreover, the studied specimen shows both ends that a very well preserved and discrete which cannot be said for the trace fossils and Recent burrows. The last but not least, careful examination of the terminal part of the studied specimen reveals the presence of a short caudal

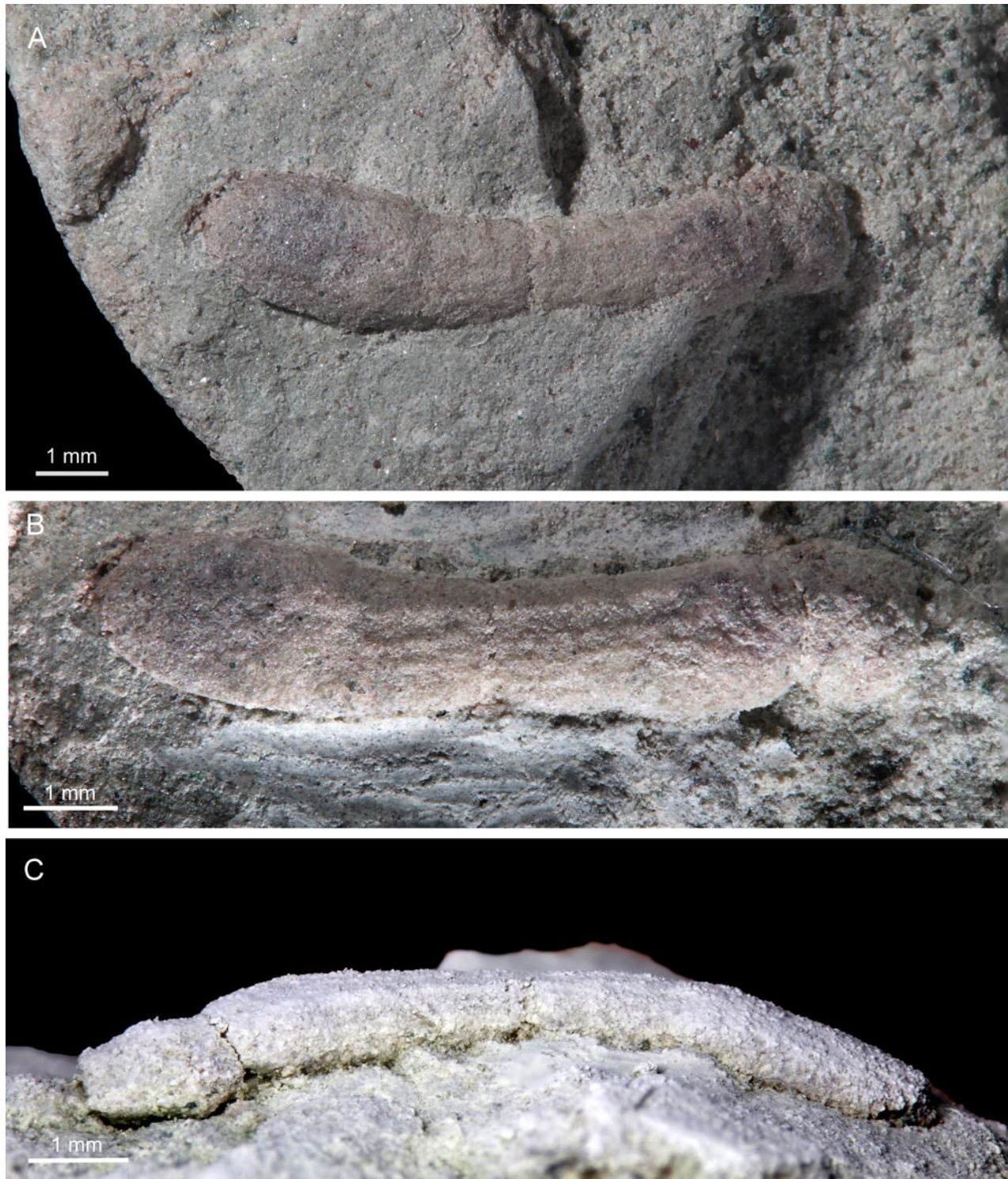


Figure 2: *Yunnanpriapulid?* sp. (GIT 293-400) from the Dominopol Stage (Cambrian, Series 2), Häädemeeste 172 borehole, depth 599.0m. A, General view in original state. B, General view in different light after some preparation. C, Lateral view of whitened specimen.

appendage preserved as cast which cannot be seen in any priapulid burrow. Thus, considering the reasons mentioned above, we are inclined to interpret our specimen as a moldic preservation of a "priapulid" worm (*i.e.*, body fossil). One could ask why we have attributed this fossil to "priapulids" as these scalidophorans have a very specific set of sensory-locomotory appendages, a peculiar symmetry of their arrangement, etc. which are not detectable on the fossil. The lack of these

characters is due to the preservation mode as mold composed of fine grained sandstone. Similarly preserved molds have been assigned to "priapulids" with confidence by KESIDIS *et al.* (2019, Fig. 3a). We acknowledge that definite Cambrian priapulids are extremely rare fossils (if any). Almost certainly studied fossil represents either total-group, or stem-group scalidophorans. It may also represent a total-group and stem-group cycloneuralians (*e.g.*, WANG *et al.*, 2025).

