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The earliest-known ancestors of Recent Priapulomorpha from the Early Cambrian Chengjiang Lagerstätte

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Abstract **The taxonomy of an early ancestor of Recent Priapulidae, *Xiaoheiqingella peculiaris* (= *Yunnanpriapulus halteroformis* Huang et al., 2004) from the Early Cambrian Chengjiang fossil Lagerstätte, is revised. Morphological characters comprise a pair of caudal appendages rather than a single appendage flanking the trunk end and a possible urogenital duct found inside the preanal region. An additional extremely rare fossil priapulid worm, *Paratubiluchus bicaudatus* gen. nov., sp. nov. is also described herein. Its diagnostic characters are: an introvert bearing 25 longitudinal rows of scalids, a distinct neck region, no annulus on the oval trunk, and a pair of caudal appendages. The proportion of body parts is similar in size to that of loricate larvae of Recent priapulids and larva-formed Palaeopriapulitidae. Taking account of the features of *Xiaoheiqingella*, bicaudal appendages are considered to be a synapomorphy of Priapulidae and Tubiluchidae. *Paratubiluchus* gen. nov. is most likely a candidate for the ancestor of the Tubiluchidae; it probably originated from a larva-formed priapulid with 25 rows of scalids, thus representing an intermediate link between the priapulids in mature-form and the priapulids with lorica.**

Keywords: Early Cambrian, Chengjiang Lagerstätte, priapulids, *Xiaoheiqingella, Paratubiluchus*.

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It was suggested and eventually has been proffered that the representatives of all extant phyla, including some minor group, occurred during the Cambrian radiations[1—10]. Many priapulid-like fossil worms have been reported from Cambrian Lagerstätten, such as the Early Cambrian Chengjiang Lagerstätte[11—16], the Middle Cambrian Burgess Shale[17], and the Middle Cambrian Kaili fauna[18]. The palaeoscolecidan worms from these Lagerstätten have been regarded as either a stem group of the priapulids[19] or nematoiids[20,21]. The Middle Pennsylvanian priapulid worm *Priapulites konecniorum*, showing striking similarities to Recent priapulids, has been regarded as one of the ancestors of living priapulids[22]. The monocaudal or bicaudal nature of the caudal appendage, however, is still obscure[17]. The recent finding of the earliest-known ancestor of the priapulids from the Chengjiang deposits, *Xiaoheiqingella peculiaris*[12], has bridged the 530 Ma temporal gap between fossil taxa and Recent priapulids. However, the introvert of *Xiaoheiqingella* was originally described as bearing 16 longitudinal rows of scalids, and was recently revised to have 25 rows[23]. *Yunnanpriapulus halteroformis*[23], which strikingly resembles *Xiaoheiqingella*, is taken as further evidence to clarify the evolutionary trend of the priapulids, and is possibly a junior synonym of *Xiaoheiqingella* based on examination of our collections from the localities near that of the holotype. Two additional worms, *Paratubiluchus bicaudatus* gen. nov., sp. nov. and form A, known from rare material, are reported herein. For the latter it is premature to use a formal taxonomy because the feature of its proboscis is not distinctive. They share the feature that the proportion of their body components is similar to that of loricate larvae of Recent priapulids and the fossil family Palaeopriapulitidae, which contains *Sicyophorus rara* Hu[12], *Palaeopriapulites parvus*[11] and *Palaeopriapulites* sp.[18], thereby providing new insights into the deep history of priapulids.

1 Materials and preservation

Totally 50 specimens are recognized and 13 of them (Eli-0001250—0001262) are described in this paper. All these specimens were collected from the Jianshan and Yunlongsi sections, which are about 1km to the east and 3 km, respectively, to the west of the famous Ercaicun section, Haikou City, Kunming City, Yunnan Province, China[16,24]. All specimens are deposited at the Early Life Institute, Northwest University, Xi'an, China.

Most of the surface area of *Paratubiluchus* gen. nov. is grayish white in color, and looks somewhat transparent whereas the pharynx and the scalids are preserved in reddish brown. It seems that the scalids and the neck folds are darker in color than other parts of the body of form A. It can be concluded that thick cuticles display darker color. The trunk of *Xiaoheiqingella* is darker than that of *Paratubiluchus* gen. nov. and form A on account of their fine annuli. The same is true when the caudal appendages of *Xiaoheiqingella* are compared with the trunk. The color of these priapulid worms appears lighter than that of the palaeoscolecidans which are usually preserved in reddish brown or dark brown in Chengjiang Lagersttäte. Therefore, this allows us to speculate that fossil priapulids might have had a thinner cuticle than those of palaeoscolecidans.

Structures such as the nerve cord (only two specimens, Pl. 12, Figs. 2—5; Text Figs. 61 and 62 in ref. [17]), muscles and gonads are well recognized in the specimens of *Ottoia prolifica* from the Middle Cambrian Burgess Shale[17]. In the Chengjiang Lagerstätte, gonads and nerve cord were known only from the yunnanozoons[5,6]. The ventral nerve cord was recently reported in a single specimen of priapulid[23]. We further present in this paper a specimen (Eli-0001252) with possible urogenital duct and three additional specimens (Eli-0001257, Eli-0001259, Eli-0001260) with distinct nerve cords to confirm the original findings[23]. All these suggest that the preservational quality of the Chengjiang fossils is on a par with the Burgess Shale fossils.

2 Systematic palaeontology

Phylum Priapulida Delage et Herouard, 1897.
Order Priapulomorpha Salvini-Plawen, 1974.
Family Priapulidae Gosse, 1855.
Genus *Xiaoheiqingella* Hu, 2002.

Emended diagnosis. Cylindrical and extensible body, divisible into four sections, i.e. an anterior proboscis, a constricted neck, a finely annulated trunk and a pair of long caudal appendages. A swollen introvert with 25 longitudinal ridges and bearing 25 longitudinal rows of scalids, anterior seven scalids standing on each ridge while the last two being located on the posterior introvert without ridges. Posterior part of the trunk with 14 circles of ring papillae. Two long caudal appendages devoid of any ornament.

Type species. *Xiaoheiqingella peculiaris* Hu, 2002.

Age and distribution. Qiongzhusi Stage, Early Cambrian; eastern Yunnan, China.

Xiaoheiqingella peculiaris Hu, 2002 (Figs.1 and 2).

