

Discussion on the systematic position of the Early Cambrian priapulomorph worms

HUANG Diying¹, CHEN Junyuan¹ & J. VANNIER²

Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China;

Université Claude Bernard Lyon 1, UFR Sciences de la Terre, UMR 5125 PEPS, Paléoenvironnements & Paléobiosphère, 69622 Villeurbanne, France

Correspondence should be addressed to Huang Diying (email: huangdiy@163.com)

Priapulid worms form a small marine phylum in present-day environments with only 18 described species, but they were the most abundant animals in the endobenthic communities of the Cambrian. They are particularly well represented in the Lower Cambrian Maotianshan Shale of China [1–3] and the Middle Cambrian Burgess Shale of Canada [4]. The priapulid worms from the 530 Ma old Maotianshan Shale may be placed within 6 basic groups: selkirkiid, corynetid, anningid, palaeoscolecidan, tylotitid and priapuliid [5]. In addition, another important endobenthic worm phylum, the Sipuncula has been also reported from the Maotianshan Shale [6].

Several studying results of priapulids from the Lower Cambrian Maotianshan Shale have been recently published. Some described species have been revised in detail and some new taxa erected. Han *et al.* described a new palaeoscolecidan worm from the Maotianshan Shale namely *Tabelliscolex* [7]. Huang *et al.* [8] revised *Xiaoheiqingella* and described a new genus *Yunnanpriapululus* that was placed in the Recent family Priapulidae. Huang *et al.* [9] revised *Corynetis* and described a new genus *Anningvermis* (with studies on the functional morphology), and two extinct priapulid families, namely the Corynetidae and the Anningidae erected. Dong *et al.* [10] reported the direct development of the worm *Makuelia hunanensis* from the Middle Cambrian of Hunan Province. This study

gives important information on the early evolutionary stages of palaeoscolecidans probably. Han *et al.* [11] recently discussed the ancestry of Priapulomorpha (Priapulidae+Tubiluchidae) in the Early Cambrian.

This paper provides new information on the Early Cambrian diversity and evolution of Priapulidae. It is based on morphological and behavioural studies of living priapulids and on the study of new fossil material. We suggest that the double-tailed priapulid *Paratubiluchus bicaudatus* (Han *et al.*, 2004) belongs to the Priapulidae and has no close relationship with Tubiluchidae.

1 Morphological comparison of *Xiaoheiqingella* and its related taxa

Xiaoheiqingella peculiaris was first assigned to the extinct family Xiaoheiqingidae¹. Huang *et al.* [8] revised *X. peculiaris* and erected a new genus and species *Yunnanpriapululus halteroformis*. *Xiaoheiqingella* and *Yunnanpriapululus* are assigned to the Recent family Priapulidae thus suggesting that the ancestors of this important family existed in the Early Cambrian already (evolutionary stasis).

Han *et al.* [11] discussed the morphology and relationship of *X. peculiaris* and *Y. halteroformis* on the basis of abundant new material from the localities near Haikou. They suggested that *X. peculiaris* was armed with a pair of caudal appendages. Their specimens ((Fig. 1 (e) and Fig. 2 (a), (b)) shows paired broad and smooth leaf-shaped caudal appendages with a tapering shape whereas other known *X. peculiaris* possess only one elongate caudal appendage [8, 12] (Fig. 1 (f)). Han *et al.* [11] attribute this difference to preservation. The elongate caudal appendage of *X. peculiaris* differs from a broad tail (near the width of the trunk) with a tapering shape from Han's material even comparing with single caudal appendages. The slightly swollen posterior trunk with papillae rings present in the double-tailed "*Xiaoheiqingella*" also differs from that of *X. peculiaris*, which is covered with only annulations (posterior trunk). In addition, Han *et al.* made no mention of any circumoral scalds in their specimens [11] although this structure is clearly visible in *X. peculiaris* and *Y. halteroformis* [8]. One possibility is that the double-tailed "*Xiaoheiqingella*" is different from other described material. The number of tail appendages (single or a

1) Hu, S. X., Priapulid worms from the Early Cambrian Chengjiang Fauna, eastern Yunnan, China, Master Thesis, Nanjing Institute of Geology and Palaeontology, 2001.

