



Introvert and pharynx of *Mafangsclex*, a Cambrian palaeoscolecidJie Yang^{1,2}, Martin R Smith³ , Xi-guang Zhang^{1,2} and Xiao-yu Yang^{1,2} ¹Key Laboratory for Palaeobiology, Yunnan University, Kunming 650091, China; ²MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, Kunming 650091, China and ³Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK

Original Article

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Abstract

Palaeoscolecid worms are widespread in the Palaeozoic period, and are of key importance to understanding the emergence of moulting animals (superphylum Ecdysozoa). However, palaeoscolecids lack a diagnostic set of morphological characters, and as such are unlikely to form a natural (monophyletic) group. Consequently, detailed anatomical study of individual taxa is necessary in order to evaluate the phylogenetic significance of palaeoscolecids. New specimens of *Mafangsclex* from the Cambrian Stage 3 Xiaoshiba Lagerstätte in Kunming, China, provide the first detailed account of a proboscis in Palaeoscolecida *sensu stricto*, a core group of palaeoscolecids characterized by having a tessellating scleritome of phosphatic plates and platelets. The eversible mouthparts of *Mafangsclex* comprise an armoured, hexaradially symmetrical introvert, a ring of coronal spines and quincuncially arranged pharyngeal armature, with a range of tooth morphologies. Taken together, this configuration strikingly resembles the proboscis arrangement inferred for the ancestral ecdysozoan. The six-fold symmetry represents an important difference from the pentaradial priapulid proboscis. The retention of key aspects of the ancestral ecdysozoan body plan suggests that palaeoscolecids represent a useful window on the earliest stages of ecdysozoan evolution.

1. Introduction

Palaeoscolecids are ecdysozoan worms whose distinctive phosphatic sclerites are a familiar component of the early Palaeozoic fossil record; isolated plates and articulated fragments of their annulated cuticle are well documented as small shelly fossils (Müller & Hinz-Schallreuter, 1993; Zhang & Pratt, 1996; Harvey *et al.* 2010) and small carbonaceous fossils (Butterfield & Harvey, 2012; Slater *et al.* 2017). The annulated nature of the cuticle and its microscopic structure was historically presumed to denote an annelid affinity (Glaessner, 1979; Kraft & Mergl, 1989), though potential similarities with priapulans, nematodes and chordates were briefly mooted (Kraft & Mergl, 1989; van den Boogaard, 1989).

A robust case for an ecdysozoan affinity was first made after the discovery of palaeoscolecids in the Chengjiang Lagerstätte (Hou & Bergström, 1994). The non-mineralized cuticle preserved in these compression fossils revealed an eversible proboscis comprising a hooked introvert (representing the anteriormost part of the trunk) and an armoured pharynx (foregut), a configuration characteristic of ecdysozoan worms (Conway Morris, 1977). Alongside the presence of posterior hooks and trunk papillae in certain ‘archaeopriapulid’ worms, the proboscis has been taken to align palaeoscolecids with priapulans (Müller & Hinz-Schallreuter, 1993; Conway Morris, 1997), a position that found early cladistic support (Wills, 1998; Harvey *et al.* 2010). On this view, palaeoscolecids may illuminate priapulid origins, but would be too derived to directly inform early ecdysozoan evolution.

Alternatively, the priapulid-like features of palaeoscolecids may simply be inherited from an ancestral ecdysozoan that was macroscopic and annulated, exhibited circumoral structures and pharyngeal teeth on an eversible proboscis, and moved by peristalsis (Budd, 2001; Harvey *et al.* 2010; Smith & Caron, 2015). If palaeoscolecids are monophyletic, they either diverged from a deep node within Ecdysozoa (Budd, 2001) or sit in the ecdysozoan stem group (Conway Morris & Peel, 2010). These possibilities are linked to the position of the root of the Ecdysozoan tree, a factor that is difficult to establish by phylogenetic analysis: rooting a tree requires a suitable outgroup, but previous cladistic analyses (Wills, 1998; Harvey *et al.* 2010; Wills *et al.* 2012) have employed *Gastrotricha*, a taxon liable to long-branch attraction given that its ecdysozoan-like features are likely convergently derived.

