

Trunk ornament on the palaeoscolecid worms *Cricocosmia* and *Tabelliscolex* from the Early Cambrian Chengjiang deposits of China

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Cricocosmia jinningensis, one of the most abundant palaeoscolecid worms from the Lower Cambrian Chengjiang deposits of south China, was originally described as bearing double longitudinal rows of lateral conical sclerites on the trunk. New observation reveals that the ventral trunk bears an additional set of ventral sclerites while the lateral sclerites display a tubercle-bearing (inner surface) and net-like (outer surface) microstructure similar to that of *Tabelliscolex hexagonus*. These findings mean that: (1) *Cricocosmia* shows a dorso-ventral and antero-posterior differentiation in trunk ornament; (2) as seen from the microstructure, *Cricocosmia* is close to *Tabelliscolex hexagonus*, supporting the idea that lobe-podians and arthropods, both of which show an upper capping layer in the outer sclerites, are more closely related than the palaeoscolecidans; and (3) the similarities among the scalids, pharyngeal teeth and the trunk spines of palaeoscolecidans are superficial. *Tabelliscolex maanshanensis* sp. nov., characterized by an inner concentric circlet of laminae in each tubercle of the lateral trunk plate, is proposed herein. Element mapping reveal that four known pathways of preservation can be found co-occurring in a single specimen of *Cricocosmia* or *Tabelliscolex*, which sheds new light on the preservation of the Chengjiang fossils.

Key words: Priapulida, Palaeoscolecida, *Cricocosmia*, *Tabelliscolex*, Chengjiang, Cambrian, China.

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Introduction

The palaeoscolecidans, a group of fossil worms bearing a variety of trunk ornaments, are known to have a long history with a stratigraphic range from Early Cambrian to Late Silurian (Conway Morris 1997). Most palaeoscolecidans around the world are preserved as trunk fragments or discrete sclerites, which fail to offer a complete picture (Whittard 1953; Kraft and Mergl 1989; Hinz et al. 1990; Müller and Hinz-Schallreuter 1993; Porter 2004; Ivantsov and Wrona 2004). However, specimens of four species from the Early Cambrian Chengjiang deposits, Yunnan Province, south China are particularly abundant and well defined with complete bodies consisting of spinose proboscis with quincunxially-arranged pharyngeal teeth, annulated trunks and a pair of terminal hooks (Hou et al. 1999; Han et al. 2003a; Hu 2005), strongly indicating of the stem group of priapulids (Huang et al. 2005a). These four species vary apparently in trunk ornament: *Maotianshaniania cylindrica* Sun and Hou, 1985 bears numerous irregularly arranged uniform trunk sclerites, SEM analysis revealing that each sclerite bears four nodes (Hu

2005); *Mafangsciolex sinensis* Hou and Sun, 1988 bears four or five transverse rows of plates with platelets in between and both plate or platelet have one small central spine (Hu 2005); *Tabelliscolex hexagonus* Han, Zhang, and Shu, 2003a is characterized by two sets of plates with a honeycomb-like structure (see also Huang 2005b); the trunk of *Cricocosmia jinningensis* Hou and Sun, 1988 is well known for bearing double rows of lateral conical sclerites, but little is yet known about the microstructure of these sclerites. Numerous individuals of *Cricocosmia* were found constituting several fossil concentrations in the Kunming and Anning regions, Yunnan Province (see Han et al. 2006). Among them three specimens of *Cricocosmia* showing different fine details of their lateral sclerites and many specimens with ventral spines has been identified. A new scenario of the evolutionary history of palaeoscolecidans, starting from a uniform cover of microplates and with subsequent increase in size of plates surrounded by minute platelets is proposed here.

Institutional abbreviation.—ELI, Early Life Institute, Northwest University, Xi'an, China.

