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NEW PALAEOSCOLECID WORMS FROM THE FURONGIAN (UPPER CAMBRIAN) OF HUNAN, SOUTH CHINA: IS *MARKUELIA* AN EMBRYONIC PALAEOSCOLECID?

by BAICHUAN DUAN[1], XI-PING DONG[1]* *and* PHILIP C. J. DONOGHUE[2]*

[1]School of Earth and Space Sciences, Peking University, Beijing 100871, China; e-mails: duanbch@pku.edu.cn; dongxp@pku.edu.cn
[2]School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK; e-mail: phil.donoghue@bristol.ac.uk
*Corresponding authors.

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Abstract: Three-dimensional fragments of palaeoscolecid cuticle have been recovered from the Furongian (upper Cambrian) of Hunan, South China. Extraordinary preservation of the fossils shows exquisite surface details indicating a three-layered structure of the cuticle. One new genus and two new species *Dispinoscolex decorus* gen. et sp. nov. and *Schistoscolex hunanensis* sp. nov. are described. The co-occurrence of these palaeoscolecid remains with those of *Markuelia hunanensis* allowed us to test the hypothesis that *Markuelia*, known hitherto only from embryonic remains, is an embryonic palaeoscolecid. The comparative anatomy of *Markuelia* and the co-occurring palaeoscolecids shows a number of distinctions, particularly in the structure of the tail; all similarities are scalidophoran or introvertan (cycloneuralian) symplesiomorphies. The available evidence does not support the interpretation of *Markuelia* as an embryonic palaeoscolecid.

Key words: Palaeoscolecida, Priapulida, Scalidophora, Introverta, Cycloneuralia, Wangcun Lagerstätte.

THE Wangcun Lagerstätte in the Furongian (upper Cambrian) Bitiao Formation of Wangcun, Yongshun County, western Hunan, has yielded a small but three-dimensional soft-bodied fauna. The fossil assemblage includes characteristic elements of the classic Orsten Fauna (Dong *et al.* 2005*b*; Maas *et al.* 2006) such as phosphatocopid (Liu and Dong 2009, 2010; Zhang and Dong 2009; Zhang *et al.* 2011*a*, *b*, 2012) and skaracarid (Liu and Dong 2007) crustaceans, as well as the finest examples of *Markuelia* (Dong *et al.* 2004*a*; Donoghue *et al.* 2006*a*), a scalidophoran worm known only from embryonic stages of development. The fauna also includes three-dimensional, albeit fragmentary, cuticular remains of palaeoscolecid worms that have not been described in previous reports (Dong *et al.* 2010; Harvey *et al.* 2010).

The discovery of palaeoscolecids in the Bitiao Formation at Wangcun is of particular significance because of their co-occurrence with *Markuelia hunanensis* (Dong *et al.* 2004*a*). Although cladistic analyses have resolved *Markuelia* as a stem-scalidophoran (Dong *et al.* 2004*a*; Dong *et al.* 2005*a*; Donoghue *et al.* 2006*a*; Dong *et al.* 2010), it has been proposed that *Markuelia* is a palaeoscolecid (Huang *et al.* 2006). The affinity of palaeoscolecids has been controversial. Although they were originally interpreted as annelids (Whittard 1953), Conway Morris (1993) suggested that they were, in effect, stem-members of Scalidophora (the clade comprised of the phyla Kinorhyncha, Loricifera and Priapulida). This hypothesis was corroborated by the subsequent discovery that palaeoscolecids possess an armoured protrusible pharynx (Hou and Bergström 1994) substantiating membership of Cycloneuralia (the clade comprised of the phyla Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera). The precise affinity of palaeoscolecids among Cycloneuralia remains the subject of debate (Müller and Hinz-Schallreuter 1993; Hou and Bergström 1994; Conway Morris 1997; Wills 1998; Dong *et al.* 2004*a*; Huang *et al.* 2004*a*, *b*, 2006; Maas *et al.* 2007*a*, *b*; Conway Morris and Peel 2010; Harvey *et al.* 2010), although formal cladistic analyses invariably resolve a stem-priapulid affinity (Wills 1998; Dong *et al.* 2004*a*, 2005*a*, 2010; Donoghue *et al.* 2006*a*; Harvey *et al.* 2010).

Although the late embryonic development of *Markuelia* has been resolved (Dong *et al.* 2005*a*, 2010; Dong 2007; Peng and Dong 2008), postembryonic stages are unknown and would provide a critical test of established phylogenetic hypotheses. Thus, we describe the cuticular remains of palaeoscolecids that co-occur with *Markuelia hunanensis* in the Late Cambrian Bitiao Formation of South China

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with the aim of testing the hypothesis that *Markuelia* is a palaeoscolecid and that these represent postembryonic remains.

MATERIALS AND METHODS

We sampled approximately seven metric tonnes from a 200-mm bed of limestone in the Furongian (upper Cambrian) Bitiao Formation, in Wangcun section, Yongshun County, western Hunan, South China (for locality details see Dong *et al.* 2004*b*). The rock was broken into blocks of approximately 10 cm^3 and subjected to dissolution using *c.* 10 per cent buffered acetic acid following Müller (1985) and the protocol described by Jeppsson *et al.* (1999). The insoluble residues were sorted under a binocular microscope. Thousands of palaeoscolecid cuticular fragments were recovered, 202 of which were examined using an FEI QUANTA 200F environmental scanning electron microscope. Figured specimens were reposited in the Geology Museum, Peking University (GMPKU). The terminology for descriptions follows Müller & Hinz-Schallreuter (1993), Conway Morris (1997) and Topper *et al.* (2010).