Diagnosis. As the genus.

Description. The body consists of a proboscis, a neck, an annulated trunk, and a pair of caudal appendages. Despite of morphological variability, the ratio of the axial length between the proboscis and trunk ranges from 1:3 to 1:4.

The proboscis is subdivided into the introvert, collar, and pharynx from the posterior to the anterior. The introvert is pear-shaped and reaches the maximal width in its posterior half. Up to 25 longitudinal parallel ridges and 25 longitudinal rows of scalids are clearly recognized on the anterior half of the introvert (Fig. 1(a)—(g); Fig. 2(a), (b), (e) and (g)). The anterior seven of the nine scalids on each ridge are evenly aligned, whereas the remaining two scalids are positioned on the posterior half of the introvert and do not stand on the ridges, with their intervals being apparently wider than those between the anterior seven scalids. The collar is armless and tapers rapidly forward (Fig. 1(f)). Similar to the living priapulids, the eversible pharynx often stays within the introvert cavity in its rest status, but infrequently appearing as a short protrusion at the anterior-most of the proboscis during eversion[25]. Its surface is densely armed with diagonally- or quincunxially-arranged spine-like teeth (Figs. 1(b) and 2(f)); at least five teeth can be recognized in each oblique row on one face of the specimen (Figs. 1(b) and 2(f)).

The neck appears as a constriction and displays as a boundary between the trunk and the introvert (Figs. 1(c), 1(d) and 2(g)). The portion described as "neck area with fine annuli"[23], should be regarded as the anterior trunk rather than a neck. The remaining part of the trunk is also finely annulated whereas the posterior bulge of the trunk, referred to here as the preanal region, generally is larger than the rest of the trunk but never exceeds the introvert in diameter in general. The preanal region is armed with ca. 14 circles of spine-like ring papillae. Each circle consists of up to 16—20 (Figs. 1(c), 2(a), 2(b), 2(d), 2(h), and 2(j)). Ring papillae in anterior circles are most prominent and arranged alternatively. The inflated preanal region and their ring papillae could have functioned to increase the friction against the sediment in the process of burrowing. The gonads and the urogenital ducts in living priapulids are bilaterally symmetrically located at the posterior end of the trunk[25], so swelling of the preanal region in *Xiaoheiqingella* may be suggestive of accommodation to these organs.

A pair of long caudal appendages is discernible bilaterally joining to the posterior end of trunk (Figs. 1(d), 1(e), 1(g), 1(h), 2(a), 2(b), 2(h), 2(d) and 2(j)), and have been compressed into different bedding planes or flattened on a single bedding plane. In the former case, only one caudal appendage associated with main part of the body is frequently exposed when the slab is opened, as seen in the holotype of *Xiaoheiqingella*[9]. Since the anterior end of the caudal appendage is not connected to the axial end of the trunk, thus the other appendage is predicted to be buried on a bedding plane deeper or above, and indeed might be exposed by careful preparation. In the latter case, two caudal appendages occur on the same bedding plane and look like a whole one. Its diameter, however, is almost equivalent to or even larger than the trunk. Together with the longitudinal line recognized through the center of the caudal appendage, it follows that it consists of two separated parts and an artifact of a whole one is produced by overlapping of the two caudal appendages (Fig. 1(h)). The cuticle of the caudal appendages is smooth-skinned and devoid of any ornament (Fig. 2(b)).

Probably due to contraction of the muscles and associated flowing of the coelomic liquid, the shapes of body parts vary significantly. For example, the introvert can be shrunk to a width equal to that of the trunk, or even be inflated to reach twice as wide as the trunk; the middle portion of the trunk can be dilated slightly, but restricted locally, thus the outline of the trunk does not appear ovum-shaped. The preanal region sometimes becomes smaller than other portions of the trunk. The caudal appendages are also stretchable and contractile.

Similar to *S. rara* and larva of *Tubiluchus corallicola*[26], the gut of *Xiaoheiqingella* appears as a narrow dark, reddish or grayish strip floating free or is slightly looped or coiled in the lumen of the trunk (Figs. 1(f), 2(c),