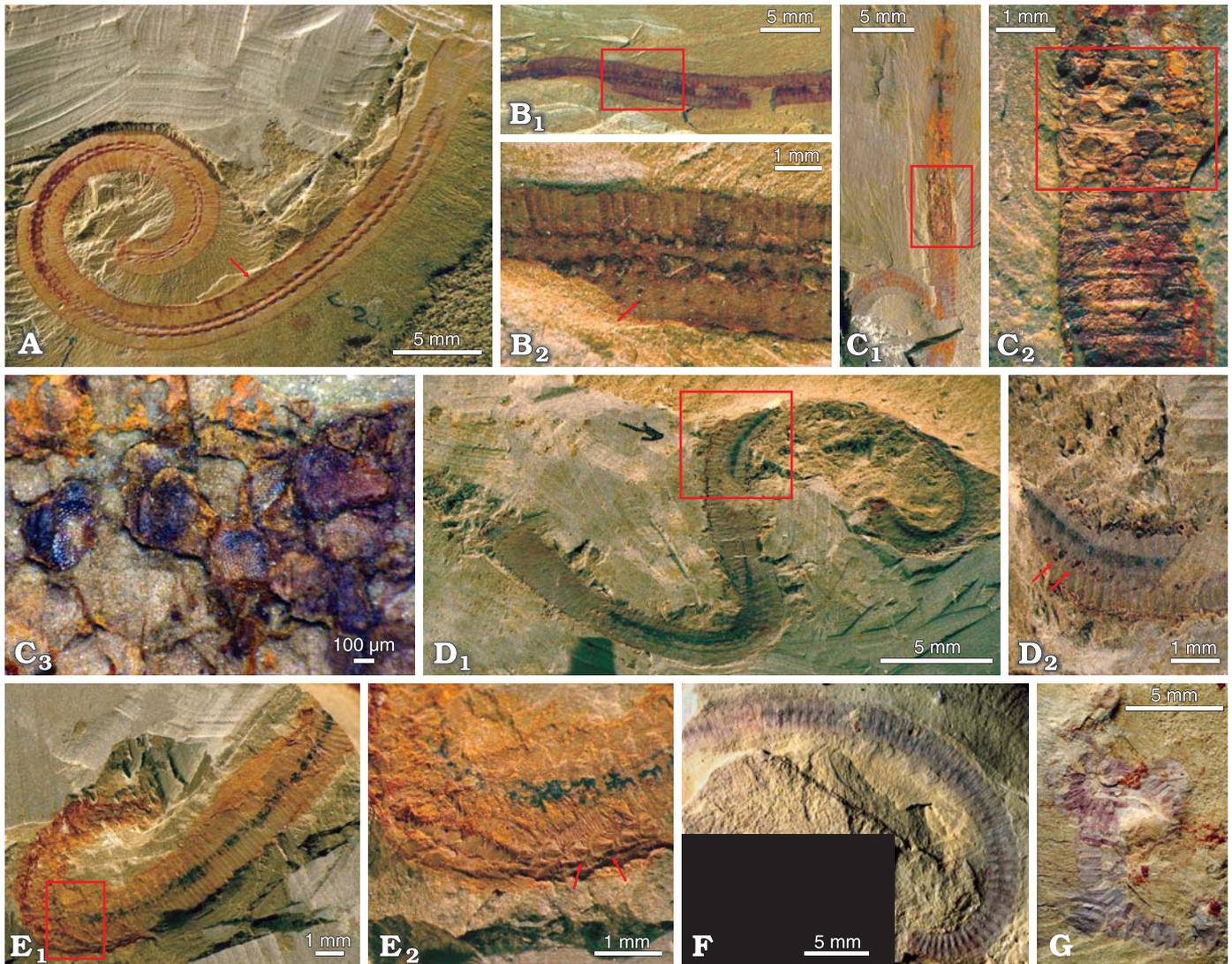


Fig. 1. Early Cambrian palaeoscolecid worms from the Early Cambrian Chengjiang deposits, China. **A–E.** *Cricocosmia jinningensis* Hou and Sun, 1988. **A.** ELI-0001400, showing the ventral trunk spines (arrow) of *Cricocosmia*. **B.** ELI-0001401, showing the ventral trunk spines (arrow); B₂ is the rectangle area on B₁. **C.** ELI-0001402; C₁, a complete specimen; C₂, lateral spines at the anterior portion of the trunk (rectangle area in C₁) preserved fine structure; C₃, showing the preserved microstructure of the lateral spines, note that sclerites colored black can preserve finer structure than those of yellow, and that sclerites showing finer structures are apparently dislocated probably due to molting. **D.** ELI-0001403; D₁, a complete specimen; D₂, posterior portion of the body (rectangle area in D₁) with several spines (arrows pointed) bearing fine structures. **E.** ELI-0001404; E₁, a fragmental specimen in burrowing; E₂, showing the trunk sclerites (arrows pointed) with a net-like structure; the marginal ridges are evident on these sclerites. **F.** *Tabelliscolex hexagonus* Han, Zhang, and Shu, 2003a, ELI-0001218, holotype, showing the general outline. **G.** *Tabelliscolex maanshanensis* sp. nov., ELI-0001219, showing molted trunk sclerites.

Materials and method

Up to date, more than three thousands specimens of *Cricocosmia* have been collected and the specimens examined here came from the Jianshan (ELI-0001400, ELI-0001402, ELI-0001403) and Yulongsi sections (ELI-0001401, ELI-0001404), Haikou town, Kunming City, Yunnan Province. However, only three specimens (ELI-0001402, ELI-0001402, and ELI-0001402) have preserved fine structures on their lateral sclerites in our collections. The holotype and paratype specimens of *Tabelliscolex hexagonus* Han, Zhang, Zhang, and Shu, 2003a (ELI-0001218, ELI-0001219) were reinvestigated under SEM for comparison and by EDX for

chemical composition. All the uncoated whole specimens were analyzed with a Philippe FEI Quanta 400-FEG with a 20.2 kV and 80 Pa in the State Key Laboratory of Continental Dynamics, Northwest University, China.

Systematic paleontology

Phylum Priapulida Delage and Hérourard, 1897
 Class Palaeoscolecida Conway Morris and Robison, 1986
 Order uncertain