CORRESPONDENCE

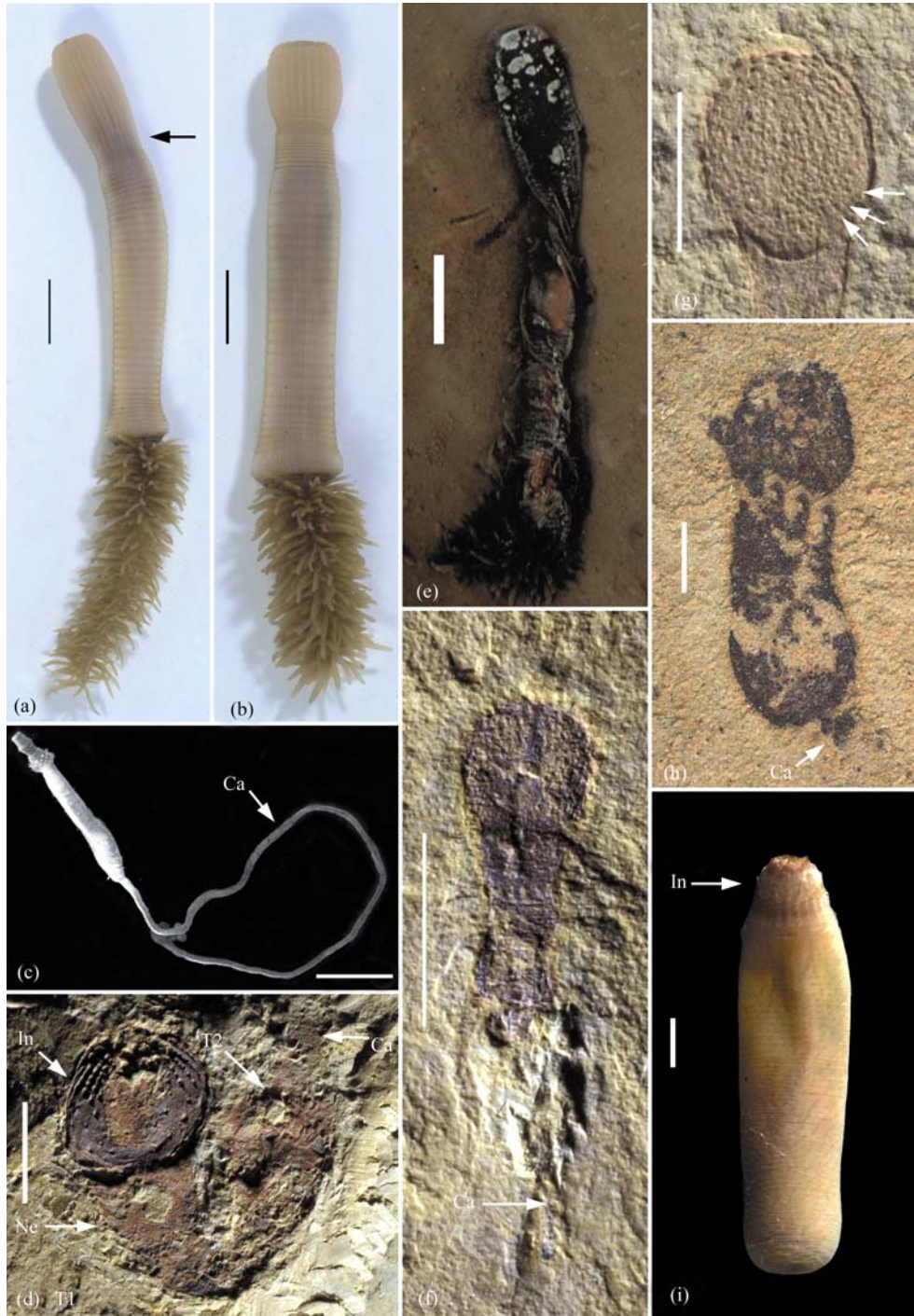


Fig. 1. Early Cambrian and Recent priapulids. (a) Living *Priapulid caudatus*; (b) *P. caudatus* in movement showing contracted anterior trunk and body; (c) Recent *Tubiluchus troglodytes* of Tubiluchidae, showing the general morphology especially a typical slender and elongate caudal appendage (from Todaro M A, Shirley T C, 2003); (d) *Yunnanpriapulid halteriformis* (EC 60382) showing the divisions of body; (e) decayed specimen of *P. caudatus* (ca. one week after death), showing the preserved cuticle (without annulations) and intestine; (f) *Xiaoheiqingella peculiaris* (EC 60302 b) showing a elongate caudal appendage with slightly swollen tip; (g) the details on introvert of holotype of *Y. halteriformis* showing the posterior scalds; (h) the post-larva of *Y. halteriformis* (EC 69500), showing a short caudal appendage; (i) Recent *Halicryptus spinulosus* showing the feature of a conical introvert and no neck. Ca: caudal appendage; In: introvert; Ne: neck; T1: anterior trunk; T2: posterior trunk. Scale bar 1 cm in (a), (b), (e); 2 mm in (d), (f), (g), (i); 500 μ m in (c), (h).