DESCRIPTION

Preservation

The cuticular fragments are preserved through calcium phosphate replication of the original tissues, preserving all three-component layers of the cuticle, as well as their histological distinction, to a resolution of approximately one micron (Harvey *et al.* 2010). Given that soft tissue replacement has occurred, it is not clear whether the sclerites on the external surface layer were mineralized *in vivo*. While palaeoscolecids are commonly represented by isolated sclerites that were mineralized *in vivo*, these sclerites were not mineralized in all palaeoscolecids, for example, *Louisella* (Conway Morris 1977). Regardless, preservation of the underlying cuticle layers maintains the relative arrangement of the sclerites and reveals the degree with which they vary in shape, size and ornamentation across large fragments of the cuticle. The specimens range in their extent from small fragments of cuticle with a low number of sclerites, through fragments of the circumference of the body and millimetres of the length of the body, to specimens that preserve the posterior ends of the organism; no fragments of the oral end of the organism were recovered. Many specimens show evidence of the shedding of sclerites from the outer layer of the cuticle (Fig. 1C), but it is not clear whether this represents an *in vivo* condition or an artefact of taphonomy or laboratory recovery. Microbial activity is invariably implicated in soft tissue replacement by mineral (Briggs 2003; Raff *et al.* 2008). Our specimens show no diagnostic evidence, such as of bacterial autolithification. However, some of the remains preserve circa 5 μm diameter anastomosing strands on inner surfaces of the cuticle, also mineralized in calcium phosphate (Fig. 1B). Crusts of calcium phosphate were also encountered, particularly on the inner surfaces of the cuticle, displaying a spherulitic or botryoidal surface texture. These are characteristic of diagenetic crusts in other conservation Lagerstätte preserving soft tissue through calcium phosphate mineral replacement (Yue and Bengtson 1999; Xiao and Knoll 2000).

Anatomy

The taxonomy of palaeoscolecids is divided between a form taxonomy based largely on isolated singular plates that provide little insight into the biology of the organism, and a biological taxonomy based upon two-dimensional sedimentary casts of partial to whole specimens that reveal considerable detail concerning gross and fine anatomy but in which the detailed morphology of the plates is difficult to discern (Conway Morris and Peel 2010). The recovery of fragments of anatomy composed of fused plates provides a means of reconciling these taxonomies, no matter how incomplete the remains are (Hinz *et al.* 1990; Müller and Hinz-Schallreuter 1993).

The ornamentation of the plates among the material recovered in the Bitiao Formation exhibits sufficient diversity in morphology and arrangement to justify as many as six distinct form taxa. However, this range of variation falls within the scope seen in individual organisms in other deposits (Hinz *et al.* 1990; Müller and Hinz-Schallreuter 1993). We recognize two taxa among the assemblage of material distinguished principally upon differences in the organization of the tail, although there are also differences in sclerite ornamentation. Nevertheless, these taxa share features concerning the nature of the cuticle that is organized into annulae. The annulae range in height and anterior-posterior width from 1.5 and 10 μm, respectively, in specimens with a diameter of 107 μm, to 17 and 88 μm, respectively, in specimens with a diameter of 424 μm. The arrangement of the sclerites on the surface of the cuticle, in paired rows on each annulus, meets with the condition in other palaeoscolecids, as defined strictly by Harvey *et al.* (2010). However, these are merely the largest of the sclerites, and they intergrade with a field of smaller sclerites that occupy the intervening spaces and, in particular, the surface of the cuticle in low relief between each annulus (Figs 1E–G, 2G).