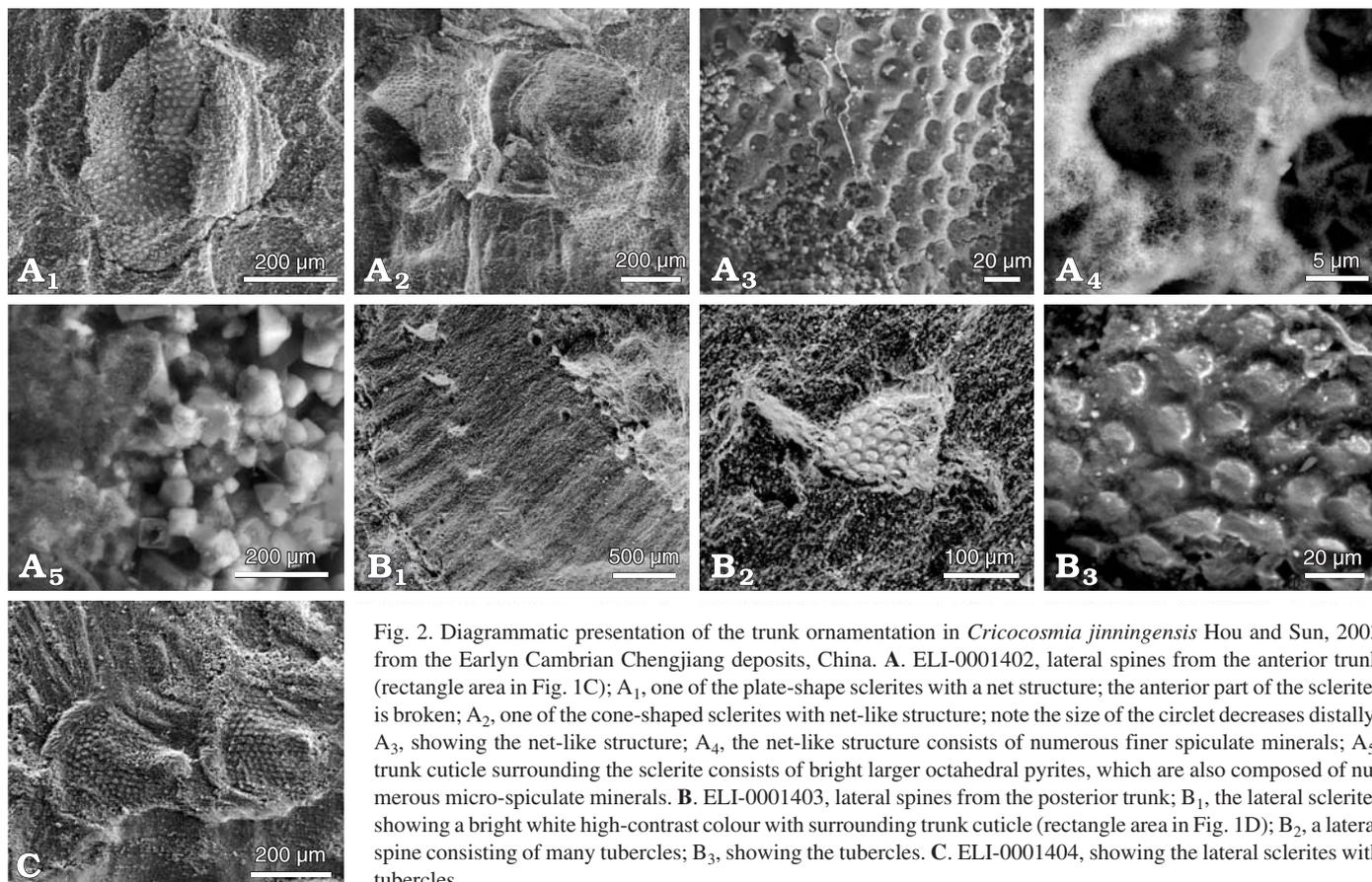


Fig. 2. Diagrammatic presentation of the trunk ornamentation in *Cricocosmia jinningensis* Hou and Sun, 2003 from the Early Cambrian Chengjiang deposits, China. **A.** ELI-0001402, lateral spines from the anterior trunk (rectangle area in Fig. 1C); A₁, one of the plate-shaped sclerites with a net structure; the anterior part of the sclerites is broken; A₂, one of the cone-shaped sclerites with net-like structure; note the size of the circllet decreases distally; A₃, showing the net-like structure; A₄, the net-like structure consists of numerous finer spiculate minerals; A₅, trunk cuticle surrounding the sclerite consists of bright larger octahedral pyrites, which are also composed of numerous micro-spiculate minerals. **B.** ELI-0001403, lateral spines from the posterior trunk; B₁, the lateral sclerites showing a bright white high-contrast colour with surrounding trunk cuticle (rectangle area in Fig. 1D); B₂, a lateral spine consisting of many tubercles; B₃, showing the tubercles. **C.** ELI-0001404, showing the lateral sclerites with tubercles.

Family Cricocosmiidae Hou, Bergström, Wang, Feng, and Chen, 1999

Diagnosis.—Elongate trunk with paired macrosclerites on each annulus that is wide and less prominent on the dorsal side. Macrosclerites composed of many tubercles on the outer surface and corresponding pits in the inner surface. Tubercles with or without inner circllet. Terminal trunk with a pair of hooks.

Remarks.—*Houscolex* Zhang and Pratt, 1996, *Cricocosmia* and *Tabellisoclex* should be assigned to this family.

Genus *Cricocosmia* Hou and Sun, 2003

Type species: *Cricocosmia jinningensis* Hou and Sun, 2003, Qiongchuanian Stage (Early Cambrian), Chengjiang, Eastern Yunnan, China.

Diagnosis.—Eversible proboscis with ten longitudinal rows of scalds; trunk with paired macrosclerites that composed of many tubercles on the outer surface and corresponding pits in the inner surface.

Cricocosmia jinningensis Hou and Sun, 2003

Figs. 1A–E, 2, 3.

Emended diagnosis.—Elongate trunk bears approximately 110 annuli that decrease in wide backwardly and usually form two sub-annuli on the dorsal side. Correspondingly,

cone-shaped macrosclerites decrease in size and increase in height. Trunk with or without ventral spines.

Description.—The proboscis of *Cricocosmia* dictates the anterior/posterior orientation of this animal while the bilateral asymmetry is defined by the paired sclerites and the comparably smooth area between the two rows of lateral sclerites which consisting with the orientation of the terminal hooks, indicate the ventral side of the trunk.

Ventral spines: Approximately 5% of *Cricocosmia* specimens in our huge collections show two roughly longitudinal rows of tiny spines at the ventral side of the trunk (Fig. 1A, B). The arrangement of these spines is not regular, but usually, one annulus bears one or two such spines (Fig. 1A, B). The specimens described here do not show any other differences from those devoid of ventral spines.