pair) is a generic diagnostic feature in modern priapulids. In present-day Priapulidae, *Priapululus* and *Acanthopriapululus* have a single caudal appendage and *Priapulopsis* has two of them. The double-tailed Recent form *Priapululus atlantisi* mentioned by Han et al. is in fact homologous with *Priapulopsis bicaudatus*^[13]. The double-tailed “*Xiaoheiqingella*” possesses a pair of caudal appendages although these broad and smooth features strongly differ from those of modern forms. We suppose that such leaf-shaped caudal appendages had an original conical shape before post-mortem compaction. However, their function remains unknown.

Han et al.^[11] analysed the morphological differences of *X. peculiaris* and *Y. halteriformis*, but they avoided discussing the most important difference (i.e. the posterior trunk swollen or not; covered with papillae rings or absent)^[8]. Han et al.^[11] attribute these differences to preservation. Some specimens of *Y. halteriformis* display a rather well-defined wider neck area (Fig. 1 (d)) different from the double-tailed “*Xiaoheiqingella*”^[8,11]. Such single short caudal appendage is also present in a new post-larval specimen of *Y. halteriformis* (Fig. 1 (h); posterior trunk with more or less axial compression). In addition, the holotype of *Y. halteriformis* is armed with scattered scalids on its posterior introvert (Fig. 1 (g)).

X. peculiaris, *Y. halteriformis* and the double-tailed “*Xiaoheiqingella*” display morphological differences and that probably indicate 3 different forms within the Early Cambrian Priapulidae. They can be clearly distinguished from their posterior trunk and caudal appendage although their introvert exhibits rather close features. One specimen (EC 60303; Figs. 2(d), 3(b)) of *X. peculiaris* illustrated by Huang et al.^[8] probably relates to double-tailed “*Xiaoheiqingella*”.

In addition, Han et al.^[11] described the possible pre-anal region. We disagree with this interpretation that is not consistent with our knowledge on extant and extinct priapulid worms^[13]. Huang et al. suggested that *Y. halteriformis* had a well-defined neck area (probably specialized from the anterior trunk^[8]). It was misunderstood by Han et al. We consider here that this structure may result from the movement of trunk. The caudal appendages of double-tailed “*Xiaoheiqingella*” resemble the forked posterior structure of the problematic animal *Kinzeria crinita* (Lower Cambrian; Pennsylvania, U.S.A.)^[14]. This finding also provides a clue of the affinity of *K. crinita*.

2 Discussion on the systematic position of *Paratubiluchus bicaudatus*

Paratubiluchus was erected by Han et al. on the basis of a single complete specimen and was assigned to the Recent Tubiluchidae. *Tubiluchus* is the most diverse genus of Priapulida with 7 species. It represents an important body plan among the modern Priapulida^[15–17]. Wills suggested that the Tubiluchidae were a link between Cambrian and Recent priapulids^[18]. The general characteristics of Tubiluchidae are: (1) an swollen introvert with 20–25 rows of scalids; (2) well-defined neck area; (3) a trunk covered with tumuli without annulations; (4) a caudal appendage smooth and slender; (5) pharyngeal teeth pectinate, arranged quincunxially without distinct circles^[15, 17, 19, 20]. Han et al. described *Paratubiluchus bicaudatus* as follows: introvert with 25 scalid rows, neck area wide, oval shaped trunk without annulations, pair of short caudal appendages^[11]. They suggested that *P. bicaudatus* is a link between Recent loricate priapulid larvae and adult priapulids^[11].