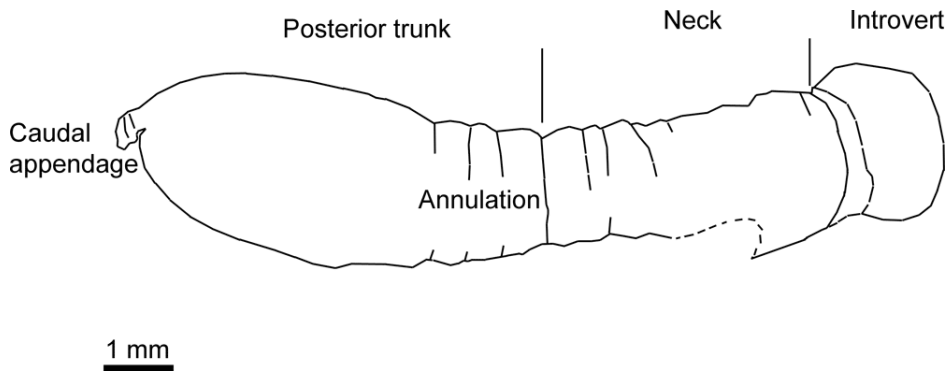


Figure 3: Schematic line drawing of *Yunnanpriapulid*? sp. (GIT 293-400).

TAPHONOMY

The specimen is preserved as a three-dimensional cast in the fine-grained sandstone and is oriented parallel to the bedding plane. The color of the fossil is light brown while the surrounding matrix is greenish-grey. We did not find sedimentological differences in the grain size between the matrix and fossil that could suggest a trace fossil. The light brown color could be caused by the higher pyrite content of the fossil as compared to the surrounding rock. The originally organic priapulid was presumably preserved via pyritization (BRIGGS, 2003). The rapid burial helped protect the organism from scavengers and decay, providing the opportunity for fossilization. The mineralization of soft tissues did not lead to a full replacement, but rather to the preservation of the organism's external form as a mold. Over time, mineral-rich waters in the sandstone could seep into the mold, hardening and preserving the fossil's shape. The further mineralization and incoming sand from surrounding sediments filled the cavity and preserved the worm as a cast. We assume that studied specimens could represent a similar way of preservation to priapulid mold from the lower Cambrian of Sweden that was recently described and illustrated by KESIDIS *et al.* (2019, Fig. 3a).

ECOLOGY

Yunnanpriapulid was likely a burrowing predator (HUANG *et al.*, 2004a, 2004b, 2014). Similarly, most other Cambrian priapulids are thought to be predators (CONWAY MORRIS, 1977; HUANG *et al.*, 2004a, 2004b; HU, 2005; HUANG, 2006; PEEL, 2017). A direct evidence of predation comes from preserved gut contents in *Ottoia* (see VANNIER, 2012). Moreover, extant priapulids are also chiefly carnivorous, though occasionally they ingest mud too (HUANG *et al.*, 2004a, 2004b). The early Cambrian priapulids had a burrowing lifestyle (ZHANG *et al.*, 2006; HAN *et al.*, 2007; VANNIER *et al.*, 2010; HUANG *et al.*, 2014; KESIDIS *et al.*, 2019). Since these animals had an endobenthic lifestyle, it is possible that a massive input of sediment made it impossible for the worm to escape and reach the water sediment-interface. The preservation of the fossil on a bedding plane likely resulted from post-mortem transportation of the dead animal, presumably due to a storm event on a relatively shallow terrigenous shelf. Fine-grained sands formed a suitable substrate for burrowing,

and during its life, *Yunnanpriapulid* was likely submerged in sediment leaving only its apertural part free on the surface of seafloor. The priapulid likely hunted a high variety of animals for food as suggested by studies of their gut content (VANNIER, 2012). The numerous worm burrows in the lower Cambrian sediments of Estonia suggest that the sea floor may have contained diverse scalidophoran fauna. The data on early Cambrian predators in the Baltic Basin is scarce (see MENS & PIRBUS, 1997), and it is possible that priapulids may have been among the top predators.

PALEOBIOGEOGRAPHY

The early Cambrian priapulids have been reported only from a few places, most of them in China. The oldest total-group scalidophoran fossils come from Kuanchuanpu Formation (WANG *et al.*, 2025). The most famous locality is Chengjiang Lagerstätte, which also contains the most diverse fauna of priapulid worms (HUANG *et al.*, 2004a, 2004b, 2014; MA *et al.*, 2014). Recently, 4 palaeoscolecidans that differ from priapulids (ZHURAVLEV *et al.*, 2011) and one corynetiid were reported from the Guanshan fossil Lagerstätte (Cambrian Stage 4, Series 2) from East Yunnan, SW China (HU *et al.*, 2012). Total-group scalidophorans also occur in Sirius Passet Lagerstätte (Cambrian Series 2, Stage 3) (PEEL, 2017). The discovery of possible priapulid in the lower Cambrian of Estonia (Baltica) indicates that these worms had wider paleobiogeographic distribution in the early Cambrian than previously known. The similarity of the Estonian specimen to the Chinese species suggests that there may have been some faunal exchange between the remote continents of Baltica and south China. On the other hand, the larval stages of modern priapulids are not swimming. They are loricate larvae (VANNIER, 2024). Thus, the larval stage was likely not the primary mode of dispersal for priapulid worms.

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