Lateral sclerites: The presence on the trunk of *Cricocosmia* of a pair of cone-shaped sclerites on each annulus is well known (Hou and Bergström 1994). Despite of the first pair of sclerites that are smaller than the second one, the lateral sclerites increase gradually in height and decrease in diameter toward the trunk end; those on the anterior part of the trunk appear to be dorso-ventrally extended elliptical inwardly-curved plates; on the middle part they are shaped as round plates each with a low-relief cone pointing backward; and the posterior sclerites are formed into curved backwardly-pointing sharp spines with a ground base (Fig. 1A).

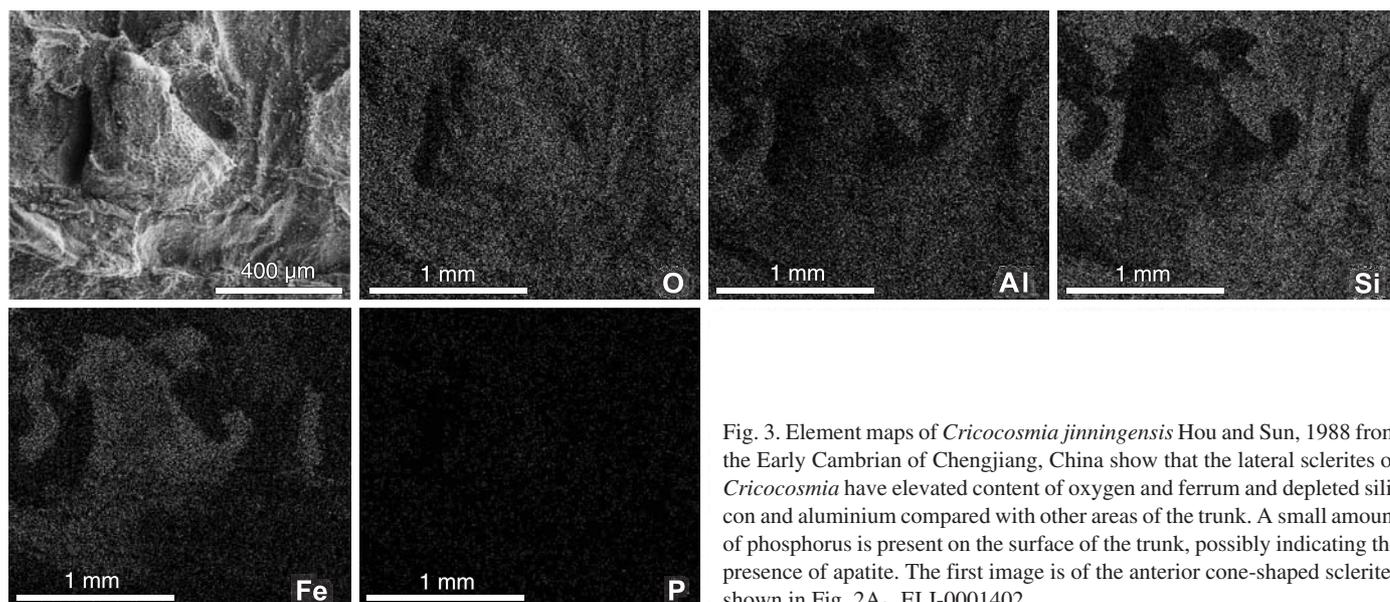


Fig. 3. Element maps of *Cricocosmia jinningensis* Hou and Sun, 1988 from the Early Cambrian of Chengjiang, China show that the lateral sclerites of *Cricocosmia* have elevated content of oxygen and ferrum and depleted silicon and aluminium compared with other areas of the trunk. A small amount of phosphorus is present on the surface of the trunk, possibly indicating the presence of apatite. The first image is of the anterior cone-shaped sclerites shown in Fig. 2A₂, ELI-0001402.

Each lateral sclerite has a marginal ridge that is wide and apparent at its part posterior (Fig. 1E).

SEM-BSE analysis reveals that the well-preserved lateral sclerites including the marginal ridges consist of a crudely diagonal meshwork of hemi-spherical tubercles or round concave pits (Figs. 1C–E, 2A–C). The surface with holes represents the inner side of the epicuticle whereas that with tubercles represents the outer side. In ELI-0001402 and ELI-0001404, the pits in the meshwork range from ca. 2 to 10 µm in diameter, and they apparently decrease in size towards the tip of the lateral sclerites (Fig. 2A₂–A₄, C). The skeleton frame separating the pits is also ca. 2–10 µm in thickness. In ELI-0001403, the tubercles, which are located on the sclerites near the trunk end, seem to be uniform in diameter. However, the distal part does not show any microstructure probably due to poor preservation. The pits at the edge of the sclerites are complete or an incomplete pit (Fig. 2A₃). Apparently, the sclerites on the posterior trunk are composed of less tubercles than the anterior ones (Figs. 1C–E, 2A–C). The thickness of the lateral sclerites is hard to estimate; possibly it is less than the diameter of the pits, ca. 10 µm.

SEM reveals that the sclerites in ELI-0001402 consist of densely packed finely spiculate mineral crystals less than 2 µm in length whereas the surrounding trunk surface is covered with iron oxide octahedral pseudomorphs of pyrite, which have been replaced by the spiculate mineral crystals (Fig. 2A₄, A₅). EDX and element mapping reveal that the lateral sclerites are composed mainly of iron oxide with fewer amounts of phosphorus, and the surrounding area is mainly composed of aluminosilicates, probably chlorite (Fig. 3), thus, the spiculate probably are limonite. It should be noted that up to 3.53 wt% of organic carbon and lesser amounts of phosphorus and sulphur can be detected from the mapping

Table 1. EDX analysis of the mapping area in Fig. 3, noting the high concentration of carbon in specimen ELI-0001402.