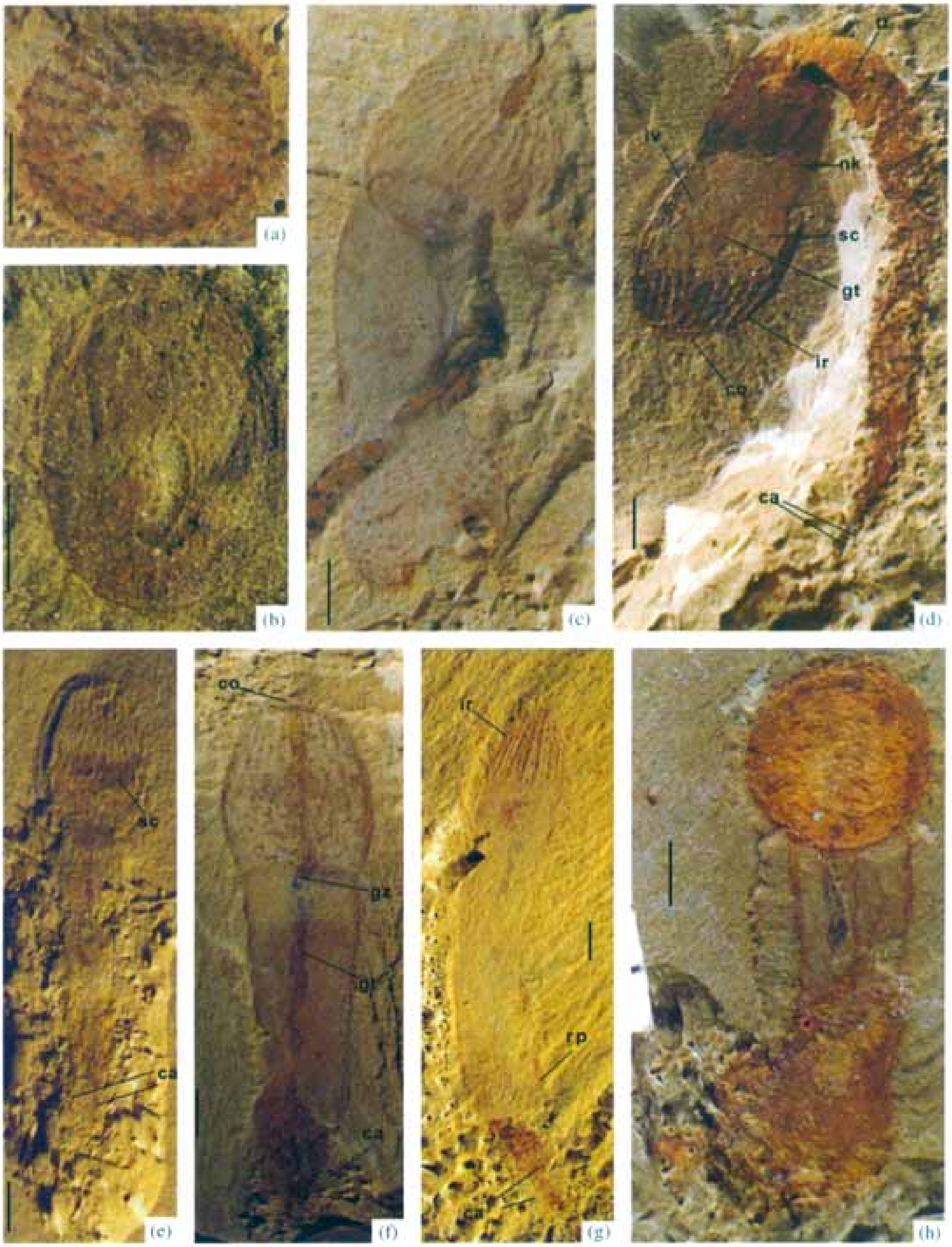

Fig. 1. *Xiaoheiqingella peculiaris* Hu, from Jianshan section, Haikou, Kunming, Yunnan. an = annuli; as = anus; bc = buccal tube; ca = caudal appendages; co = collar; es = esophagus; gc = gut content; gt = gut; gz = gizzard; ir = introvert ridge; iv = introvert; mo = mouth opening; nk = neck; ph = pharynx; pr = preanal region; rp = ring papillae; sc = scalids; tr = trunk; ?ud = ?urogenital duct. Scale bar represents 1 mm. (a) Eli-0001250, the introvert is axially compressed, all scalid rows are visible; (b) Eli-0001251, showing the diagonally-arranged pharynx teeth; (c) Eli-0001252A, showing possible urogenital duct, gizzard and esophagus; the neck looks like a constriction between the introvert and the trunk, the scalid rows and ring papillae are prominent; (d) Eli-0001253, a complete specimen, the body lies across to the bedding plane, the trunk tissue appears to be harder than introvert and the neck, a pair of caudal appendages are rather slender, its bicaudal nature only can be recognized at the distal end; (e) Eli-0001254, showing a pair of caudal appendages; (f) Eli-0001255, showing the gizzard and the collar, the trunk tapers backward; (g) Eli-0001256, almost complete specimen, introvert ridges and the ring papillae are distinct, the caudal appendages are not completely exposed; (h) Eli-0001257, showing the curved gut and the straight nerve cord.