Some authors suggested that the priapulid larva-like animal *Sicyophorus* was a priapulid^[11, 21]. *Sicyophorus* has a lorica with longitudinal ridges that resembles Recent priapulid larvae especially those of Tubiluchidae (e.g. lorica rather rounded in cross-section)^[17,22,23]. Adults of *Sicyophorus* can reach up to 2.5 cm long (usually nearly 1 cm long). They are distinctly larger than the modern priapulid larvae (less than 2 mm)^[13, 23]. Therefore, *Sicyophorus* is not a priapulid larva. It is also remarkably different from all extant and extinct adult priapulids. Thus, the position of *Sicyophorus* remains questionable. Loricifera is a small phylum with a body plan comparable to that of priapulid larvae^[24–26]. Warwick suggested that loriciferans were paedomorphic priapulids^[27] (adult loriciferans 50–485 µm long^[28]) but most authors consider it as a proper phylum or related to isolated taxa^[24–26, 28–30]. Our hypothesis is that perhaps, macrobenthic loriciferans originated from priapulid larvae via paedomorphic processes in the course of evolution. *Sicyophorus* and its related taxa were possibly the earliest representatives of Loricifera. The morphological adaptations which characterize modern loriciferans most probably appeared after the Cambrian¹⁾.

The present paper analyzed and compared the mor-

1) Huang, D. Y., Early Cambrian worms from SW China: morphology, systematics, lifestyles and evolutionary significance, University of Lyon, Ph. D thesis, 2005.

CORRESPONDENCE

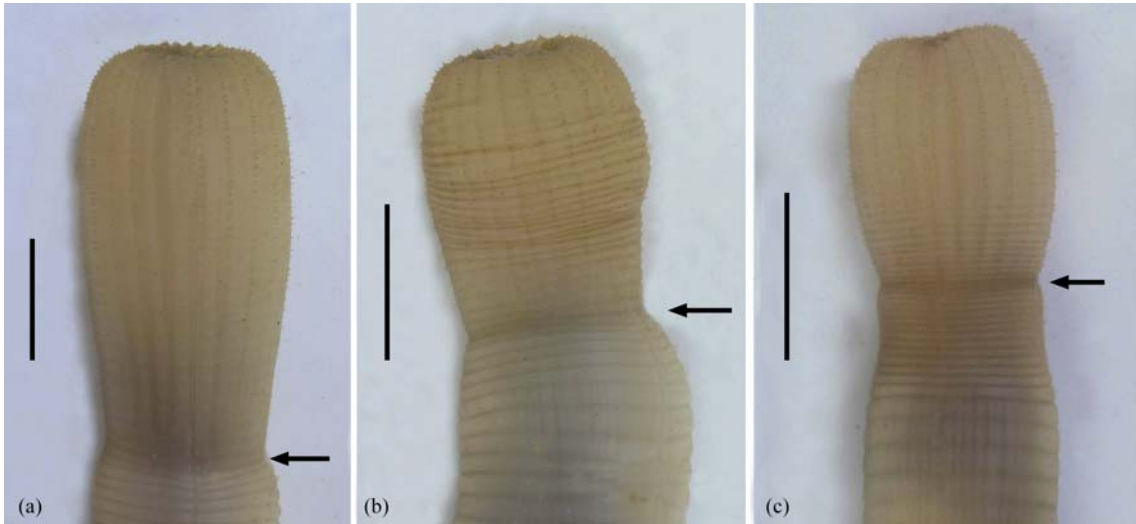


Fig. 2. *Priapululus caudatus* showing the contraction of its introvert and its anterior trunk. (a) Normal situation of introvert; (b) contraction of introvert, showing the ring-like wrinkles in the formerly non-annulated area; (c) contraction of anterior trunk. Arrows showing the neck constriction. Scale bar is 1 cm.



Fig. 3. Comparisons between the new form of the Early Cambrian Priapulidae, *Paratubiluchus bicaudatus* and the Recent *Priapululus caudatus*. (a) New form of Priapulidae from the Maotianshan Shale, showing the paired caudal appendages (black arrows); (b) general morphology of the new form, showing that the neck area (black arrows) is a constriction and the anterior trunk is tapering forwards; (c) holotype of *P. bicaudatus* showing the so-called well-defined neck area [11]; (d) *P. caudatus* in movement, showing a contracted anterior trunk area. Scale bar is 5 mm.

phologies of *P. bicaudatus* with Tubiluchidae as follows:

General shape: All tubiluchids are meiofaunal with interstitial habits.