Finally, palaeoscolecids may represent a paraphyletic grade that straddles the base of the ecdysozoan tree, with the implication that the ancestral ecdysozoan was itself a palaeoscolecid-grade organism. This situation is supported by cladistic results that place palaeoscolecids in the stem lineages of Nematomorpha (Hou & Bergström, 1994) and Priapulida (Wills *et al.* 2012), and by the mounting evidence that palaeoscolecids with lobopodian-like paired

trunk sclerites (Steiner *et al.* 2012) may be stem-group panarthropods (Dzik, 1991; Han *et al.* 2007; Smith & Caron, 2015).

Despite the relative abundance of palaeoscolecid in Burgess Shale-type deposits (Zhao *et al.* 2014; Wang *et al.* 2014; Martin *et al.* 2016; Vannier & Martin, 2017), and the potential value of pharyngeal and introvert armature in taxonomic and phylogenetic study (Smith *et al.* 2015), detailed reconstructions of palaeoscolecid proboscides are scarce. Besides the ambiguous toothed proboscis (pharynx?) of *Palaeoscolex* from the Ordovician Fezouata biota (Kouraiss *et al.* 2018), a pharynx has been described in atypical members of the group, including *Cricocosmia*, whose dorsal plates mark it as a possible stem-panarthropod (Steiner *et al.* 2012; Smith & Caron, 2015); *Xystoscolex*, whose preservation does not allow straightforward comparison with other palaeoscolecid taxa (Conway Morris & Peel, 2010); and *Tylotites* (Han *et al.* 2007); the latter two taxa may be close relatives of *Louisella*, which is no longer considered a palaeoscolecid (Smith, 2015). *Guanduscolex* (Hu *et al.* 2008), *Scathascolex* (Smith, 2015) and *Utahscolex* (Whitaker *et al.* 2020) more closely resemble *Palaeoscolex*, but are excluded from the palaeoscolecids *sensu stricto* by the absence of tessellating microplatelets (Harvey *et al.* 2010); the same is likely true of *Maotianshania* (García-Bellido *et al.* 2013). As such, the only direct observations of the proboscis in Cambrian palaeoscolecids *sensu stricto* come from *Wronascolex* (García-Bellido *et al.* 2013) and *Mafangsclex* (Hu, 2005). Previous reports have lacked detail (Hou & Bergström, 1994), a full written description (D. Y. Huang, unpub. Ph.D. thesis, Univ. Claude Bernard Lyon 1, 2005) or illustration (Hu, 2005; García-Bellido *et al.* 2013), leaving it difficult to critically evaluate proboscis morphology.

Here we present new specimens of *Mafangsclex* from the Xiaoshiba biota (Yang *et al.* 2013, 2018), which provide new details of the morphology and armature of the introvert and pharynx, resolving the configuration of the archetypal palaeoscolecidan proboscis.

2. Material and methods

All fossils dealt with in this study were collected from mudstone beds within the lower part of the Hongjingshao Formation at the Xiaoshiba section, which contains the index trilobite *Zhangshania typica* (Hou *et al.* 2017). Specimens were photographed using a Leica DFC 500 digital camera mounted to a Leica M205-C Stereoscope under bright-field illumination, a Leica DFC7000 T monochrome digital camera attached to a Leica M205 FA fluorescence stereomicroscope and a FEI Quanta 650 scanning electron microscope under low vacuum. Figure 2a is a composite image to maximize armature visibility; each pixel's luminance has been calculated using the Grain Merge algorithm in the GNU image manipulation program (www.gimp.org) from two source images with complementary lighting directions, with the value of the blue RGB channel inverted; chroma and hue correspond to original colour values under bright-field illumination. Specimens are deposited at the Yunnan Key Laboratory for Palaeobiology (YKLP), Yunnan University, Kunming, China.