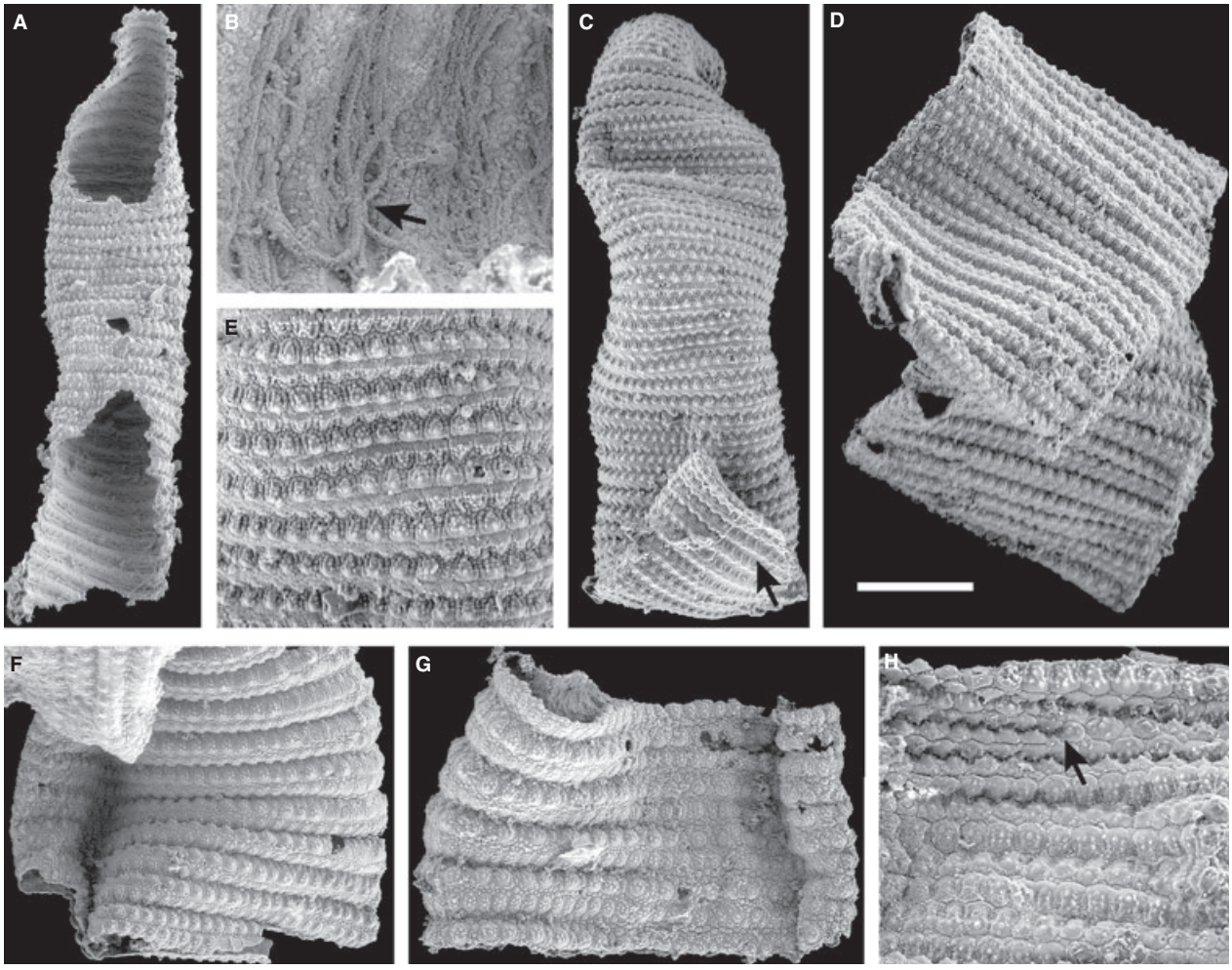

FIG. 1. *Dispinoscolex decorus* gen. et sp. nov. without the aboral end preservation. A–B, GMPKU2395; A, cuticle fragment with thread-like structure; B, details of the thread-like structure of A; arrow points to the anastomosing strands on inner surfaces of the cuticle. C, E, GMPKU2399; C, dorsal view of cuticle fragment; arrow points to the exfoliation of outer layer of cuticle; E, details of C. D, GMPKU2400; lateral view of a twisted cuticle fragment. F, GMPKU2401; lateral view of cuticle fragment. G, GMPKU2402; lateral view of cuticle fragment. H, GMPKU2403; cuticle fragment showing bifurcation of annulus; arrow points to the bifurcation of annulus. Relative scale bars represent 259 μm (A), 46 μm (B), 120 μm (C), 200 μm (D), 54 μm (E), 176 μm (F), 164 μm (G), 55 μm (H).

The key distinction between the two taxa, however, is the number of tail spines, with *Dispinoscolex decorus* possessing one pair of recurved spines (Fig. 2) and *Schistoscolex hunanensis* possessing two symmetrical pairs aligned in parallel and recurved in the same orientation, the smaller pair positioned behind the larger (Fig. 3A–B, E). In both taxa, the tail spines are arranged about a central furrow that is aligned parallel to the direction of spine curvature (Figs 2A–D, H, 3B). Tail spines are not an unusual feature of palaeoscolecids, of living or fossil priapulids or of scalidophorans more generally (Harvey *et al.* 2010); however, Harvey *et al.* (2010) identified as a shared derived character of palaeoscolecids the presence of one or two pairs of ventrally recurved hooks arranged about a dorsoventrally oriented terminal posterior orifice.

SYSTEMATIC PALAEONTOLOGY

NEPHROZOA Jondelius, Ruiz-Trillo, Baguñà and Riutort, 2002

ECDYSOZOA Aguinaldo, Turbeville, Linford, Rivera, Garey, Raff and Lake, 1997

INTROVERTA Nielsen, 1995

SCALIDOPHORA Lemburg, 1995

PRIAPULIDA (total group) Delage and Hérouard, 1897

PALAEOSCOLECIDA Conway Morris and Robison, 1986

PALAEOSCOLECIDAE Whittard, 1953

Genus DISPINOSCOLEX gen. nov.

Type species. *Dispinoscolex decorus* sp. nov.