They live in relatively warm and well-oxygenated environments. Their body (excluding caudal appendage)

is ca. 2 mm long and bears a very elongate smooth tube-like caudal appendage (several times the body length; see Fig. 1 (c)) [17,31]. The size of *P. bicaudatus* (nearly 1 cm long; excluding caudal appendages) was close to other Cambrian forms of Priapulidae [8]. The macrobenthic worm *P. bicaudatus* was a burrower. The

size is one of characters for identifying priapulid families^[15, 16]. The different adaptations of meiofaunal and macrobenthic priapulids are responsible for their morphological differences. The trunk of *P. bicaudatus* (from reference [11] (Fig. 3 (a), (c)) has a short cone shape that resembles some Recent Priapulidae such as *Priapulus caudatus* (Fig. 3 (d)). The trunk of Tubiluchidae is rather elongate and clearly differs from that of *P. bicaudatus*. The relatively short trunk of *P. bicaudatus* is probably a preservational artifact. We do not think “oval-shaped”^[11] is an exact word for describing this worm.

Neck: The so-called neck area of *P. bicaudatus* is considered as a natural well-defined constriction. It is one important character for *P. bicaudatus* assigning to Tubiluchidae^[11]. *P. caudatus* uses the evertion of its introvert and the retraction of its trunk for moving on and through the sediment. Sometimes, the anterior end of the trunk contracts that creating a relatively well-defined area with denser annulations. At the same time, the length of trunk also contracts during this motion (Fig. 1 (a), (b)). This situation is very similar to the attitude of *P. bicaudatus* (Fig. 2 (c); Fig. 3 (d)). The “neck” of *P. bicaudatus* is armed with transverse wrinkles and small warts^[11]. Similar irregularly ring-like wrinkles are also present along the introvert of living *P. caudatus* (no annulations in normal situation) when moving (Fig. 2 (a), (b)). Perhaps, such wrinkles of *P. bicaudatus* play also a role in burrowing or crawling. Such warts are also visible on both the neck and trunk^[11]. Thus, we suppose that the holotype represents an animal which was buried alive. Its so-called defined neck is a contracted area of anterior trunk. The neck of *P. bicaudatus* in fact is only a constriction between the introvert and the trunk.

Trunk annulations: No visible annulations are present on the trunk of *P. bicaudatus*^[11]. This character is found also in a new priapulid worm from the Maotianshan Shale. However, very weak annulations of new form are visible after careful observation. This new form is characterized by: (1) a swollen oval-shaped introvert; (2) an introvert armed with a circle of rather elongate circumoral scalids, 25 rows of anterior scalids, posterior larger scatter scalids; (3) a neck area as a constriction; (4) a rather short trunk armed with weak annulations; (5) a posterior section with ca. 5 circles of papillae; (6) a pair of elongate and smooth caudal appendages (Fig. 3 (a), (b)). This worm can be firmly placed within the Priapulidae (Huang et al., detailed

description and discussion in preparation). Its general features are comparable with those of *P. bicaudatus*, especially the trunk without distinct annulations. However, the posterior introvert of the new form is covered with larger scalids and its posterior trunk is armed with papillae rings and bears a pair of longer caudal appendages. The neck of the new form is represented by a constriction, but the anterior trunk displays a slight tapering shape (Fig. 3 (b)). The cuticular annulations of *P. caudatus* do correspond with internal ring muscles (observations and dissections of living specimens). The cuticle and the intestine seem to be more decay-resistant than the other parts of the animal (without distinct annulations, ca. one week; see Fig. 1 (e)). Thus, the poorly developed annulations of *P. bicaudatus* and the new form indicate that the underlying muscle system was relatively weakly developed. A possible implication of that is a relatively low mobility. We suppose that the trunk was similarly playing an important role in the locomotion of the Early Cambrian priapulids. This hypothesis is supported by the fact that these worms had probably no eversible introvert at that stage of their evolution. The meiofaunal tubiluchids are found in/on subtidal sand, muddy bottoms and subtidal stromatolite^[32, 33]. Some characters of Tubiluchidae (e.g. poorly developed annulations and pharynx with no distinct circles) are specialized (adaptation to interstitial habits). Other meiofaunal priapulids such as *Meiopriapulus* and *Maccabeus* have atypical annulations. Thus, the annulations indicate moving abilities and have no important value in systematics for macrobenthic burrowers.

Caudal appendage: *P. bicaudatus* has a pair of short caudal appendages^[11] that differ from the typical slender and elongate tail of Tubiluchidae^[13, 17, 22, 31]. In addition, the grayish band-like structure of the caudal appendages of *P. bicaudatus* has been interpreted as possible retractor muscles^[11]. We suggest that this structure merely represents the cavities of the caudal appendages due to no comparable muscle system in the tails of Recent priapulids^[13].

