Soft-part preservation in a linguliform brachiopod from the lower Cambrian Wulongqing Formation (Guanshan Fauna) of Yunnan, South China

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Hu, S., Zhang, Z., Holmer, L.E., and Skovsted, C.B. 2010. Soft-part preservation in a linguliform brachiopod from the lower Cambrian Wulongqing Formation (Guanshan Fauna) of Yunnan, southern China. *Acta Palaeontologica Polonica* 55 (3): 495–505.

Linguliform brachiopods were important components of early Cambrian benthic communities. However, exceptionally preserved soft parts in Cambrian linguliform brachiopods are extremely sparse, and the most important findings are from the early Cambrian Chengjiang Konservat Lagerstätte of Kunming, southern China. Here we describe the first record of preserved soft-part anatomy in a linguliform brachiopod from the early Cambrian Guanshan fauna (Wulongqing Formation, *Palaeolenus* Zone); a unit which is considerably younger than the Chengjiang fauna. The well preserved soft anatomy include linguliform pedicles, marginal setae and, in a few cases, an intact lophophore imprint. The pedicle has pronounced surface annulations, with its proximal-most part enclosing the apex of the ventral pseudointerarea; the pedicle is up to 51 mm long, corresponding to more than 4 times the sagittal length of the shell, and 12% of the maximum valve width. In details of their preservation, these new fossils exhibit striking similarities with the linguliforms from the older Chengjiang fauna, and all specimens are preserved in a compressed state as flattened impressions. The new linguliform has an elongate oval to subtriangular shell and an elongate triangular ventral pseudointerarea; the pedicle emerged from an apical foramen through a poorly preserved internal pedicle tube. The new linguliform is most similar to the mostly organic-shelled siphonotretoid-like brachiopod *Acanthotretella spinosa*, recently described from the classic middle Cambrian Burgess Shale Konservat Lagerstätte, British Columbia, Canada. The new species *Acanthotretella decaius* sp. nov. is described; it differs from *A. spinosa* in having a slightly thicker pedicle, and a larger and more rigid, probably partly mineralised shell, indicating that the mostly organic shell of *A. spinosa* may represent a secondary reduction of shell mineralisation. However, the spine-like setae of the new species are unfortunately poorly preserved only at the margin of the shell, but the new species is referred tentatively to the Superfamily Siphonotretoidea. The occurrence of *A. decaius* in the Guanshan fauna is the first lower Cambrian (Series 2, early Stage 4) record of both *Acanthotretella* and siphonotretoids, and it represents the first description of a lophophore and digestive tract from the siphonotretoid lineage.

Key words: Brachiopods, Linguliformea, Konservat Lagerstätte, early Cambrian, China.

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Received 12 November 2009, accepted 26 March 2010, available online 13 April 2010.

Introduction

Brachiopods are solitary marine coelomates with their soft body enclosed by a bivalved shell, which is composed of either calcium phosphate or calcium carbonate. This group of benthic animals made their first appearance in the lowermost Cambrian (Holmer and Popov 1996; Popov et al. 1996), and became an important component of marine communities during the early Paleozoic. Although fossil brachiopods in the Palaeozoic era are common and abundant, most of them are known exclusively from their shell, as soft parts are exceptionally preserved only in Konservat Lagerstätten, most notably the lower Cambrian Chengjiang deposits (Luo et al. 1999; Zhang et al. 2008, 2009, 2010 and references therein) and the middle Cambrian Burgess Shale (e.g., Holmer and Caron 2006; Pettersson Stolk et al. 2010). Such remarkable occurrences provide unique insights into the body plan and palaeoecology of early brachiopods that are not available from the study of shells alone (Jin et al. 1993; Zhang et al. 2003, 2004a, b, 2005, 2006, 2007a, b, c, 2008, 2009, 2010; Holmer and Caron 2006; Pettersson Stolk et al. 2010).