3. Systematic palaeontology

Class PALAEOSCOLECIDA Conway Morris & Robison, 1986
 Family PALAEOSCOLECIDAE Whittard, 1953
 Genus *Mafangsclex* Hu, 2005

Type species. The type species of *Mafangsclex*, *Palaeoscolex sinensis* Hou & Sun, 1988, is now regarded as a junior synonym of *Sabellidites yunnanensis* Luo & Zhang, 1986 (Luo *et al.* 2014). Note that, contra Luo *et al.* (2014), the name of the type species remains unchanged under Article 67.1.2 of the International Code of Zoological Nomenclature. Luo *et al.* (2014) recognized *Sabellidites badaowanensis* Luo & Zhang, 1986 as a junior synonym of *S. (=M.) yunnanensis*, which renders *Mafangsclex* monospecific.

Emended diagnosis (after D. Y. Huang, unpub. Ph.D. thesis, Univ. Claude Bernard Lyon 1, 2005; Luo *et al.* 2014). Elongate palaeoscolecid, 30 to 50 times longer than wide. Introvert narrower than trunk, bearing 12 longitudinal rows of quincuncially arranged hook-like scalids. Proximal pharynx with small cuspidate teeth; distal pharynx sparsely ornamented with larger teeth. Trunk densely annulated, with each annulus comprising two to three transverse rows of alternating plates near each edge of an annulation. Plates round, with one central node. Space between plates occupied by platelets. Gut undifferentiated. Single pair of tail hooks.

Mafangsclex cf. yunnanensis
 Figures 1–3

Material. Thirteen specimens: YKLP 12374–12386.

Description. Two specimens preserve the full length of the trunk: the trunk and introvert of YKLP 12374 (Fig. 1h) measure 98 mm in length and 2.0–2.4 mm in diameter; the everted pharynx measures an additional 6.6 mm. The respective measurements for YKLP 12379 (Fig. 1c) are 76 mm, 1.5–2.0 mm and 8.4 mm. The smallest specimen, YKLP 12376a, is 1.2 mm wide and over 52 mm long, consistent with a constant length:width ratio of ~40–50.

Five specimens display an everted proboscis (Fig. 1), whose construction follows the conventional ecdysozoan configuration (Conway Morris, 1977; Smith & Caron, 2015; Smith *et al.* 2015): it comprises an introvert armed with posterior-directed hooks (Zone I of Conway Morris, 1977); an unarmed proximal pharynx (Zone II) and a distal region of the pharynx bearing anterior-directed armature (Zone III) (Fig. 2).

The introvert is slightly narrower than the trunk, ~1.5 mm wide and 3.4 mm long, representing ~4 % of the length of the trunk (Fig. 1a, c, h). It bears 12 longitudinal rows of posterior-directed hooks, arranged quincuncially: six rows can be observed on a single side of the compressed introvert (Fig. 2a, b), and excavation of the margins of the preserved introvert reveals corresponding hooks at a lower level in the matrix (Fig. 2c, d). The vertical position of these hooks, and the absence of displaced hooks elsewhere on the introvert, suggests that this hook belongs to a separate row. Consequently, each of the six visible rows corresponds to one unseen at a deeper plane within the fossil. Each row contains nine or more hooks, whose size decreases from the anterior to the posterior (Fig. 2a, b, f, k–n); the anteriormost hook is ~170 µm in height and 300 µm in width (Fig. 2e).