Elements	Weight (%)	Atom (%)
C K	3.53	6.40
O K	45.61	62.15
Mg K	1.69	1.52
Al K	7.56	6.11
Si K	18.30	14.20
P K	0.15	0.11
S K	0.09	0.06
K K	2.61	1.46
Ti K	0.26	0.12
Fe K	20.19	7.88
Total	100.00	

area (Table 1). EDX analysis in ELI-0001403 and ELI-0001404 shows similar results to ELI-0001402.

Genus *Tabelliscolex* Han, Zhang, and Shu, 2003

Type species: Tabelliscolex hexagonus Han, Zhang, and Shu, 2003, Qionghusian Stage (Early Cambrian), Chengjiang, Eastern Yunnan, China.

Tabelliscolex chengjiangensis sp. nov.

Figs. 1G, 4A.

Derivation of the name: After the type locality.

Holotype: ELI-0001219, part and counterpart.

Type locality: Ma'anshan section, Changing County, Yunnan Province, China.

Type horizon: (*Eoredlichia*–*Wutingaspis* Zone) Yu'anshan Member, Heilinpu Formation, Early Cambrian.

Material.—Holotype only.

Diagnosis.—Elongate trunk with annuli that bear a pair of elongate elliptic macroplates on each, constructed by hexag-

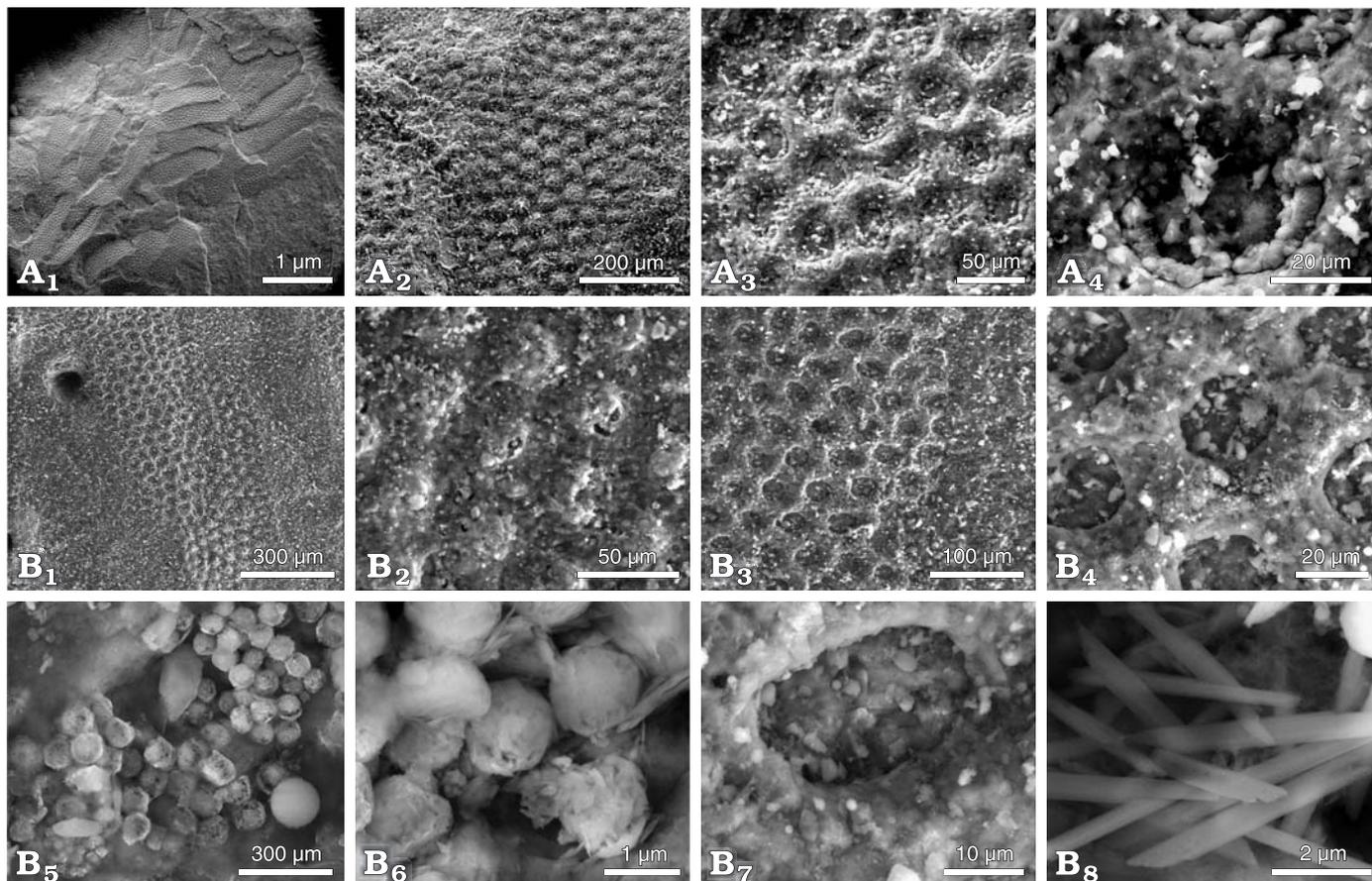


Fig. 4. SEM-BSE images of uncoated specimens of *Tabelliscolex* from the Early Cambrian of Chengjiang, China. **A.** *Tabelliscolex maanshanensis* sp. nov., ELI-0001219, holotype; A₁, molted elongate sclerites; A₂, shows the tubercles and the pits on the inner side; A₃, showing each pit has a inner circllet of concentric laminae; A₄, close-up showing the pit and the inner lamina. **B.** *Tabelliscolex hexagonus* Han, Zhang, and Shu, 2003a, ELI-0001218, holotype; B₁, two over-lapping plates, one plate showing the tubercles (B₂) and another showing the pits (B₃); B₄, the skeleton of the plate, noting the framboidal pyrites within the skeleton; B₅, close-up showing framboidal pyrites replicated by finer minerals (B₆); B₇, close-up of the pit; B₈, some needle-like minerals within the pit in B₇.