doi:10.4202/app.2009.1106

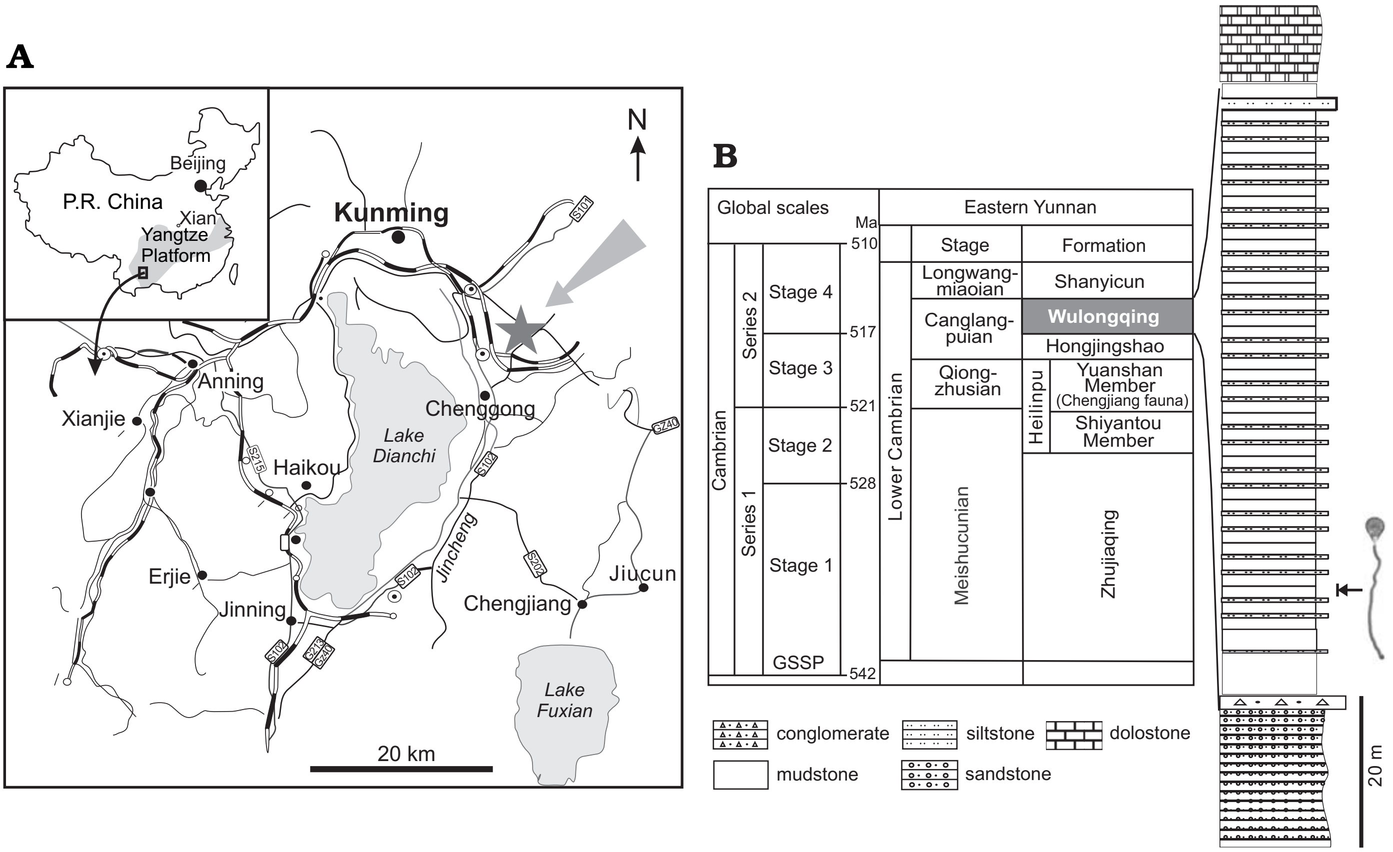

Fig. 1. **A**. Map showing the locality (star) where the brachiopod *Acanthotretella decaius* sp. nov. was collected. **B**. Stratigraphical correlation of the muddy deposits yielding the Guanshan fanua including *A. decaius* sp. nov. in Gaoloufang section near Guangwei village, Kunming, southern China.