The fully everted pharynx extends about three times the length of the introvert (Fig. 2). Its base is encircled by a band of anterior-directed coronal spines, measuring 150 µm high and 80 µm wide (Fig. 2e). The unarmed proximal region of the pharynx (i.e. Conway Morris's Zone II) is approximately as long as wide; the distal region (Zone III) bears quincuncially arranged teeth until it flares to form a distal bulb (Fig. 1c). The proximalmost teeth of Zone III (Fig. 2h–j), like those of *Ottoia* or *Selkirkia*, exhibit a prominent triangular arch culminating in a distinct prong (see Smith *et al.* 2015 for terminology), though their preservation is



Fig. 1. (Colour online) Specimens of *Mafangsolex cf. yunnanensis* with proboscis structure from the Xiaoshiba Lagerstätte. (a, b) YKLP 12385: (a) part; (b) counterpart. (c) YKLP 12379, complete specimen. (d) YKLP 12380, preserving part of pharyngeal teeth. (e, f) YKLP 12386: (e) almost complete specimen; (f) view of tail hook. (g, h) YKLP 12374: (g) view of tail hook; (h) complete specimen. Abbreviations: pr – proboscis; thk – tail hook. All scale bars represent 2 mm, except (f) and (g), which are 500 μ m.

insufficient to establish the presence or nature of any denticles or pad. Distally, the teeth become wider, and the prong is diminished (Fig. 2g). Insofar as the limited preservation allows a meaningful comparison, the gradient of tooth morphology resembles the transition from Type B to Type D teeth in *Ottoia* (Smith *et al.* 2015).

The trunk is densely annulated with about four annulations per millimetre (Figs 1, 3a, b). Annulations are delimited by intercalary furrows (Fig. 3a–c). Each annulation is ornamented with two sclerite bands, occupying three quarters of the annulation width, separated by a median zone, occupying the remaining quarter