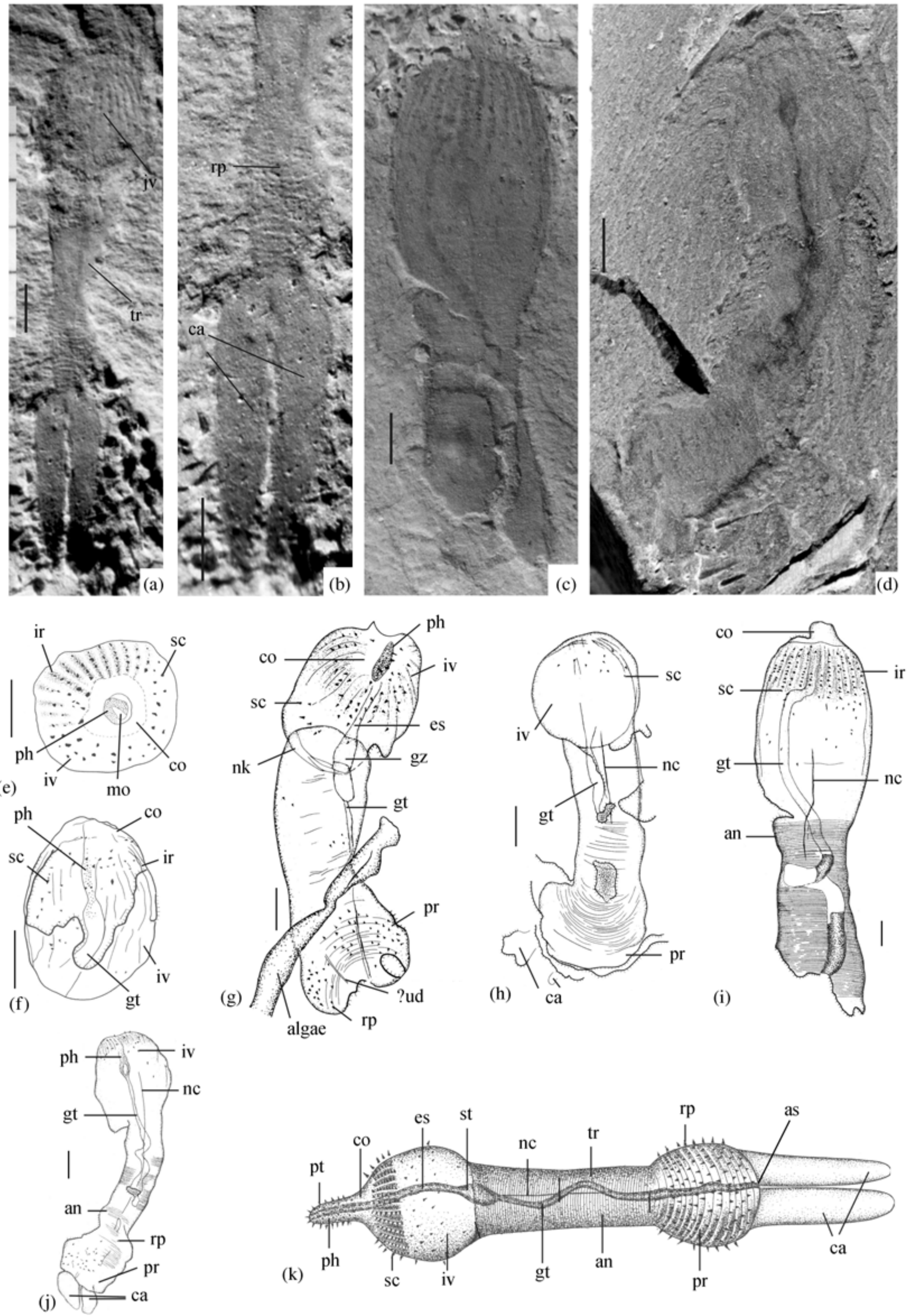

Fig. 2. *Xiaoheiqingella peculiaris* Hu, from Jianshan section, Haikou, Kunming, Yunnan. nc = nerve cord, other abbreviations (see Fig. 1). Scale bar represents 1 mm. (a) Eli-0001258, a complete specimen, showing the introvert, trunk and caudal appendages; (b) Eli-0001258, close-up showing a pair of caudal appendages and the ring papillae; (c) Eli-0001259, showing the curved gut and the straight nerve cord; (d) Eli-0001260, showing the curved gut, the straight nerve cord and a pair of caudal appendages beneath the bedding plane of the trunk; (e)—(j) explanation drawing of Fig. 1(a), 1(b), 1(h), 1(d), 2(c), 2(d) and 2(k) reconstruction of *Xiaoheiqingella peculiaris*.

2(d), 2(i) and 2(j)). The emptied gut is uniform in diameter, except its anterior swelling (Figs. 1(c), 1(f) and 2(g)), referred to here as a gizzard. Thus the short portion between the pharynx and the gizzard should represent an esophagus. The anus opening is located between proximal end of the caudal appendages and the posterior end of the trunk.

The ventral nerve cord is distinguishable by its comparatively fine line-shape and its reddish brown color near to that of the trunk but significantly different from grayish color of the gut. The bending of nerve cord corresponded with the curving of the trunk (Figs. 1(h), 2(c) and 2(d)), it therefore seems to be intra-epidermal like that of Recent priapulids. A short and narrow grayish stripe, visible in the lateral side of the preanal region (Figs. 1(c) and 2(g)), is alternatively interpreted as a urogenital duct or, less possibly, a posterior retractor muscle.

Stratigraphy and locality. Qiongzhusi Formation, Yu'anshan Member (*Eoredlichia* zone), Lower Cambrian. Meishucun section of Jinning, Jianshan section, Ercaicun section and Yulongsi section of Haikou, Kunming.

Comparison and discussion. Huang et al.[23] has argued that the differences between *Xiaoheiqingella* and *Yunnanpriapulus* are (i) the posterior swollen trunk of *Yunnanpriapulus* that bears ring papillae, which are absent in *Xiaoheiqingella*; (ii) the caudal appendage of *Xiaoheiqingella* is rather slender, whereas it is very short in *Yunnanpriapulus*; (iii) the neck area of *Yunnanpriapulus* is well delimited as a constriction between introvert and trunk in *Xiaoheiqingella*. However, there are several contradictions in their argument: at least one scalid is discernible in the posterior introvert of the most complete specimen of *Xiaoheiqingella* (EC60301 in ref. [23], Fig. 2(a); Fig. 3(a)), sharing a feature with *Yunnanpriapulus*; EC60381 (ref. [23], Fig. 4(a); Fig. 5(a)); the holotype of *Yunnanpriapulus* bears remarkable ring papillae, but scalids are invisible on its posterior introvert. Furthermore, none of the three differences mentioned above is supported by our observation: specimens orienteding obliquely to bedding planes are usually shorten their diameters backwardly (Fig. 1(d)—(f)), giving the appearance that the diameters of preanal and caudal appendage are markedly decreased; the scalids and the ring papillae on these specimens are obscure, showing more features of *Xiaoheiqingella*. On the contrary, specimens lying parallel to bedding plane express more characteristics of *Yunnanpriapulus* (Figs. 1(c), 2(a), 2(b), 2(d), 2(g) and 2(j)). Otherwise, specimens preserved with bicaudal appendages, short or long, co-occur with the phenomena that their posterior introvert bears scalids and the neck appears as a constriction between introvert and trunk (Figs. 1(c), 1(d), 1(g), 2(a), 2(b), 2(d), 2(g) and 2(j)). Therefore, *Yunnanpriapulus* is most probably a synonym of *Xiaoheiqingella*. Our reconstruction of *Xiaoheiqingella* is presented in Fig. 2(k) in which a protruded pharynx is drawn intentionally to show the arrangement of the teeth.

Acanthopriapulus horridus of Recent Priapulidae is recognized by 25 longitudinal rows of scalids. Its middle and posterior scalids, although smaller in size, are loosely arranged with little trace of longitudinal rows[27]. This character is very reminiscent of the posterior scalids of *Xiaoheiqingella*. It should be noted that spinous ring papillae on the preanal region of *Xiaoheiqingella* show no distinct difference with scalids and pharyngeal teeth in shape, suggesting that all kinds of ornaments in the cuticle of Recent priapulids might be derived from spines, which are known as the most common form of ornament on the surface of Cambrian taxa. The character that spines of the pharynx, the introvert and the trunk are commonly arranged quincunxially or diagonally is speculated to be a primitive condition of the priapulids.

Tubiluchidae van der Land, 1970.

Genus *Paratubiluchus bicaudatus* gen. nov.

Etymology. The genus name refers to the body that closely resembles living *Tubiluchus*.

Diagnosis. Pear-like introvert with 25 longitudinal rows of scalids, the posteriormost one of six or seven scalids is located with a distance from the others, and all the posteriormost scalids themselves align circumferentially. Neck area distinct. Middle part of the oval-shaped trunk with many spines. Trunk end flanked by two long caudal appendages with transverse striations.

Type species. *Paratubiluchus bicaudatus* gen. et sp. nov.

Age and distribution. Qiongzhusi Stage, Early Cambrian; eastern Yunnan, China.