P. bicaudatus differs markedly from the tubiluchids by its size and shape, and by the morphology of its caudal appendage. Morphological evidence supports the placement of *P. bicaudatus* within the Priapulidae rather than within the Tubiluchidae. The hypothesis according which Tubiluchidae would have undergone no major changes in morphology over the past 530 Ma^[11] is not strongly supported because *P. bicaudatus* may be

CORRESPONDENCE

placed in Priapulidae and display remarkably morphological differences with Tubiluchidae.

In addition, Han et al.^[11] described an unnamed form A, which they compare with *Paratubiluchus*. However, its interpreted neck area is in fact corresponds to the median portion of the trunk. Form A has no distinguishable neck area. This new form is distinctly different from Priapulomorpha but resembles Recent *Halicryptus* (Priapulida; see Fig. 1 (i)) in outline.

3 Evolutionary significance of the Early Cambrian double-tailed priapulids

The priapulids from the Middle Cambrian Burgess Shale fauna^[4,34] and the Kaili fauna^[35] have so far not yielded a priapulid with a paired caudal appendage. *Priapulites konecniorum* (Priapulidae) from the Late Carboniferous Mazon Creek fauna was first described with two tails^[36], then considered as a monocaudal worm^[4] or occurred a few monocaudal specimens^[37]. The present authors (DYH and JV) re-observed the holotype and a few other specimens of *P. konecniorum*. We believe that it is a very advanced form resembling modern Priapulidae.

The rather smooth caudal appendages formed by equal branches probably represents a primitive feature for bicaudal priapulids. This conclusion is supported by our discussions on the Early Cambrian priapulids. We agree with Adrianov and Malakhov^[15] on that monocaudal priapulids are more primitive than bicaudal forms, although both mono- and bi-tailed priapulids co-occurred in the Early Cambrian. This hypothesis is also supported by other extinct and extant families such as Anningidae (one caudal appendage)^[9] and Tubiluchidae^[13,15]. In addition, Han et al. suggested that the paired caudal appendages are probably homologous with the paired posterior papillae of *Maccabeus* and *Halicryptus*^[15, 38, 39]. However, this opinion seems to lack strong support.

The Early Cambrian priapulids are highly diverse with 11 priapulid genera and species described to date^[5]. Among them, *Tylotites petiolaris* is firstly described as a lobopodian^[2]. Han et al. assigned it to Introverta (uncertain position) after the discovery of its pharynx^[40]. Recent studies indicates that *Tylotites* is a typical priapulid with pentagonally arranged pharyngeal teeth. The discovery of Early Cambrian double-tailed pri-

apulids has deep implications on the early evolution of Priapulida and particularly that of Priapulidae. It indicates that the ancestries of Priapulidae can be traced back to the Cambrian Explosion with a remarkable evolutionary stasis over the last more than half a billion years. These Cambrian forms differ from modern ones by the scald distribution of their introvert (e.g. scalds present only on anterior introvert in the Early Cambrian forms; scalds present on whole introvert in Recent forms) and caudal appendage(s) (e.g. rather smooth in the Early Cambrian forms; covered with various ornaments in the Recent forms). Recent studies of the Lower Cambrian trace fossils, *Trichophycus pedum*, indicate that the origin of priapulid worms (even Priapulidae) can be traced back to the Precambrian-Cambrian boundary¹⁾.

Acknowledgements Huang Diying is grateful to Dr. Hu Shixue from Yunnan Institute of Geological Sciences for his re-observing the holotype of *Xiaoheiqingella peculiaris* and to Dr. Han Jian from Northwest University for helpful discussions. Huang Diying and J. Vannier would like to acknowledge the Kristineberg Marine Research Station (Sweden) for support our study of Recent priapulids and the Muséum National d'Histoire Naturelle for providing us with our comparable recent priapulid material of *Halicryptus spinulosus*. We thank M. N. Podelvigne for photography (Université Claude Bernard Lyon 1). This work was supported by the National Natural Science Foundation of China (Grants Nos. 40302004, 40432006), Chinese Academy of Sciences (Grant No. KZCX3-SW-141), and the Ministry of Science and Technology of China (Grant No. 200077700).