onally arranged tubercles. It differs from *Tabelliscolex hexagonus* by having a concentric lamina in each tubercle and possibly lacking a dorsal sclerite on each annulus.

Description.—The holotype, ELI-0001219, is completely composed of more than 76 pairs of long elliptical sclerites. All these sclerites are constructed from hexagonally arranged hemi-spherical tubercles (pits) (Fig. 4A₁, A₂) same with that of *Tabelliscolex hexagonus* (see Figs. 1F, 4B₁–B₃; see also Han et al. 2003a: pl. 1; Huang 2005: figs. 44–46), thus each sclerite usually has six others surrounding it while the marginal ones have four others. These tubercles are ca. 30 μm and the inner surface of the sclerites has an additionally inner circllet within the pit (Fig. 4A₃, A₄).

SEM analysis of *Tabelliscolex hexagonus* reveals that the plates are mainly preserved as irregularly shaped argillaceous mineral crystals (Fig. 4B₄) and microspherules that further consist of short plate-like mineral crystals (Fig. 4B₅, B₆). Some needle-like minerals are present within the pit of a plate (Fig. 4B₇, B₈). This is also the case for *Tabelliscolex chengjiangensis* sp. nov. EDX and element mapping shows that the plates of *Tabelliscolex chengjiangensis* sp. nov. are

mainly composed of oxygen, aluminum, and silicon, representing aluminosilicates, with a lesser amount of iron representing iron oxide, and phosphorus and calcium representing apatite phosphate, as well as organic carbon (6%) that can be found in the mapping area (Fig. 5; Table 2). The plates could not be distinguished from the surrounding trunk in the element mapping, but it did reveal that the fossil is composed mainly of oxygen, aluminum, silicon, components of the aluminosilicates.

Discussion.—*Tabelliscolex hexagonus* was described as bearing two sets of trunk sclerites, one row of elliptic plates on the dorsal side and two lateral rows of elongate elliptical plates, so that each annulus has three sclerites (Han et al. 2003a). The holotype specimen of *T. chengjiangensis* sp. nov. does not preserve the equivalent dorsal sclerites of *T. hexagonus*; thus, such structure need more specimens to be confirmed.

It seems unlikely that the concentric laminae in *T. chengjiangensis* sp. nov. are artefacts of preservation; they are also not newly secreted cuticle replacing older ones because the holotype specimen had already been molted.

Stratigraphic and geographic range.—Type locality only.

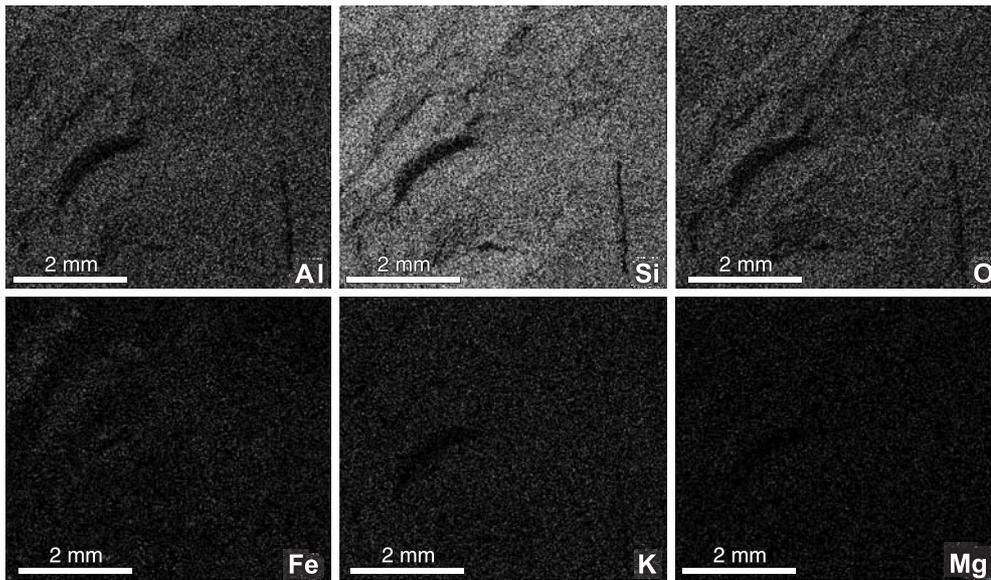


Fig. 5. Element maps of *Tabelliscolex maanshanensis* sp. nov. from the Early Cambrian Chengjiang deposits, China. Mapping area is the upper right part in Fig. 4A₁, ELI-0001219. Images show that lateral sclerites of *Tabelliscolex maanshanensis* are composed predominantly of silicon, oxygen, and aluminum, with lesser amounts of iron, potassium, and magnesium.

Table 2. EDX analysis of the mapping area in Fig. 5, noting the high concentration of carbon in the current specimen (ELI-0001219). Phosphorus and calcium indicate apatite, sulphur indicates pyrite.