Discussion. The Family Tubiluchidae was originally defined as: pharynx with pectinate teeth of equal size; polythyridium at entrance of intestine; introvert with 20 rows of scalids; trunk not annulated; larvae with radially symmetrical lorica[25]. A definition of the Tubiluchidae given by Adrianov et al.[27] contains additional items: meiobenthic worms; introvert and trunk separated by distinct neck area; neck folded or with soft cuticular plates; trunk densely covered with tumuli, without annuli; tail monocaudal, long, smooth and slender, introvert bearing 25 rows of scalids. The last item has also been supported by other works[28,29]. It should be pointed out that features including "meiobenthic worms" and "polythyridium" are shared by *Meiopriapulus*, which is devoid of any caudal appendage and was assigned to the Tubiluchidae[30]. Therefore, it seems the definition given by Adrianov et al.[27] is too detailed to contain another genus. Features of *Paratubiluchus* gen. nov. coincide with the definition of the Tubiluchidae except for its bicaudal appendages. In short, the monocaudal appendage should represent a feature of *Tubiluchus* rather than the Tubiluchidae.

Paratubiluchus bicaudatus gen. et sp. nov. (Fig. 3(a)—(d)).

Etymology. The species name refers to two caudal appendages.

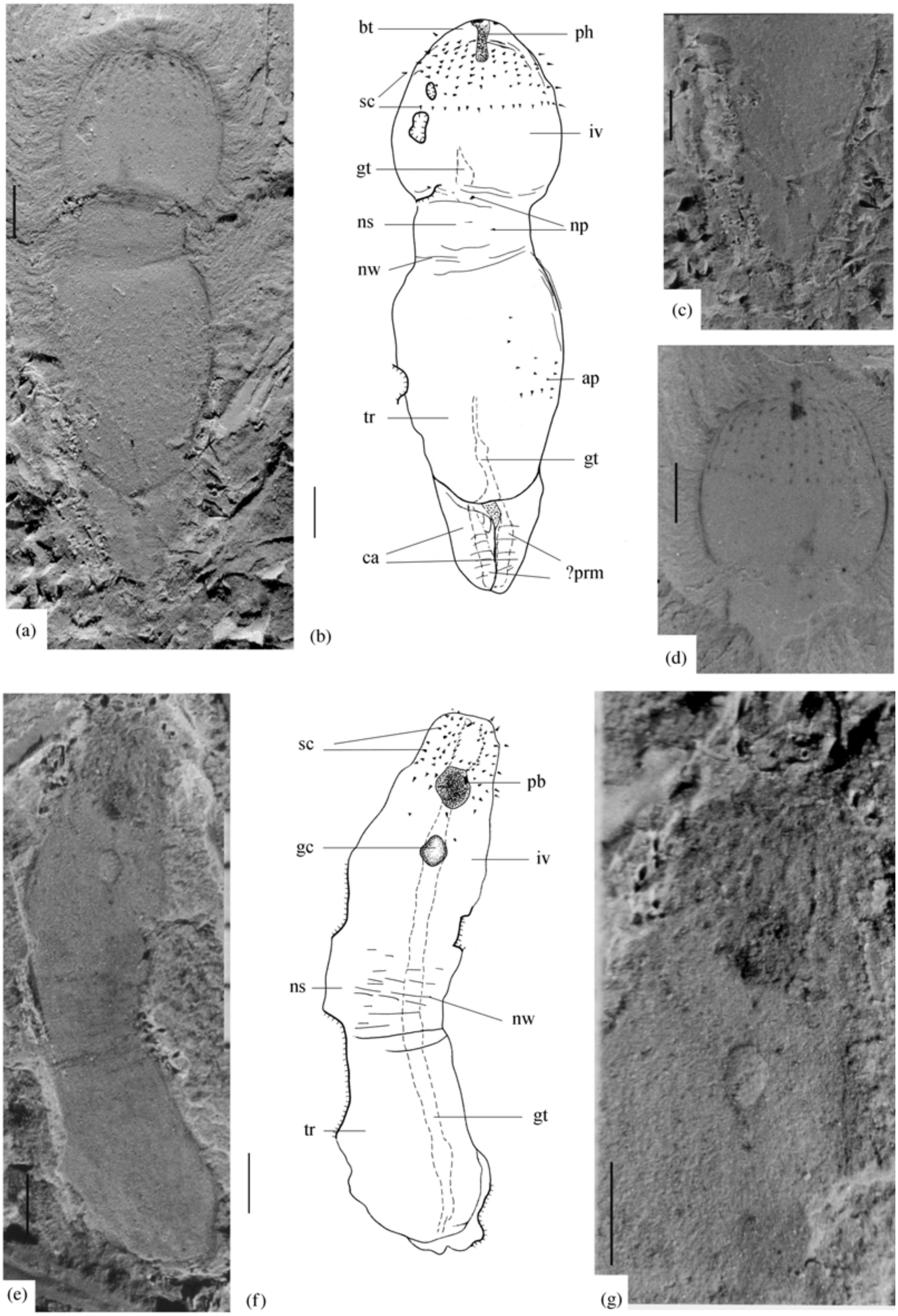

Fig. 3. (a)—(d) *Paratubiluchus bicaudatus* gen et sp. nov., from the Jianshan section, Haikou, Kunming, Yunnan. (a) Eli-0001261A, holotype; (b) explanation of (a); (c) close up of (a); (d) Eli-0001261B, holotype, showing the proboscis. (e)—(g) form A, from the Jianshan section, Haikou, Kunming, Yunnan. (e) Eli-0001262, a complete specimen, one fourth area of the introvert bears 18—20 longitudinal rows of spine-formed scalids followed by additional scalids loosely scattered, the neck area is well defined by transverse wrinkles, the short trunk lacks annuli, likely without caudal appendage; (f) explanation drawing of (e); (g) close-up showing the introvert, the scalids and the pharyngeal bulb which seems to be armed. pb = pharyngeal bulb; prm = posterior retract muscles; nw = neck wrinkle; ns = neck section; other abbreviations (see Fig. 1). Scale bar represents 1 mm.