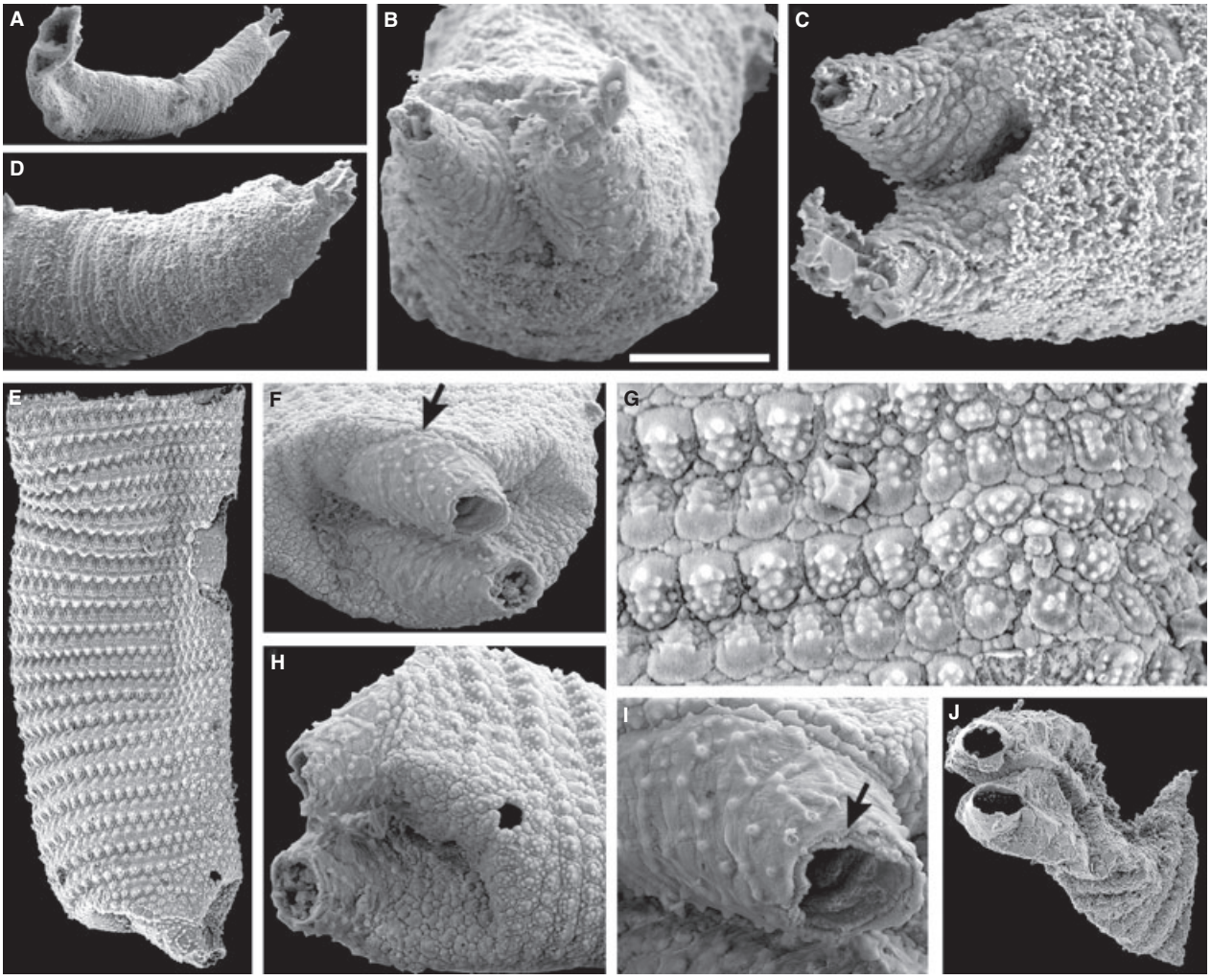

FIG. 2. *Dispinoscolex decorus* gen. et sp. nov. A–D, GMPKU2393; A, lateral view of a very small trunk fragment with aboral end, the annulations are clear but surface ornamentation is faint; B, posterior view of A, showing a two-spined configuration; C, ventral view of A, showing the opening between two spines; D, lateral view of A. E–I, GMPKU2394 holotype; E, a compressed cuticle fragment with aboral end, showing the dorsal/ventral differentiation; F, postero-lateral view of the aboral end of C, showing detailed surface structure of the aboral end; arrow points to the furrow between trunk and tail spine; G, close-up of cuticle ornamentation of C; H, ventral view of the aboral end of C; I, close-up of one of the spines of C, showing the two-layered structure and net-like pattern of surface; arrow points to the two-layered structure of spine cuticle; J, a specimen recovered from the Late Cambrian of Wangcun section in western Hunan, exhibiting one pair of fractured aboral spines (an unnamed specimen in Harvey *et al.*, 2010, fig. 2E). Relative scale bars represent 306 μm (A), 50 μm (B), 43 μm(C), 115 μm (D), 140 μm (E), 68 μm (F), 26 μm (G), 54 μm (H), 31 μm (I), 231 μm (J).

Derivation of name. From *di-*, Latin, two, and *spino*, Latin, spinous, referring to the two-spined tail configuration of the worm, and *scolex*, Greek, worm.

Occurrence. Westergaardodina cf. *calix–Prooneotodus rotundatus* conodont zone in Bitiao Formation of Paibian Stage, Furongian Series (conventional upper Cambrian) from Wangcun section which represents a margin of the Yangtze platform, Yongshun County, western Hunan, South China.

Diagnosis. Palaeoscolecid with one pair of spines at the aboral end. Annulations narrow. Intercalations indistinct. Plates densely arranged. Ornamentation of plates highly decorated.