References

1. Chen, J. Y., Zhou, G. Q., Biology of the Chengjiang fauna, Bulletin of the National Museum of Natural Science, 1997, 10: 11—106.
2. Luo, H. L., Hu, S. X., Chen, L. Z. et al., Early Cambrian Chengjiang Fauna from Kunming Region, China (in Chinese with English-summary), Kunming: Yunnan Science and Technology Press, 1999, 129.
3. Hou, X. G., Aldridge, R., Bergström, J. et al., The Cambrian Fossils of Chengjiang, China: the Flowering of Early Animal Life, Oxford: Blackwell Science Ltd., 2003, 1—233.
4. Conway Morris, S., Fossil priapulid worms, Special Papers in Palaeontology, No. 20, 1977, 1—95.
5. Huang, D. Y., Chen, J. Y., Vannier, J., Diversity of the Early Cambrian priapulid worms, in Proceedings of 19th International Congress of Zoology, 2004, 26.
6. Huang, D. Y., Chen, J. Y., Vannier, J. et al., Early Cambrian sipunculan worms from southwest China, Proceedings of the Royal Society of London B, 2004, 271: 1671—1676.[\[DOI\]](#)

1) Huang, D. Y., Zhu, M. Y., Vannier, J. et al. Priapulid worms are the possibly trace makers of the Early Cambrian *Trichophycus pedum*: Experiment on the burrowing behaviour of living *Priapulid caudatus*, in Sino-German Symposium Environmental and Biological Processes of the Cambrian Explosion, 2004, 37—38.