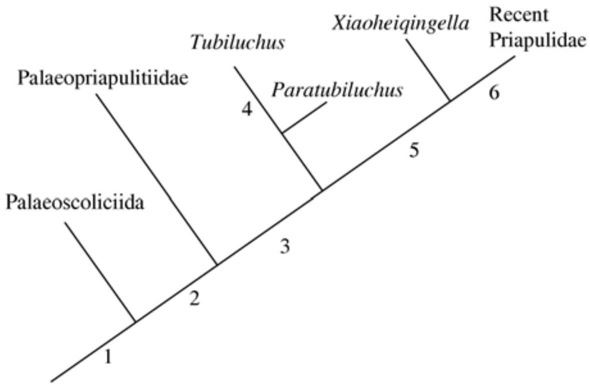

Fig. 4. Simplified cladogram of fossil priapulids and Recent taxa (modified from ref. [23]). 1, Pharyngeal spines and spine-formed scalids arranged in quincunx; 2, body divided into three sections: anterior introvert bearing 20 longitudinal scalid rows; neck well developed, oval trunk enclosed in a radial symmetrical lorica; 3, body divided into four sections: 25 longitudinal rows of scalids, trunk not annulated in adults, bicaudal appendages; 4, meiobenthic worm, monocaudal appendages; 5, cylindrical trunk with fine annuli and sub-region, no visible neck; 6, scalids covering full length of the introvert, lorica differentiated dorso-ventrally.

Diagnosis. As the genus.

Holotype. Eli-0001261A, B.

Description. The body consists of a proboscis, a well delimited neck section, a trunk without annuli and a pair of caudal appendages. The ratio of the four parts in axial length measured from the holotype is about 2∶1∶3∶1.5.

The introvert is also pear-shaped, and its maximal width is positioned at the posterior half. Up to 13 evenly spaced longitudinal rows of spine-shaped scalids are clearly recognized on the anterior half surface of the introvert in one face of specimen. Thus total rows can be count ca. 25. Anterior six of seven scalids on each row increase their intervals slightly, whereas the posteriormost scalid is far away from the anterior six and slightly apart from the regular longitudinal row. Thus it appears that all the posteriormost scalids on each row are arranged nearly in a circle. The collar is armless and tapers rapidly forward. The pharynx is invaginated into the introvert and its dark colored surface indicates that it might have been densely armed by tiny spines (Fig. 3(a), (b) and (d)).

The neck is fairly well delimited as a short constricted section between introvert and trunk. It is also characterized by sparse papillae and some transverse wrinkles, which differ remarkably from the annuli. The trunk is oval-shaped, reaching its maximal width in the anterior 1/3 portion. The trunk is ornamented with some papillae but without any annuli (Fig. 3(a) and (b)).

The lateral end of the trunk is flanked by a pair of short tubular caudal appendages with faint transverse wrinkles or striations. As seen in the holotype, the distal portions of the appendages are somewhat overlapped at their median margins (Fig. 3(c)). A pair of grayish white stripes, with almost equal length and 1/4 width of the caudal appendages, is visible within the inner sides of the appendages. They display a color similar to that of the gut, are possibly separately bifurcated from the gut end stretching into the caudal appendages (Fig. 3(a)—(c)) and are not imprinted by the overlapping area of caudal appendages. This might be interpreted as the posterior retractor muscle, although no comparable structures are found in extant priapulids. The gut is partially visible as a light grayish white stripe. The anal opening is in the same position as that in *Xiaoheiqingella*.

Comparison. *Paratubiluchus* gen. nov. differs mainly from *Xiaoheiqingella* and Recent Priapulidae in its oval trunk with papillae but without annuli. Similarities between the former two include: the last one or two scalids are disposed distinctly far away from anterior scalids; both have a pair of caudal appendages. Compared with *Tubiluchus*, *Paratubiluchus* gen. nov. is a macrobenthic worm possessing a bigger but relatively shorter trunk, a pair of caudal appendages, and a body proportion similar to extant loricate larvae and *S. rara*. *Paratubiluchus* gen. nov. also shows some resemblances to form A in having a well delimited neck area, in lacking annuli on the trunk and having a similar body ratio; hence they differ in the detailed arrangement of scalids and caudal appendages.

The genera of Priapulidae, Tubiluchidae and Halicryptidae generally experience several stages of loricate larvae in their ontogeny. During larval development, the scalids are arranged in 20 longitudinal rows in the first stage, and are increased to 25 rows at later stages[26]. Considering the assemblage of characteristics found in *Paratubiluchus* gen. nov., it may be concluded that the nearest common ancestor of them is a loricate larva-formed worm with 25 rows of scalids. It mostly resembles the older larvae of *Tubiluchus*, which has commonly been considered to retain more primitive features. Further deductions include that the nearest ancestor may be derived from loricate priapulids with 20 rows of scalids, resembling *S. rara* and the first stage of loricate larvae of recent priapulids. *Paratubiluchus* gen. nov. is conceived to be a link between larva-formed priapulids and mature-formed priapulids (Fig. 4).

Stratigraphy and locality. Qiongzhusi Formation, Yu'anshan Member (*Eoredlichia* zone), Lower Cambrian, Jianshan section, Haikou, Kunming.

3 Ancestral features of early Priapulomorpha

Clues about the ancestral features of early Priapulomorpha chiefly come from the ontogenies of recent priapulids, and from comparison of fossil priapulids with related phyla such as kinorhynchs and loriciferans. However, relationships among them are still unresolved[31]. Although the palaeoscolecidans[32] are believed to occupy a more basal position than crown priapulids[19], we will exclude them in the following discussion because their phylogenetic position is still controversial.

Introvert. The number of scalids row are 20 in Palaeopriapulitidae, 25 in Family Priapulidae, Tubiluchidae, Halicryptidae and Chaetostephanidae (including tentacle), and more than 25 in Meiopriapulidae[33−35]. So it is suggested that introvert bearing less scalid rows should be a primitive feature (Fig. 4). Scalids entirely covering the introvert as in Recent Priapilidae have been interpreted as a derived state, and those restricted to the anterior region of the introvert in fossil Priapulidae as a primitive condition[23].

Neck. The neck as a well defined short section is probably a primitive state[23]. The speculation that “the neck is a specialized trunk” among Priapulomorpha[23] is not supported. Because the main components of the body, such as introvert, neck and trunk are also present in other cephalorhynchs such as kinorhynchs and loriciferans[31], investigating their origin should not be limited in a single phylum.

Trunk. An oval trunk is more primitive than an elongate trunk; and a loricate trunk is more primitive than a trunk without lorica in the adult. A trunk lacking annuli is more primitive than one with annuli. A trunk with a distinct sub-region is an advanced feature[23]. Ring papillae at the trunk end of *Halicryptus* are probably homologous with the preanal hooks of *Maccabeus*[33].