Dispinoscolex decorus sp. nov.
Figures 1, 2

v. 2010 unnamed Harvey, Dong and Donoghue, p. 181, fig. 2E.

Derivation of name. From *decorus*, Latin, decorated, referring to the highly decorated plate pattern.

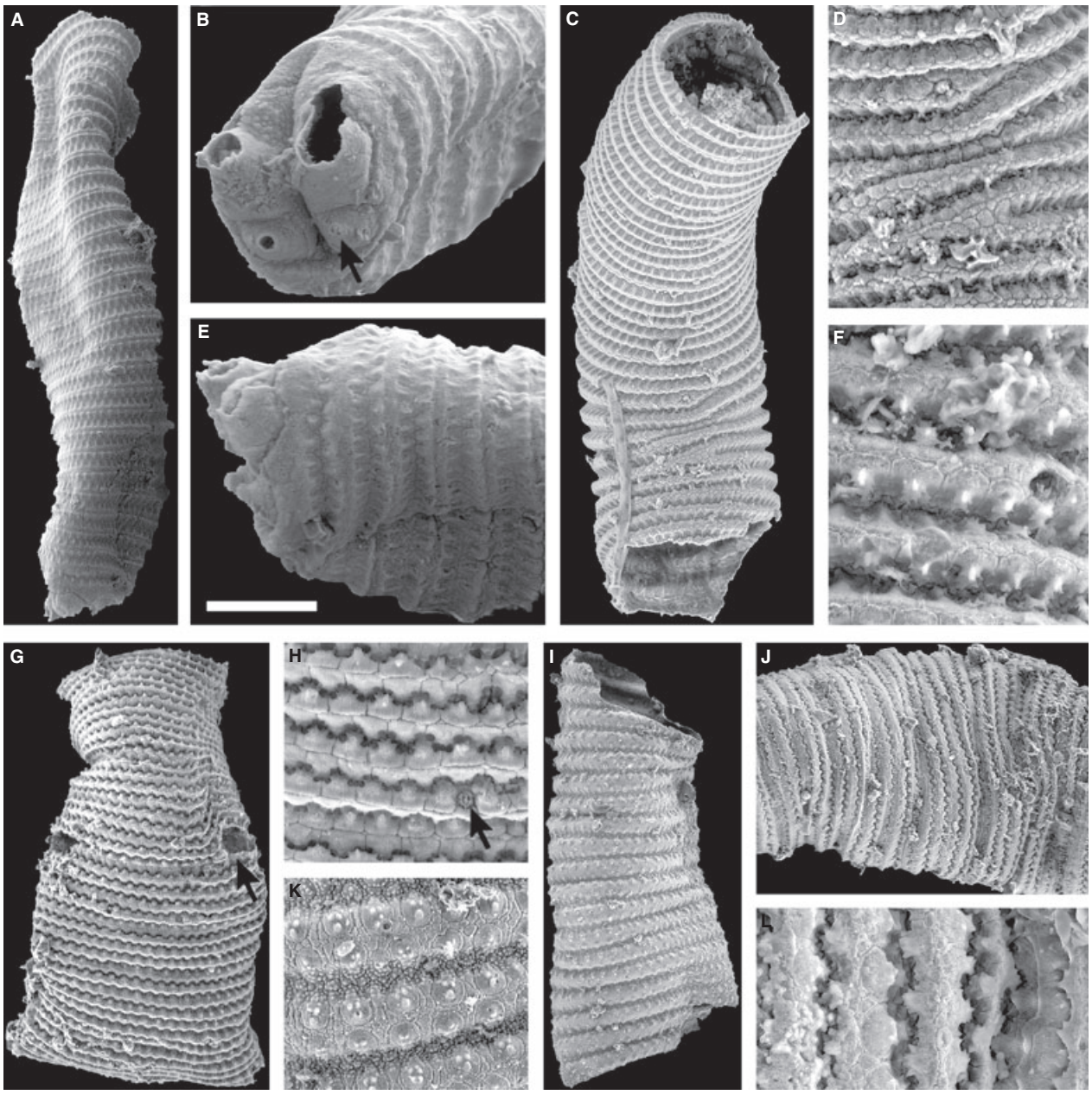

FIG. 3. *Schistoscolex hunanensis* sp. nov. A–B, E, GMPKU2404 holotype; A, lateral view of a compressed cuticle fragment with two pairs of aboral spines; the surface ornamentation details are vague; B, postero-lateral view of the aboral end of A with ventral side on the top, showing a two-pair-spine configuration and the ventral pair (upper pair) is larger than the dorsal pair (lower pair); arrow points the tip of tail spine appearing as a small round opening; E, lateral view of aboral end of A. C–D, GMPKU2405; C, ventral view of cuticle fragment with bifurcation; D, details of C, showing bifurcation of annulus. F, GMPKU2406; details of cuticle decoration. G–H, GMPKU2407; G, dorsal view of cuticle fragment, showing deformation and rupture of cuticle; arrow points to the rupture and deformation of cuticle; H, details of G, showing plates with outstanding central elevation; arrow points to the broken tubule in the median annular zone. I, K, GMPKU2408; I, lateral view of cuticle fragment; K, details of I, showing narrow intercalations and flat microplates. J, L, GMPKU2409; J, cuticle fragment showing extreme contraction; L, details of J, showing highly contracted annuli. Relative scale bars represent 124 μm (A), 52 μm (B), 75 μm(C), 33 μm (D), 50 μm (E), 18 μm (F), 84 μm (G), 26 μm (H), 217 μm (I), 86 μm (J), 63 μm (K), 17 μm (L).