Recent geological survey of the Yangtze Platform of South China has led to the discovery of further fossil localities, where brachiopods with exceptional preservation of soft anatomy occur (Zhang and Hua 2005; Luo et al. 2008; Zhang et al. 2008). In this paper, we describe the first record of exceptional preservation in a linguliform brachiopod from the early Cambrian Guanshan fauna. The Guanshan fauna, although less well known and overshadowed by the older comprovincial Chengjiang fauna (Hou et al. 2004), still represents a very significant Burgess Shale-type Lagerstätte. The Guanshan fauna comes from the Wulongqing Formation (Canglangpuian Stage), which is widely exposed around the Kunming-Wuding and Malong-Yiliang areas, Yunnan Province (Luo et al. 1999, 2008). The faunal assemblages are numerically dominated by abundant trilobites (see Luo et al. 2008), and an assortment of non-mineralised Burgess Shale-type fossils of soft-bodied organisms including some eocrinoids (Hu et al. 2007), *Vetulicola* (Luo et al. 2005), palaeoscolecid worms (Hu et al. 2008), chancelloriids, anomalocaridids, sponges, bradoriids, *Tuzoia*, *Isoxys*, and other bivalved arthropods (Luo et al. 2008 and references therein; Liu et al. 2006), as well as a moderately diverse brachiopod fauna (also see Luo et al. 2008: pls. 33–35). The brachiopods comprise *Diandongia pista* (Rong 1974), *Lingulellotreta malongensis* (Rong 1974; Holmer et al. 1997), abundant *Heliomedusa*-like fossils (Luo et al. 2008: pl. 35: 9–12), some small-sized acrotheloid and acrotretoid brachiopods (ZZ unpublished data), as well as the new linguliform brachiopod *Acanthotretella decaius* described herein. *Acanthotretella decaius* is the first brachiopod from the Guanshan fauna with exceptionally preserved soft parts, and it shows a comparable preservation as that found in the Chengjiang brachiopods (Zhang et al. 2004a, 2005, 2007a, 2008), including the fine preservation of the pedicle, setal fringes, and imprints of the lophophore. The genus *Acanthotretella* is otherwise only known from the middle Cambrain (Series 3) Burgess Shale (Holmer and Caron 2006) and, due to its unusual combination of characters including an apparently only weakly mineralised shell and shell-penetrating spines or setae, plays a potentially crucial role in deciphering character transformations along the stem-crown transition among linguliforms, particularly siphonotretids. The new discovery of exceptionally preserved *A. decaius* from the Guanshan fauna extend the occurrence of this taxon back to Series 2 and provides further insights into the morphology and ecology of this probably basal brachiopod.

Institutional abbreviations.—GKG, Yunnan Institute of Geological Sciences, Kunming, China; NWU, Northwest University, Xi’an, China.

Materials and methods

A total of 20 individuals in 16 specimens of *Acanthotretella decaius* were collected from the lower Cambrian Wulongqing Formation of Gaoloufang section at Guangwei Village in Kunming of Yunnan Province (Fig. 1). Of them, 12 individuals have well-preserved pedicle impressions (e.g., Figs. 2A–D, F, 3A–D) while seven are provided with some preserved setal fringes around the shell margin (Fig. 2D–F). Two specimens preserve paired lophophore imprints; only one is illustrated here (Fig. 2B, C) and the other omitted because of somewhat weak preservation. In addition, another two specimens show U-shaped digestive tracts (Fig. 3C, D). All the material in this work comes from the collections made by Yunnan Institute of Geological Sciences, Kunming, China. The fossils were derived from a 40–50 m thick, fine-grained laminated mudstone, occasionally intercalated with thin layers of siltstone or sandstone. Abundant silt-mud couplets with normal grading are commonly observed within the mudstone layers containing the soft-bodied linguliform brachiopods. The Wulongqing Formation contains two trilobite zones: the lower part of *Palaeolenus* Zone and the upper part of *Megapalaeolenus* Zone. The specimens of *A. decaius* were collected from mudstone deposits in the *Palaeolenus* Zone, generally thought to correlate with the upper Botomian Stage of the early Cambrian in Siberia (Luo et al. 1994, 1999). *Acanthotretella decaius* are commonly preserved as reddish-brown impressions or grayish films of shell valves with flattened reddish impression of pedicles, in striking color contrast to the surrounding fine-grained matrix, which is deeply weathered to yellowish green. The shells of *A. decaius* are invariably strongly compressed parallel to the bedding plane, and most shells appear to be flattened into a thin film so that the two valves are indistinguishable from each other. The elongate pedicle is also strongly compressed, and preserved as a reddish impression. Judging from the excellent preservation of the pedicles, and also from the fact that the distal part of the pedicle commonly is obliquely oriented, and cutting through several bedding planes, it is reasonable to suggest that these animals could have been buried alive in situ or transported only a short distance, as has been suggested for the Chengjiang lingulids (Jin et al. 1991; Zhang et al. 2005). It is thus assumed that the specimens might have been entombed alive, possibly as a result of storm-induced burial (Hu et al. 2009).