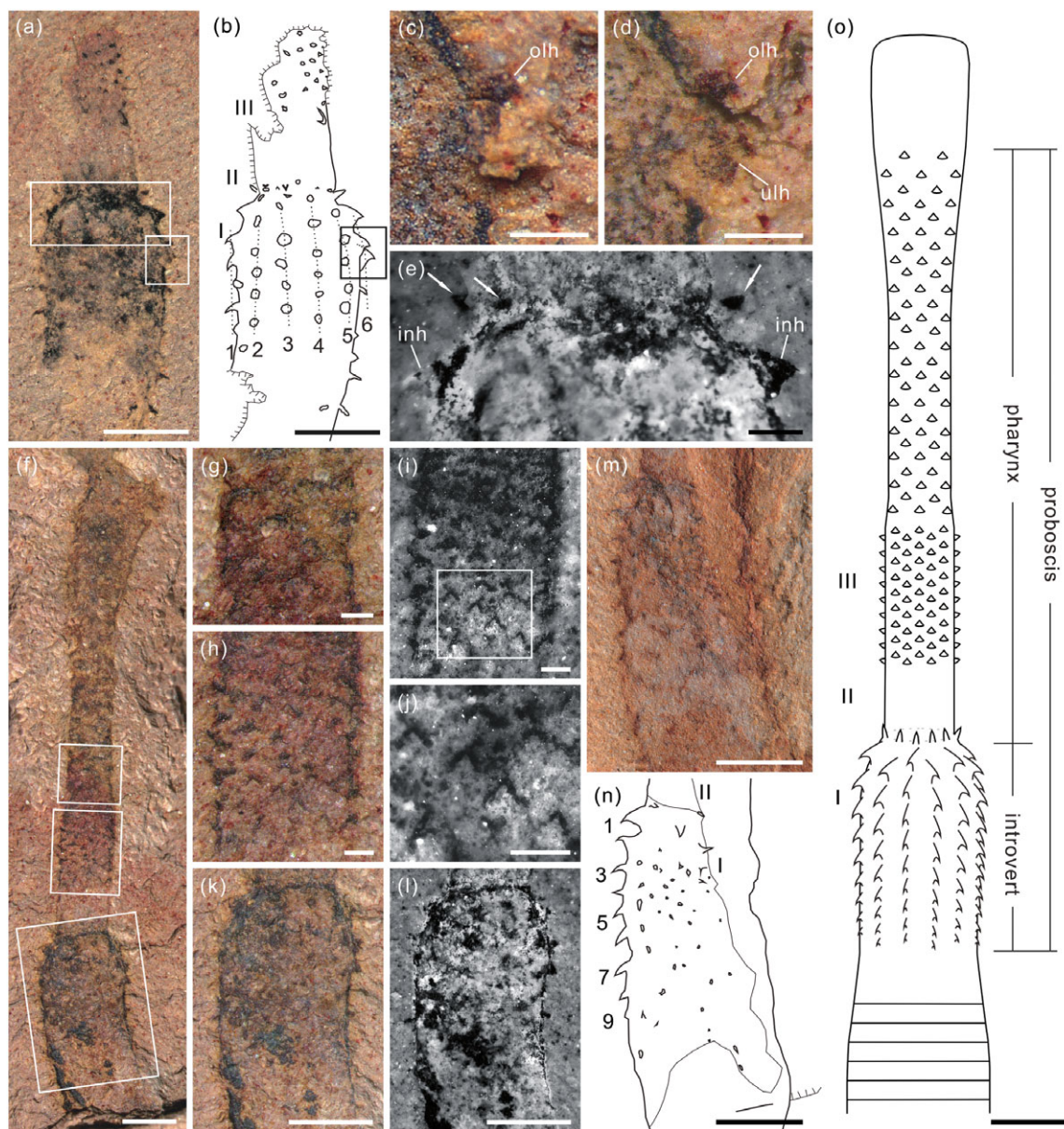


Fig. 2. (Colour online) Proboscides of *Mafangscölex* cf. *yunnanensis*. (a–e) YKLP 12385a: (a) close-up of proboscis; (b) line drawing; (c) original state of (d), showing the overlying hook; (d) enlargement of the boxed area in (a), showing the underlying hook exposed after matrix around being peeled off; (e) fluorescence image showing the coronal spines (white arrow) and two anteriormost Zone I hooks. (f–l) YKLP 12385b: (f) close-up of proboscis; (g) enlargement of the boxed area in (f), showing the distal teeth of Zone III; (h) enlargement of the boxed area in (f), showing the proximal teeth of Zone III; (i) fluorescence image showing the proximal teeth of Zone III; (j) enlargement of the boxed area in (i); (k) enlargement of the boxed area in (f), showing Zone I; (l) fluorescence image showing the lateral introvert hooks of Zone I. (m, n) YKLP 12379: (m) close-up of proboscis; (n) line drawing of (m). (o) Reconstruction of proboscis. Abbreviations: I, II, III – armature associated with Conway Morris’s (1977) Zone I, II and III; inh – introvert hook; olh – overlying hook; ulh – underlying hook. Scale bars represent 1 mm (a, b, f, k–o); 200 µm (c–e, g–j).

(Fig. 3b, c). Each band comprises two to three transverse rows of alternating plates, which are round and closely spaced, 35–50 µm in diameter, with one prominent central node (Fig. 3b–d). Platelets, resembling the plates but 10–15 µm in diameter, fill the gaps between plates (Fig. 3c, d).

Most specimens are coiled (Fig. 1), presumably reflecting stress or post-mortem processes (Zhao *et al.* 2012). The worms exhibit more coils than *Cricocosmia* or *Maotianshania* of equivalent width (D. Y. Huang, unpub. Ph.D. thesis, Univ. Claude Bernard Lyon 1, 2005), presumably reflecting the greater body length of *Mafangscölex*.

The gut occupies a slightly ventral position and terminates at a posterior anus flanked by a robust pair of hooks (Fig. 1e–h). The gut is generally preserved as a flat carbonaceous film, but occasional regions exhibit relief (Fig. 1d), recalling the situation in Sirius Passet palaeoscolecid (Peel, 2017).