Holotype. GMPKU2394 (Fig. 2E–I).

Type locality and horizon. Westergaardodina cf. *calix–Prooneotodus rotundatus* conodont zone in Bitiao Formation of Paibian Stage, Furongian Series (conventional upper Cambrian) from Wangcun section, Yongshun County, western Hunan, South China.

Material. GMPKU2385, GMPKU2393-2395, GMPKU2399-2403, GMPKU2410 (143 specimens).

Occurrence. As for type locality and horizon.

Diagnosis. A species of palaeoscolecid with a pair of robust spines positioned at the aboral end. Annulations narrow with two rows of regularly close-packed, highly decorated plates of similar size. Ornamentation of plate with broad central elevation, composed of one or two large central nodes and about 10 nodes surrounding them; marginal nodes notable. Intercalation indistinct or narrow. Median annular zone narrow, with microplates of convex surface.

Description. Numerous specimens of cuticle fragments were recovered, but only three specimens are preserved with complete aboral ends; the oral end is unrepresented. Aboral end with a pair of robust tail spines, inclining towards the ventral side and connected to the trunk with a furrow (Fig. 2E–F, H). There is an invagination between the two spines in the sagittal plane representing a dorsoventral aperture, considered a terminal aboral orifice by Harvey *et al.* (2010). The spines are conical in shape, and the tips are mostly broken, revealing that the spines are hollow and, therefore, not completely composed of cuticle (Fig. 2I). The preserved length of the broken spines ranges from 49 to 85 μm; intact spines may have exceeded 100 μm. The cross-sectional profile of the spine bases is circular to oval, with a maximum diameter of 140 μm and average diameter of 70 μm. The cuticle of the spines is two layered, while trunk cuticle is three layered. The outer layer of the tail spine cuticle differs from the trunk in bearing uniformly distributed papillae and transverse wrinkles; the inner layer is thicker (Fig. 2E–F, H–I). Trunk cuticle includes an additional middle layer that expands to accommodate the thickness of the plates (Harvey *et al.* 2010).

The median annular zone is underdeveloped, with microplates distributed sparsely in the gaps between two rows of directly contacting plates. The outline of each microplate is round to oval, with a convex outer surface. Pores, representing the sockets of tubuli (Brock and Cooper 1993; Müller and Hinz-Schallreuter 1993), are distributed irregularly in the median annular zone (Figs 1E–G, 2G).

Annulations are narrow with dorsoventral differentiation. Intercalations indistinct. Plate outline polygonal to oval. Plates on the dorsal side are decorated with an elongate central elevation with one large central node positioned towards the midline of the annulus, and 8 to 10 marginal nodes semi-encircling the large node, forming a 'V' or 'U' shape, tapering towards the annular border. Ventral plates are decorated with a polygonal central elevation, and the central node is of regular size. Tubercles on the lower outer margin develop towards the annular border (Figs 1E–G, 2G).

Remarks. Palaeoscolecids with a pair of tail spines were first recognized in macroscopic specimens with a pair of or only a left/right hook associated with and arranged about a terminal orifice interpreted as an anus (Hou and Bergström 1994; Han *et al.* 2007; Hu *et al.* 2008; Harvey *et al.* 2010). However, the terminal hooks in macroscopic specimens show a high degree of curvature, not seen in *Dispinoscolex decorus*.

The closest comparisons with *Dispinoscolex decorus* include the following: an unnamed specimen from the Middle Cambrian of Australia figured in Harvey *et al.* (2010, Fig. 2F) in which similar tail spines are encountered, but in association with a more elongate and broader terminal aperture, smooth with sparsely distributed plates, not ornamented as in *Dispinoscolex decorus*; the scleritome of close-packed plates, indistinct median annular zone and intercalation draws comparison with *Schistoscolex angustosquamatus* Müller and Hinz-Schallreuter, 1993, but *Dispinoscolex decorus* is distinguished by the complex ornamentation of the cuticular plates; *Shergoldiscolex nodosus* Müller and Hinz-Schallreuter, 1993, bears comparably ornamented cuticular plates bearing a nodular central elevation and tubercles on lower outer margin, but *Dispinoscolex decorus* can be distinguished by bearing similarly sized plates within each annulus, and an indistinct median annular zone.

Genus SCHISTOSCOLEX Müller and Hinz-Schallreuter, 1993

Type species. Schistoscolex umbilicatus Müller and Hinz-Schallreuter, 1993.

Occurrence. From the Middle Cambrian of Australia and the *Westergaardodina* cf. *calix–Prooneotodus rotundatus* conodont zone in Bitiao Formation of Paibian Stage, Furongian Series (conventional upper Cambrian) from Wangcun section which represents a margin of the Yangtze platform, Yongshun County, western Hunan, South China.

Emended diagnosis. Two pairs of spines at the aboral end; the dorsal pair smaller than the ventral pair. Annulation narrow, partly furcated. Intercalations small. Annuli with two rows of plates in contact with each other. Surface of plates with elevated centre. Marginal tubercles may be developed towards annulus borders.