7. Han, J., Zhang, X. L., Zhang, Z. F. et al., A new platy-armored worm from the Cambrian Chengjiang Lagerstätte, South China, *Acta Geologica Sinica*, 2003, 77 (1): 1—6.
8. Huang, D. Y., Vannier, J., Chen, J. Y., Recent Priapulidae and their Early Cambrian ancestors: comparisons and evolutionary significance, *Geobios*, 2004, 37: 217—228. [\[DOI\]](#)
9. Huang, D. Y., Vannier, J., Chen, J. Y., Anatomy and lifestyles of Early Cambrian priapulid worms exemplified by *Corynetis* and *Anningvermis* from the Maotianshan Shale (SW China), *Lethaia*, 2004, 37: 21—33. [\[DOI\]](#)
10. Dong, X. P., Donoghue, P. C. J., Cheng, H. et al., Fossil embryos from the Middle and Late Cambrian period of Hunan, South China, *Nature*, 2004, 427: 237—240. [\[DOI\]](#)
11. Han, J., Shu, D. G., Zhang, Z. F. et al., The earliest-known ancestors of recent Priapulomorpha from the Early Cambrian Chengjiang Lagerstätte, *Chinese Science Bulletin*, 2004, 49 (17): 1860—1868.
12. Chen, L. Z., Luo, H. L., Hu, S. X. et al., Early Cambrian Chengjiang fauna in Eastern Yunnan (in Chinese with English summary), Kunming: Yunnan Science and Technology Press, 2002, 1—199.
13. Land, J. van der., Systematics, zoogeography, and ecology of the Priapulida, *Zool. Verh., Leiden*, 1970, 112: 1—118.
14. Capdevila, D. G-B., Conway Morris, S., New fossil worms from the Lower Cambrian of the Kinzers Formation, Pennsylvania, with some comments on Burgess Shale-type preservation, *J. Paleont.*, 1999, 73: 394—402.
15. Adrianov, A. V., Malakhov, V. V., The phylogeny, classification and zoogeography of the class Priapulida. I. Phylogeny and classification, *Zoosyst. Rossica*, 1996, 4: 219—238.
16. Adrianov, A. V., Malakhov, V. V., Priapulida: Structure, Development, Phylogeny and Classification (in Russian with English summary), Moscow: KMK Scientific Press, 1996, 1—268.
17. Todaro, M. A., Shirley, T. C., A new meiobenthic priapulid (Priapulida, Tubiluchidae) from a mediterranean submarine cave, *Ital. J. Zool.*, 2003, 70: 79—87.
18. Wills, M. A., Cambrian and recent disparity: The picture from priapulids, *Paleobiology*, 1998, 24: 177—199.
19. Calloway, C. B., Morphology of the introvert and associated structures of the priapulid *Tubiluchus corallicola* from Bermuda, *Marine Biology*, 1975, 31: 161—174. [\[DOI\]](#)
20. Adrianov, A. V., Malakhov, V. V., Symmetry of priapulids (Priapulida). I. Symmetry of adults. *Journal of Morphology*, 2001, 247: 99—110. [\[DOI\]](#)
21. Hou, X. G., Bergström, J., Wang, H. F. et al., The Chengjiang Fauna — Exceptionally Well-preserved Animals from 530 Million Years Ago (in Chinese with English summary), Kunming: Yunnan Science and Technology Press, 1999, 1—170.
22. Kirsteure, E., Note on adult morphology and larval development of *Tubiluchus corallicola* (Priapulida), based on in vivo and scanning electron microscopic examinations of specimens from Bermuda, *Zoologica Scripta*, 1976, 5: 239—255.
23. Higgins, R. P., Storch, V., Evidence for direct development in *Meiopriapululus fijiensis* (Priapulida), *Trans. Am. Microsc. Soc.*, 1991, 110: 37—46.
24. Kristensen, R. M., Loricifera, a new phylum with aschelminthes characters from the meiobenthic, *Z. Zool. Syst. Evolut.-forsch.*, 1983, 21: 163—180.
25. Higgins, R. P., Kristensen, R. M., New Loricifera from southeastern United States coastal waters, *Smithson. Contr. Zool.*, 1988, 438: 1—70.
26. Brasca, R. C., Brusca, G. J., *Invertebrates*, Sinauer, Sunderland, Massachusetts, 1990, 1—922.
27. Warwick, R. M., Are loriciferans pedomorphic (progenetic) priapulids? *Vie. Et. Milieu.*, 2000, 50: 191—193.
28. Kristensen, R. M., Brooke, S., Phylum Loricifera, in *Atlas of Marine Invertebrate Larvae* (eds. Young, C. M., Sewell, M. A., Eice, M. E.), London: Academic Press, 2002, 179—187.
29. Adrianov, A. V., Malakhov, V. V., The phylogeny and classification of the phylum Cephalorhyncha, *Zoosyst. Rossica*, 1995, 3: 181—201.
30. Adrianov, A. V., Malakhov, V. V., *Cephalorhyncha of the World Ocean* (in Russian with English summary), Moscow: KMK Scientific Press, 1999, 1—400.
31. Land, J. van der., A new aschelminth, probably related to the Priapulida, *Zoologische Mededelingen*, 1968, 42: 237—250.
32. Kirsteure, E., Land, J. van der., Some notes on *Tubiluchus corallicola* (Priapulida) from Barbados, West Indies, *Marine Biology*, 1970, 7: 230—238. [\[DOI\]](#)
33. Kirsteure, E., Rützler, K., Additional notes on *Tubiluchus corallicola* (Priapulida), based on scanning electron microscope observations, *Marine Biology*, 1973, 20: 78—87. [\[DOI\]](#)
34. Briggs, D. E. G., Erwin, D. H., Collier, F. J., *The Fossils of the Burgess Shale*, Washington: Smithsonian Institution Press, 1994, 114—125.
35. Zhao, Y. L., Yang, R. D., Yuan, J. L. et al., Cambrian stratigraphy at Balang, Guizhou Province, China: candidate section for a global unnamed series and stratotype section for the Taijiangan stage, *Palaeoworld*, 2001, 13: 189—208.
36. Schram, F. R., Pseudocoelomates and a nemertine from the Illinois Pennsylvanian, *J. Paleont.*, 1973, 47: 985—989.
37. Fitzhugh, K., Sroka, S. D., Nonannelid worms. In: *The Fossil Fauna of Mazon Creek* (eds. Shabica, C. W., Hay, A. A.), Illinois: Northeastern Illinois University Press, 1997, 84—88.
38. Por, F. D., Bromley, H. J., Morphology and anatomy of *Maccabeus tentaculatus* (Priapulida: Seticoronaria), *J. Zool., Lond.*, 1974, 173: 173—197.
39. Shirley, T. C., Storch, V., *Halicryptus higginsi* n. sp. (Priapulida), a giant new species from Barrow, Alaska, *Invertebrate Biology*, 1999, 118: 404—413.
40. Han, J., Zhang, Z. F., Shu, D. G., Discovery of the proboscis on *Tyrolites petiolaris*, *Northwestern Geology* (in Chinese), 2003, 36 (1): 87—92.

(Received March 4, 2005; accepted June 13, 2005)