Elements	Weight (%)	Atom (%)
C K	6.38	10.55
O K	48.76	60.50
Na K	0.14	0.12
Mg K	1.02	0.83
Al K	9.26	6.81
Si K	23.22	16.41
P K	0.08	0.05
S K	0.34	0.21
K K	3.72	1.89
Ca K	0.62	0.31
Ti K	0.46	0.19
Fe K	6.01	2.13
Total	100.00	

Comparison and implications for evolution of the palaeoscolecidans

Certain fossil and extant priapulids show structures comparable to the ventral spines of *Cricocosmia*. For example, the trunk of *Louisella pedunculata* (Conway Morris, 1977) from the Middle Cambrian Burgess Shale bears two rows of ventral papillae, which was conceived to have a respiratory function; the female Recent priapulid *Tubiluchus corallicola* bears many more tumuli on the ventral side of the trunk than the male (Kirsteuer and Land 1970; Land 1970) and our new observations confirm that *Mafangscoplex* specimens also occasionally bear roughly two rows of trunk papillae (our unpublished observation). Thus, it seems reasonable to interpret the morphs with ventral spines as a female of *Crico-*

cosmia jinningensis rather than a new species. Correspondingly, those devoid of ventral spines would be males or an artifact of preservation. The ventral spines may have functioned for respiration, help in fertilization, to increase friction in burrowing, or for mucus secretion from glands.

Similar structures of the tubercle-bearing sclerites are widely seen in other palaeoscolecidans: e.g., *Houscolex* Zhang and Pratt, 1994, *Utahphospha* (Müller and Müller 1976), *Kaimenella* (Märss 1988: pl. 3: 10), *Plasmuscolex*, *Gamascolex*, *Hadimopanella* (Wrona 1982, 1987, 2004; Kraft and Mergl 1989: pl. 5, pl. 6: 1), as well as various *Palaeoscolex* (Whittard 1953; Conway Morris 1997) species described by Müller and Hinz-Schallreuter (1993). However, the sclerites of *Cricocosmia* and *Tabelliscolex* are apparently larger than those mentioned above and each annulus of the trunk bears only one pair of such sclerites (see Fig. 6). In other palaeoscolecid worms each annuli usually have one to two rows of plates, and the remaining area is tightly packed with platelets or microplates.

We propose that the trunk ornament of palaeoscolecidans is classified in five types: microplate, platelet, plate and macroplate as well as various trunk protuberances, i.e., tubules, nipple-like projections, possible seta and ventral spines. The last type, that is few in number and occurs relatively occasionally, is of little significance in genus-level classification (Müller and Hinz-Schallreuter 1993; Zhang and Pratt 1994; Han et al. 2003a). Because the platelets or microplates are microscopic versions of the plates in some species, i.e., *Palaeoscolex lubovae* (Ivantsov and Wrona 2004) and *Palaeoscolex piscatorum* (Conway Morris 1997), most probably they are homologous structures. This allows us to propose that: (1) the trunks with only one kind of uniform microplate or platelet most represent the primitive condition, which is represented by *Maotianshania* (see Hou and Bergström 1994; Hu 2005); (2) the trunks with plates and platelets represent the advanced condition as seen in most palaeoscolecidans, especially because the platelets are mi-

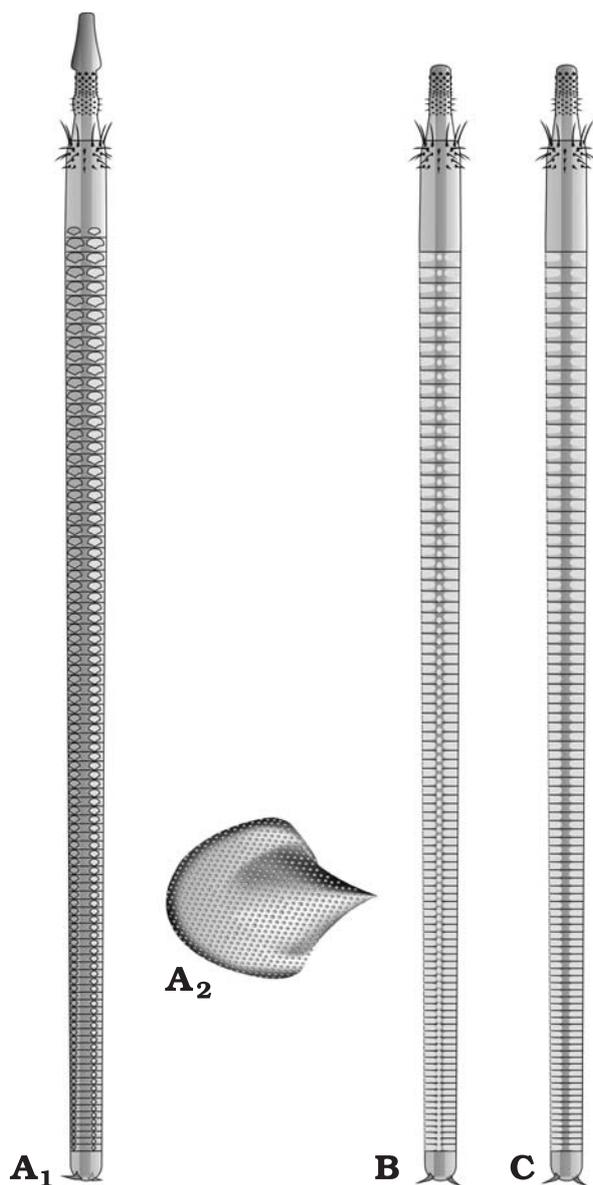


Fig. 6. Reconstructions of the palaeoscolecid worms *Cricocosmia* and *Tabelliscolex* (modified from Huang 2005b). A. *Cricocosmia jinningensis*; A₁, whole animal; A₂, typical lateral sclerite of *Cricocosmia jinningensis*. B. *Tabelliscolex hexagonus*. C. *Tabelliscolex maanshanensis* sp. nov.

crossopic versions of the plates; (3) the trunks with macroplates and/or platelets most likely represent the most specialized level presented by *Cricocosmia* and *Tabelliscolex*.