Caudal appendage. The terminal structures of the body in Priapulidae, Tubiluchidae, Halicryptidae and Chaetostephanidae vary significantly. *Maccabeus* lacks a caudal appendage, but its anal opening bears a pair of tubuli-like processes[33]. *Halicryptus* also lacks a caudal appendage, but possesses a pair of large setae flanking the anus[25]. *Tubiluchus* bears a slender monocaudal appendage. Two species of *Priapulopsis* and *Priapulus atlantisi* of the Priapulidae are bicaudal[36], while the other species of this family can have or lack appendages. Monocaudal-bicaudal has been suggested as an evolutionary route for the caudal appendage[27], and the bicaudal appendage should represent an autapomorphy of *Priapulopsi* being regarded as the most advanced genus of the Priapulidae (Fig. 4). Combining with the present two fossil species, we conclude that bicaudal appendages should be a synapomorphy of the Priapulidae and Tubiluchidae, rather than an autapomorphy of *Priapulopsis*. The right appendage of *Priapulopsis australis* is much smaller than the left one[27], indicating that the bicaudal appendages could be converted to a monocaudal appendage by degeneration. The macroscopic tubular caudal appendages of Priapulidae, the tubuli-like processes of *Maccabeus*, as well as the terminal setae of *Halicryptus*, might be homologous.

Gut. A Pharyngeal bulb or polythyridium is present in the Tubiluchidae, Meiopriapulidae[26,27], Palaeopriapulitidae and form A (Fig. 3(e)—(g)). These organs are conceived to be primitive features.

Ventral nerve cord. The ventral nerve cord found in living priapulids and the fossil materials in the present study is a primitive character, which may have little phylogenetic significance.

Huang et al.[23] suggested that the body plan of the Priapulidae has undergone very little changes over the last 530 millions years. Considering the feature of *Paratubiluchus*, Tubiluchidae may be the case. And the priapulomorphs probably show anatomical conservatism and failed to create any new macroscopic structures in the later stages of their evolutionary history.

4 Lifestyle

The caudal appendages of *Xiaoheiqingella* might have served as a device to adjust the body fluid rather than having a respiration function contrasting with the vesicular tail of living *Priapulus caudatus*[25]. *Xiaoheiqingella* probably burrowed in a fashion similar to those of Recent priapulomorphies[37]. The bodies of *Xiaoheiqingella* are frequently preserved lying at an angles about 30°—40° in the rocks (Fig. 1(d)). It could be concluded that the animal had the ability to move vertically in the sediment if the high compression ratio of the rocks is concerned. The specimens of *Xiaoheiqingella* are occasionally associated *S. rara* on the same bedding, suggesting that they occupied similar ecological niches. Annuli on the trunk of Recent priapulids correspond to bundles of circle muscles beneath the cuticle[27], which thus give the trunk a more effective contractile ability and so the animal is more active in burrowing. form A and *Paratubiluchus* gen. nov. lack annuli in their trunk, indicating that they are less effective and passive in burrowing. The neck of *S. rara* is well delimited and served as a hinge to bend the body, whereas the neck in both *Xiaoheiqingella* and living Priapulidae has a very limited role. Thus the body bending in these animals may have depended on the elongate cylindrical trunk instead of the neck. In this aspect, the short trunks and neck sections of form A and *Paratubiluchus* gen. nov. might represent an intermediate link between these two styles of body bending.

Xiaoheiqingella was chiefly carinivorous with possible occasional mud-eating habits[23]. A similar fashion is suggested for *Paratubiluchus* gen. nov., whereas presence of a pharyngeal bulb in the form A indicates a higher percentage of mud-eating.

5 Palaeoecology

The arthropods today make up 80% of the whole animal kingdom. Their dominance in diversity was scarcely less in the history record, a view well supported in the Cambrian Lagerstätten[38,39]. The priapulid-like worms, especially the palaeoscolecidans, are a rather diversified group in diversity, disparity and richness in the Lower Paleozoic records[32]. For example, they are nearly as rich as the arthropods in the localities of Haikou[24,38,40], having reached 10 genera from all sections of Chengjiang deposits, and making up 10% of benthic communities, nearly equivalent to population structure of the Middle Cambrian Burgess Shale[1]. However, they have not been reported in the fossil record younger than Silurian[32]. Identified as a stem group of priapulids, the Palaeopriapulitae are very common in sections of Chengjiang deposits[11,16], especially in the Haikou region, Kunming, and might have been extinct after the Middle Cambrian. *Xiaoheiqingella* and *Paratubiluchus* gen. nov., which undoubtedly belong to Priapulomorpha, are extremely rare and not recorded in other Lagerstätten. This set of evidence supports that the palaeoscolicidans and stem group of priapulids except priapulomorphs played important roles at least in Cambrian benthic communities represented by the Chengjiang fauna and Burgess Shale fauna. The priapulomorphs are very low in diversity (2 fossil species and 18 living species) and rare in richness in both the Cambrian and the extant ecological system[38]; this condition might have been maintained throughout their history.

In conclusion, the anatomy, feeding habit, locomotion style and ecological niche of the priapulomorphs remained stagnant since they rapidly diversified in the Early Cambrian. The roots of the main clades of the Priapulida may have occurred, therefore, at that time or not far before.