Schistoscolex hunanensis sp. nov.
Figure 3

v. 2010 unnamed Harvey *et al.*, p. 181, fig. 2A.

Derivation of name. From *Hunan*, referring to its occurrence in Hunan, South China.

Holotype. GMPKU2404 (Fig. 3A–B, E).

Type locality and horizon. Westergaardodina cf. *calix–Prooneotodus rotundatus* conodont zone in Bitiao Formation of Paibian Stage, Furongian Series (conventional Upper Cambrian) from Wangcun section, Yongshun County, western Hunan, South China.

Material. GMPKU2404-2409, GMPKU2411 (38 specimens).

Occurrence. As for type locality and horizon.

Diagnosis. A species of palaeoscolecid with two pairs of robust spines positioned at the aboral end, ventral pair larger than dorsal pair. Annulations narrow with two rows of small, close-packed plates. Ornamentation of plate with narrow, highly convex central elevation; tubercles on the elevation partly fused; marginal tubercles faded. Intercalation indistinct or narrow. Median annular zone narrow, with microplates of flat surface.

Description. Cuticle fragments showing aboral end; oral end missing. Aboral end with two pairs of spines, bilaterally symmetrical about the sagittal plane. The dorsal pair distinctly smaller than the ventral pair. A dorsoventral invagination in the sagittal plane between the spines, more extensive on the ventral side than the dorsal. No obvious aperture observed. Both the dorsal and ventral pairs of aboral spines are conical in shape. The tips of the dorsal pair of spines are preserved intact, appearing as a small round opening instead of narrowing into a closed sharp distal point (Fig. 3B). The tips of the ventral pair of spines are broken, revealing that the spines are hollow. The dorsal pair of spines is smaller, 19 μm in length; the ventral pair is significantly larger, though broken, exceeding 26 μm in length. The basal section of the ventral spines is twice that of the dorsal spines. All of the spines are inclined to the ventrum (Fig. 3A–B, E).

Plates are spaced closely, with an indistinct median annular zone and intercalation. Pores are spaced irregularly in the median annular zone. Annuli are comparatively narrow with two rows of plates per annulus. Ornamentation of some sclerites is difficult to discern because of poor preservation or ecdysis (i.e. replacement cuticle not developed premortem). Intact plates are ornamented with a narrow, elongate nodular central elevation, and tubercles on it are partly fused; marginal nodes are small (Fig. 3C–L).

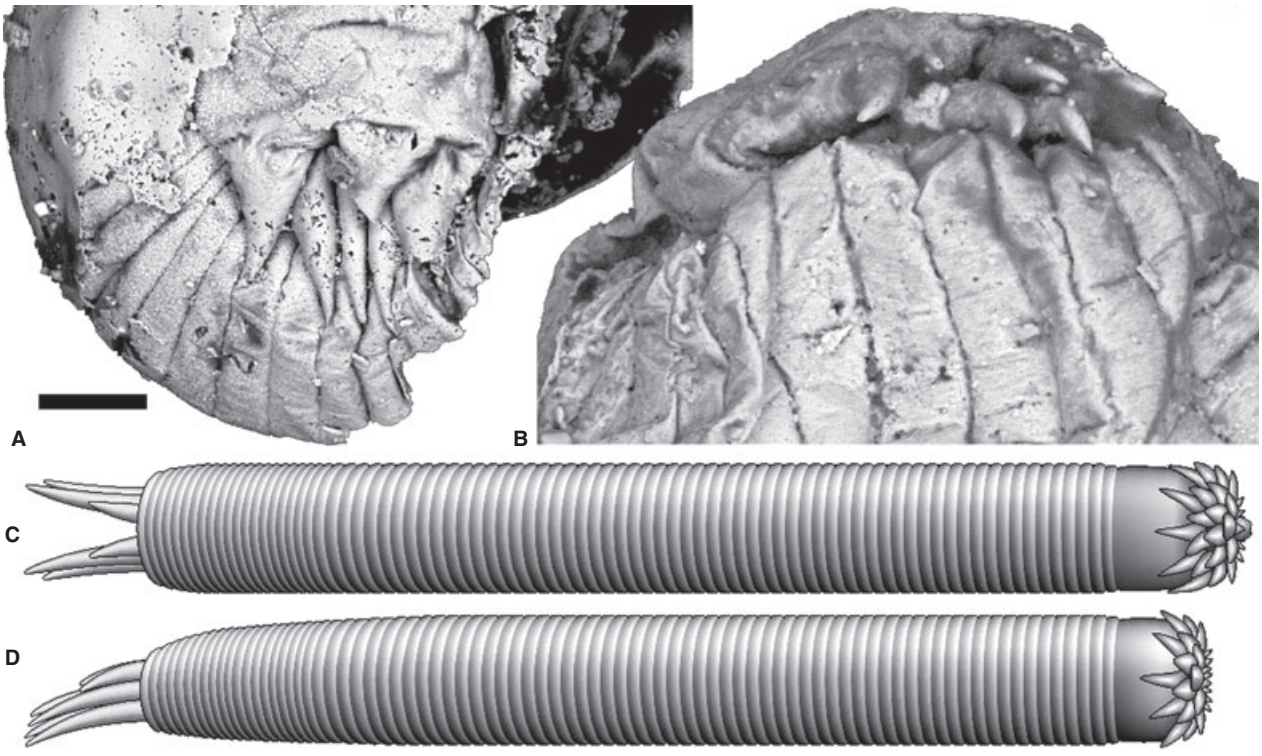

FIG. 4. Embryos of *Markuelia hunanensis* Dong and Donoghue, 2004 from the Late Cambrian Bitiao Formation at Wangcun, Hunan Province, South China. A, GMPKU2017; the six terminal spines associated with the posterior. B, GMPKU2018; view of posterior pole with appendages surrounding central depression; C–D, schematic drawing; the complete animal in an unfurled position as if it had hatched; scalids are illustrated in the everted position; C, dorsal view; D, lateral view. Relative scale bars represent 23 μm (A), 29 μm (B); C–D, not to scale.