Well-preserved specimens show that nearly all the remaining area left by the plates is occupied by microplates and platelets, and thus this seems to be one of the key diagnostic features of palaeoscolecidans. *Cricocosmia* and *Tabelliscolex* lack tightly-packed microplates or platelets, which is possibly an artefact of preservation because the inner surface of these sclerites resembles the platelets of some palaeoscolecidans, e.g., *Gamascolex herodes* (Kraft and Mergl 1989: pl. 5: 1–4, pl. 6: 1; Hinz et al. 1990: fig. 2g) and *Houscolex lepidotus* (Zhang and Pratt 1994: fig. 2), thus suggesting homology.

Because the scalids, pharyngeal teeth and trunk spines share a cone-shaped outline, Han et al (2003b) conceived that these structures are homologous. However, the tubercle-bearing or net-like microstructure is not found in the scalids of extant priapulids and other introvertians. Thus, the similarities between these structures are superficial.

It was widely known that the dorsal sclerites on some Cambrian lobopods, e.g., *Microdictyon* (Bengtson et al. 1986, 1990; Hao and Shu 1987; Chen et al. 1989, 1995), show a compound eye-like microstructure with various nodes (tubercles) at the point of the coalescence of the walls, somewhat similar to the sclerites of our palaeoscolecid material. This structure has been conceived as possibly having a function similar to the compound eyes of insects and trilobites (Dzik 2003; Chen 2004). However, such structures are also shared in the compound eyes and carapace of some bivalve arthropods (Shu et al. 1990; Dzik 2003), and recently have been reported in the eyes on the small heads of some lobopods (Collins 2002; Liu et al. 2004), thus, providing a crucial clue to understanding the origin of the compound eye.

A gradual evolutionary change from palaeoscolecidans to lobopods to arthropods was proposed by Dzik and Krumbiegel (1989) and has been indirectly supported by molecular analysis of recent forms of ecdysozoans (Aguinaldo et al. 1997; Mallatt et al. 2004). Fossil evidence supports the hypothesis that the two later forms are closer in phylogeny because of the presence of walking appendages (see Briggs et al. 1994; Hou et al. 2004). The microstructure of the sclerites in their cuticle also lends support to the idea of their close relationship. Although the trunk ornaments of palaeoscolecidans are rather diverse in morphology, no structure that could have given origin to a compound eye-like structure is known there. Additionally, the trunk of palaeoscolecidans is covered by tightly packed platelets or microplates, and this phenomenon is unseen in known lobopodians and arthropods. This, in this sense, indicates a closer relationship between the latter two.

Implications for preservation

It has been generally accepted that in the Chengjiang fossils the pyrite has been replicated by iron oxide, but sulphur has not previously been reported. The studied specimens have retained a rather small amount of sulphur (ca. 0.09 wt% in *Cricocosmia* and ca. 0.34 wt% in *Tabelliscolex*) (Tables 1, 2). Organic carbon was reported from dorsal sclerites in *Microdictyon*, the gill arches of *Haikouella*, the gut trace of palaeoscolecidans and *Stellostomites*, the grasping appendages of *Anomalocaris* (Zhu 2005), as well as *Isoxys* carapace (Gabbott et al. 2004). Approximately 6.38 wt% and 3.53 wt% of organic carbon were detected in the studied specimens (see Tables 1, 2), higher than ever reported (2.1 wt%), supporting that organic carbon and sulphur have high potential to be retained in decay-resistant structures, but were lost later possibly through intense weathering, as suggested by Butterfield (2002, 2003). Whether the source of the organic

carbon in the gut of an animal is an original composition of the gut or gut contents, needs wide examination because the gut has generally been accepted as a labile structure. It should be noticed that the concentration of organic carbon and sulphur are higher in the sclerites of *Tabelliscolex* than in those of *Cricocosmia*, probably indicating that the larger mass of decay-resistant structures can retain a relatively high content of such light elements or that the sclerites of the former are more resistant to decay.

Our specimens show that the sclerites of palaeoscolecidans are mainly composed of fine crystals whereas the surrounding trunk area is composed of larger crystals, indicating that the highly sclerotized decay-resistant structure has a higher potential than labile tissue to retain delicate structures and the original chemical composition of the animal.

It has been illustrated that the exceptional preservation of Chengjiang organisms has occurred by at least four ways: (1) coalification; (2) pyritization; (3) phosphatization, as well as (4) aluminosilicatization (Zhu et al. 2005). It has been reported that the surface of *Cricocosmia* and *Maotianshania* is composed predominantly of pyrite whereas *Mafangsolex* (*Palaeoscolex*) has high concentrations of phosphorus and calcium (Hu 2005; Zhu et al. 2005). Taken together with the present analysis of *Cricocosmia* and *Tabelliscolex*, all four pathways of preservation that can be found in the Chengjiang palaeoscolecidans are supported, and can even be found co-occurring in a single specimen of *Cricocosmia* or *Tabelliscolex*, and this should shed new light on the preservation of the Chengjiang fossils.

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