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References

1. Briggs, D. E. G., Erwin, D. H., Collier, F. J., The Fossils of the Burgess Shale, Washington: Smithsonian Institution Press, 1994, 114—125.
2. Shu, D. G., Conway Morris, S., Han, J. et al., Primitive deuterostomes from the Chengjiang Lagerstätte, Lower Cambrian, China, Nature, 2001a, 41(4): 419—424.
3. Shu, D. G., Luo, H. L., Conway Morris, S. et al., Lower Cambrian vertebrates from South China, Nature, 1999, 402: 42—46.[DOI]
4. Shu, D. G., Chen, L., Han, J. et al., An Early Cambrian tunicate from China, Nature, 2001b, 411: 472—473. [DOI]
5. Shu, D. G., Conway Morris, S., Zhang, Z. F. et al., A new species of Yunnanozoan with implications for Deuterostome Evolution, Science, 2003, 299: 1380—1384. [DOI]
6. Chen, J. Y., Dzik, J., Edgecombe, G. D. et al., A possible Early Cambrian chordate, Nature, 1995, 377: 720—722. [DOI]
7. Conway Morris, S., The Crucible of Creation: The Burgess Shale and the Rise of Animals, Oxford: Oxford University Press, 1998, 1—242.
8. Chen, J. Y., Zhou, G. Q., Zhu, M. Y. et al., The Chengjiang Biota: A Unique Window of the Cambrian Explosion (in Chinese), Taichung: National Museum of Natural Science, 1996, 1—222.
9. Chen, J. Y., Zhou, G. Q., Biology of the Chengjiang fauna, Bulletin of the National Museum of Natural Science, 1997, 10: 33—37.
10. Chen, J. Y., Huang, D. Y., A possible Lower Cambrian Chaetognath (arrow worm), Science, 2002, 298 (4): 187. [DOI]
11. Hou, X. G., Bergström, J., Wang, H. F. et al., The Chengjiang Fauna: Exceptionally Well-Preserved Animals from 530 Million Years Ago (in Chinese). Kunming: Yunnan Science and Technology Press, 1999, 53—64.
12. Chen, L. Z., Luo, H. L., Hu, S. X. et al., Early Cambrian Chengjiang Fauna in Eastern Yunnan, China (in Chinese), Kunming: Yunnan Science and Technology Press, China, 2002, 163—166.
13. Han, J., Zhang, X. L., Zhang, Z. F. et al., A new platy-armored worm from the Early Cambrian Chengjiang Lagerstätte, South China, Acta Geologica Sinica, 2003, 77(1): 1—6.
14. Hou, X. G., Sun, W. G., Discovery of the Chengjiang fauna in the Meishucun, Jinning, Yunnan, Acta Palaeontologica Sinica (in Chinese), 1988, 27: 1—12.
15. Sun, W. G., Hou, X. G., Early Cambrian Worm from Chengjiang Yunnan, China, Acta Palaeontologica Sinica (in Chinese), 1987, 26 (3): 257—271.
16. Luo, H. L., Hu, S. X., Chen, L. Z. et al., Early Cambrian Chengjiang Biota from Kunming Region, China (in Chinese), Kunming: Yunnan Science and Technology Press, 1999, 76—83.
17. Conway Morris, S., Fossil priapulid worms, Special Papers in Palaeontology, London, 1977, 20: 1—95.
18. 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 Taijiangian stage, in the Cambrian System of South China (eds. Peng, S., Babcock, L. E., Zhu, M.), Palaeoworld, 2001, 10: 189—208.
19. 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]
20. Hou, X. G., Bergström, J., Palaeoscolecid worms may be nematomorphs rather than annelids, Lethaia, 1994, 27: 11—17.
21. Budd, G. E., Why are arthropods segmented? Evolution & Development, 2001, 3(5): 332—342. [DOI]
22. Schram, F. R., Pseudocoelomates and a nemertine from the Illinois Pennsylvanian, Journal of Paleontology, 1973, 47: 985—989.
23. 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]
24. Zhang, X. L., Shu, D. G., Li, Y. et al., New sites of Chengjiang fossils: Crucial windows on the Cambrian explosion, Journal of the Geological Society, London, 2001, 158: 211—218.
25. Land, V. D. J., Systematics, zoogeography and ecology of the Priapulida, Zoologische Verhandelungen, Leiden, 1970, 112: 1—118.
26. Kirsteuer, E., Notes on adult morphology and larvae development of *Tubiluchus corallicaola* (Priapulida), based on *in vivo* and scanning electron microscopic examinations of specimen from Bermuda, Zoologica Scripta, 1976, 5: 239—255.
27. Adrianov, A. V., Malakhov, V. V., Priapulida: Structure, Development, Phylogeny, and Classification, Moscow: KMK Scientific Press, 1996, 1—268.
28. Calloway, C. B., Morphology of the introvert and associated structures of the priapulid *Tubiluchus corallicola* from Bermuda, Marine Biology, 1975, 31: 161—174.
29. Lemburg, C., Ultrastructure of the introvert and associated structures of the larvae of *Halicryptus spinulosus* (Priapulida), Zoomorphology, 1995, 115: 11—29.
30. Land, J. van der, Nørrevang, A., Affinities and intraphyletic relationships of the Priapulida, in the Origins and Relationships of Lower Invertebrates (eds. Conway Morris, S., George, J. D., Gibson, R. et al.), Oxford: Oxford University Press, 1985, 261—273.
31. Nielsen, C., Animal Evolution: Interrelationships of the Living Phyla, New York: Oxford University Press Inc., 2001, 1—563.
32. Conway Morris, S., The cuticle structure of 495 Myr-old type species of the fossil worm Palaeoscolex, *P. pricatorum* (? Priapulida), Zoological Journal of the Linnean Society, 1997, 119: 69—82. [DOI]
33. Por, F. D., Class Seticoronaria and phylogeny of the phylum Priapulida, Zoologica Scripta, 1983, 12: 267—272.
34. Will, M. A., Cambrian and Recent disparity: the picture from priapulids, Paleobiology, 1998, 24: 177—199.
35. Morse, M. P., *Meiopriapulus fijiensis* n. gen., n. sp.: An interstitial priapulid from coarse sand in Fiji, Transactions of the American Microscroscopy Society, 1981, 100: 239—252.
36. Sanders, H. L., Hessler, R. R., *Priapulus atlantisi* and *Priapulus profundus*, Two new species of priapulids from bathyal and abyssal depth of the North Atlantic, Deep Sea Research, 1962, 9: 125—130.
37. Hammond, R. A., The burrowing of *Priapulus caudatus*, Journal of Zoology London, 1970, 162: 469—480.
38. Briggs, D. E. G., Fortey, R. A., Wills, M. A., Morphological disparity in the Cambrian, Science, 1992, 256:1670—1673.
39. Budd, G. E., Ecology of nontrilobite arthropods and lobopods in the Cambrian, in the Ecology of the Cambrian Radiation (eds. Zhuravlev, A. Y., Riding, R.), New York: Columbia University Press, 2001, 404—427.
40. Zhu, M. Y., Zhang, J. M., Hu, S. X. et al. The Early Cambrian Chengjiang Biota: New quarry and discoveries near Earcaicun, Haikou town, Kunming county, Yunnan province, China, in the Cambrian System of South China (eds. Peng, S., Babcock, L. E., Zhu, M.), Palaeoworld, 2001, 10: 236—238.

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