Remarks. Schistoscolex hunanensis shares with *Schistoscolex umbilicatus* the presence of two pairs of aboral spines and close-packed plates. However, in *S. umbilicatus,* the aboral end has a broader aperture, and the difference in size between the dorsal and ventral pairs of spines is less distinct than in *Schistoscolex hunanensis* (Müller and Hinz-Schallreuter 1993, text-fig. 11B, G; Harvey *et al.* 2010, fig. 2G), and plate ornamentation is distinct. *Schistoscolex angustosquamatus* also bears two unequally sized pairs of spines, but can be distinguished by the ornamentation of its characteristic cuticular plates, which lack marginal nodes and have a less elaborately ornamented central elevation than *Schistoscolex hunanensis*.

DISCUSSION

Comparison with Markuelia

There are obvious similarities in the gross anatomy of the late embryonic stages of the direct developing *Markuelia* and the postembryonic stages known of palaeoscolecids. These include a vermiform bodyform, terminal eversible mouth associated with an armature of circumoral scalids, the presence of appendages in association with a terminal anus and homonomous annulation (Fig. 4A–D) (Dong *et al.* 2010). However, these shared characteristics have been identified as symplesiomorphies of Scalidophora and, more broadly, Introverta (= Cycloneuralia) (Harvey *et al.* 2010). Given the stem-Priapulida classification of Palaeoscolecida (Wills 1998; Dong *et al.* 2004*a*, 2005*a*, 2010; Donoghue *et al.* 2006*a*; Harvey *et al.* 2010), these characters cannot be potential synapomorphies of Palaeoscolecida + *Markuelia*. There are a number of significant differences between *Markuelia* and the co-occurring palaeoscolecids *Dispinoscolex decorus* and *Schistoscolex hunanensis*, as well as palaeoscolecids more generally. Most obviously, *Markuelia* lacks the cuticular sclerites characteristic of palaeoscolecids (Fig. 4A, B). *Markuelia* also lacks the armoured protrusible pharynx seen in palaeoscolecids and exhibits a lower number of radii in the arrangement of its oral scalids than have been described from palaeoscolecids, as well as a smaller number of circlets (Harvey *et al.* 2010). These differences could be explained away as ontogenetic because, for example, extant priapulids have been described to exhibit ontogenetic differences in the structure of their pharynx and number of circlets of scalids present on their introvert (Wennberg *et al.* 2008; Janssen *et al.* 2009). However, fossilized embryos of *Markuelia* are comparatively common by virtue of the precocious embryonic development of cuticle (Donoghue *et al.* 2006*b*), and so the absence of cuticular sclerites cannot be explained away by arguing that cuticle has not yet developed. Most significantly, perhaps, is the distinction in the anatomy of the aboral end of both *Markuelia* and palaeoscolecids, most particularly *Dispinoscolex decorus* and *Schistoscolex hunanensis*. All species of *Markuelia*, including *Markuelia hunanensis*, possess three pairs of bilaterally arranged spines associated with the terminal anus (Fig. 4A–D), while *Schistoscolex hunanensis* possesses two pairs of spines and *Dispinoscolex decorus* possesses just a single pair of spines; other palaeoscolecids have been described to possess a single spine, or one to two pairs of spines bilaterally disposed about the anus. These differences appear sufficient to preclude the interpretation of *Markuelia* as an embryonic palaeoscolecid.

CONCLUSIONS

We describe two new species of palaeoscolecid, *Dispinoscolex decorus* and *Schistoscolex hunanensis,* from the Furongian (upper Cambrian) Bitiao Formation of Wangcun, Yongshun County, western Hunan. These fossil remains co-occur with *Markuelia hunanensis*, a scalidophoran known from numerous species and geological and geographical localities, but only from preserved embryonic remains. This allows us to test the hypothesis proposed by Huang *et al.* (2006) that *Markuelia* is an embryonic stage of palaeoscolecid development. The anatomy of *Dispinoscolex decorus* and *Schistoscolex hunanensis* conforms to the range of variation already known from palaeoscolecids. There are notable differences between *Markuelia* and palaeoscolecids, including the absence in *Markuelia* of (1) palaeoscolecid cuticular plates, (2) an armoured protrusible pharynx, a smaller number in *Markuelia* of (3) scalid radii, (4) scalid circlets, and the presence in *Markuelia* of (5) a greater number of paired aboral terminal appendages, than seen in any palaeoscolecids including *Dispinoscolex decorus* and *Schistoscolex hunanensis*. The available evidence does not support the interpretation of *Markuelia* as an embryonic palaeoscolecid.

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