Remarks. The new specimens evidently belong to *Mafangscölex*, but the details of the pharynx differ from the situation previously described in *M. yunnanensis* (= *Palaeoscolex sinensis*). Hou & Bergström (1994) described a ‘priapulid-type proboscis’, but their text, illustration and interpretative drawing do not allow a detailed evaluation of the proboscis armature. Hu (2005) reports 15

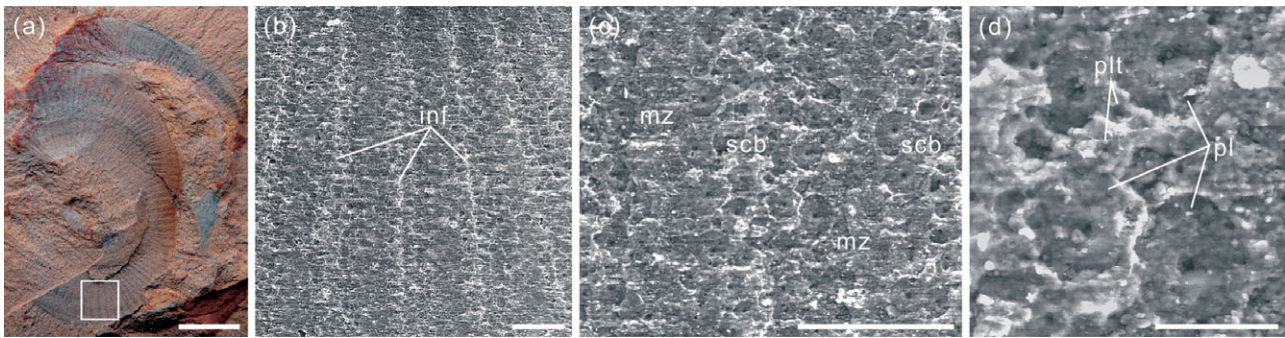


Fig. 3. (Colour online) Cuticle ornamentation of *Mafangsclex* cf. *yunnanensis*. (a–d) YKLP 12381: (a) whole view; (b) enlargement of the boxed area in (a), SEM micrograph showing sclerite bands on annulations; (c) enlargement of (b); (d) details of plate and platelet. Abbreviations: inf – intersegmental furrow; mz – median zone; plt – platelet; pl – plate; scb – sclerite band. Scale bars represent 2 mm (a); 200 μ m (b, c); 50 μ m (d).

longitudinal rows of seven scalids each in the proximal region of Zone III, with ten further rows of seven scalids more distally, and implies an absence of armature in Zones I and II. If accurate, this would justify the erection of a separate species for our material. Unfortunately, no figures are provided in support of this interpretation, making it difficult to evaluate these claims; we suspect that these scalids may instead belong to Zone I. Two proboscides of *M. yunnanensis* figured elsewhere (but not described in detail) (D. Y. Huang, unpub. Ph.D. thesis, Univ. Claude Bernard Lyon 1, 2005) appear to bear introvert and possibly coronal spines, and do not obviously differ from our own material. Even if the younger age and separate provenance hint that our material may represent a separate species, we do not consider the type material of *M. yunnanensis* to be sufficiently well described to support the diagnosis of a separate species.

4. Discussion

Notwithstanding the tubicolous *Selkirkia* (Lan *et al.* 2015) and the lobopodian *Collinsium* (Yang *et al.* 2015), this is the first report of a free-living ecdysozoan worm from the Xiaoshiba biota, though we note that further vermiform material from this deposit awaits formal description.

The new material of *Mafangsclex* is most instructive in its detailed preservation of the everted introvert and pharynx. Proboscis morphology in the Palaeoscolecida *sensu stricto* (Harvey *et al.* 2010) has hitherto been known only from *Palaeoscolex* cf. *tenensis* from the Ordovician Fezouata biota (Kouraiss *et al.* 2018), but the details of this material are ambiguous. Whereas Kouraiss and colleagues described five longitudinal rows of sclerites on a pharynx, they observed six unarmed areas (their fig. 3f), which implies that the total number of sclerite rows around the circumference is 12. Indeed, we believe that a sixth row of sclerites is faintly visible in the lateral margins of the described structure. Rather than a pharynx, we also speculate that the organ described is an introvert: all other occurrences of sclerites in longitudinal rows occur on introverts, whereas pharyngeal teeth are quincuncially disposed (van der Land, 1970; Conway Morris, 1977; Adrianov & Malakhov, 2001).

Based on current data, we therefore consider the symmetry and configuration of the *Palaeoscolex* pharynx to be ambiguous. The introvert and pharynx of *Mafangsclex* thus provide the first clear indication of proboscis morphology in Palaeoscolecida *sensu stricto*, establishing a six-fold symmetry and a construction that conforms to the wider ground plan shared by the majority of

Cambrian ecdysozoan worms (Conway Morris, 1977): an introvert with multiple circlets of posterior-directed hooks, a ring of coronal spines, an unarmoured proximal pharynx and quincuncially arranged teeth with a gradation of morphology in the distal pharynx. The single circlet of introvert hooks reconstructed in *Scathascolex* (Smith, 2015) is thus not representative of palaeoscolecids more broadly, and conceivably connects this taxon to nematomorph-like taxa with a single ring of introvert teeth (Maas *et al.* 2007). In view of the faint preservation of the coronal spines in our material, we postulate that the reported absence of equivalent structures in *Guanduscolex* (Hu *et al.* 2008) (and the type material of *Mafangsclex*) likely represents a lack of preservational fidelity rather than a genuine absence; this would leave the problematic *Ancalagon* as the only Cambrian ecdysozoan worm to lack coronal spines.

On a simplistic view, the morphological conservatism of the *Mafangsclex* mouthparts could be interpreted as the retention of the ancestral ecdysozoan ground plan in the Palaeoscolecida *sensu stricto*. This said, superficially similar introverts characterize Cambrian worms ascribed to the distantly related gastrotrichs (Chen *et al.* 2018) and sipunculans (Smith & Zhang, 2018), suggesting that the broad-scale morphology of the palaeoscolecid introvert may be constrained by its presumed locomotory function.

Because six-fold symmetry is not inherent to the function of the introvert, this detail is less straightforward to attribute to convergence. A hexaradially arranged introvert was likely the primitive condition for Ecdysozoa: not only does it characterize all ecdysozoans from the Fortunian (earliest Cambrian) period (Liu *et al.* 2014, 2019), but its vestiges are apparent in the majority of extant phyla, including stem- and crown-group loriciferans (Sørensen *et al.* 2008; Peel *et al.* 2013), nematomorphs, larval nematodes (despite the lack of introvert armature) (Maas *et al.* 2007) and certain panarthropods, in the form of the six oral papillae of *Aysheaia* (Whittington, 1978) and the six oral plates of tardigrades (Boesgaard & Kristensen, 2001; Biserova & Kuznetsova, 2012; Guidetti *et al.* 2013).

In contrast, five-fold introvert symmetry characterizes a rarefied subset of Ecdysozoa comprising the kinorhynchs (Sørensen *et al.* 2008) and most fossil and modern priapulans (Adrianov & Malakhov, 2001; Huang *et al.* 2004; Dong *et al.* 2010; Kesidis *et al.* 2019). Whether or not this pentaradial pattern is derived, it militates against the close grouping of palaeoscolecids with priapulans.

Given the great disparity of Cambrian ecdysozoan worms, observations of a single taxon are not in themselves sufficient to

resolve the evolutionary origins of ecdysozoans. Nevertheless, Palaeoscolecida *sensu stricto* ought not to be considered as a derived subset of the priapulid lineage; instead, the close correspondence between the proboscis observed in *Mafangscplex* and that reconstructed in the ancestral ecdysozoan is consistent with a deep phylogenetic origin of palaeoscolecoid worms.

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