The specimens are deposited in the Yunnan Institute of Geological Sciences. They were examined and observed under an Olympus Zoom Stereo Microscope, at the Early Life Institute, Northwest University, Xian, and photographed with a Nikon Camera mounted on a photomicrographic system with different illuminations for particular views when high contrast images were required. Measurements were made directly with a millimeter ruler. The photographs were first processed under PhotoShop 7.0 and edited and organised together in CorelDraw 9.0 and finally converted to TIF format.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

Subphylum Linguliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996

Class Lingulata Gorjansky and Popov, 1985

?Order Siphonotretida Kuhn, 1949

Remarks.—The presence of hollow spines has been considered to represent the most important unique character of the Order Siphonotretida (Holmer and Popov 2000). However, Williams et al. (2004) showed that some of the oldest well-established siphonotretides from the upper middle Cambrian are completely imperforated, whilst other Cambrian–Ordovician siphonotretides are perforated, but lack spines. Recently, Holmer and Caron (2006) described a soft-shelled siphonotretide-like brachiopod, *Acanthotretella spinosa* from the middle Cambrian Burgess Shale, whose shell surface is covered by long and slender "spine"-like setae. The setal spines may be considered as potentially homologous with the inferred non-mineralised structures that would emerge from the pores of the siphonotretides *Helmersenia* and *Gorchakovia* (Williams et al. 2004), and they can also be compared closely with the exceptionally preserved setal structures emerging from stunted spines in siphonotretides from Iran (Popov et al. 2009). However, *Acanthotretella* was originally referred to the "stem group Brachiopoda" in view of the lack of a mineralised shell and enigmatic combination of characters. The new older record of an *Acanthotretella* with a better-preserved and possibly more mineralised shell could indicate that the "soft-shelled" nature of the middle Cambrian *A. spinosa* might be a secondary loss; however, it is also possible that this is due to differences in preservation between Guanshan and the Burgess Shale faunas. Here we provisionally assign *Acanthotretella* to the Siphonotretida in view of the presence of a small circular apical foramen, internal pedicle tube and an elongate, large subtriangular pseudointerarea lacking flexure lines, which is also typical of the Siphonotretida.

?Superfamily Siphonotretoidea Kutorga, 1848

Genus *Acanthotretella* Holmer and Caron, 2006

Type species: *Acanthotretella spinosa* Holmer and Caron, 2006. Fossil ridge between Wapta Mountain and Mount Field; Emerald Oncolite Shale Member and Walcott Quarry Shale Member (Greater Phyllopod bed), Burgess Formation.

Emended diagnosis.—Shell mostly organic with variable amount of phosphatic mineral component, inequivalved, biconvex or ventri-biconvex; ventral valve probably apsacline, with elongate and thin pedicle with a central coelomic region, emerging through a short tube with a small circular apical foramen; ventral pseudointerarea elongate, triangular or V-shaped, extending posteriorly far beyond the hinge line; setae variably developed elongate, spine-like; visceral region of both valves, short, triangular, not extending to mid-valve.

Remarks.—As mentioned above, the genus *Acanthotretella* was first described from the Burgess Shale. The shell valves were strongly flattened and evidently torn apart in some

doi:10.4202/app.2009.1106

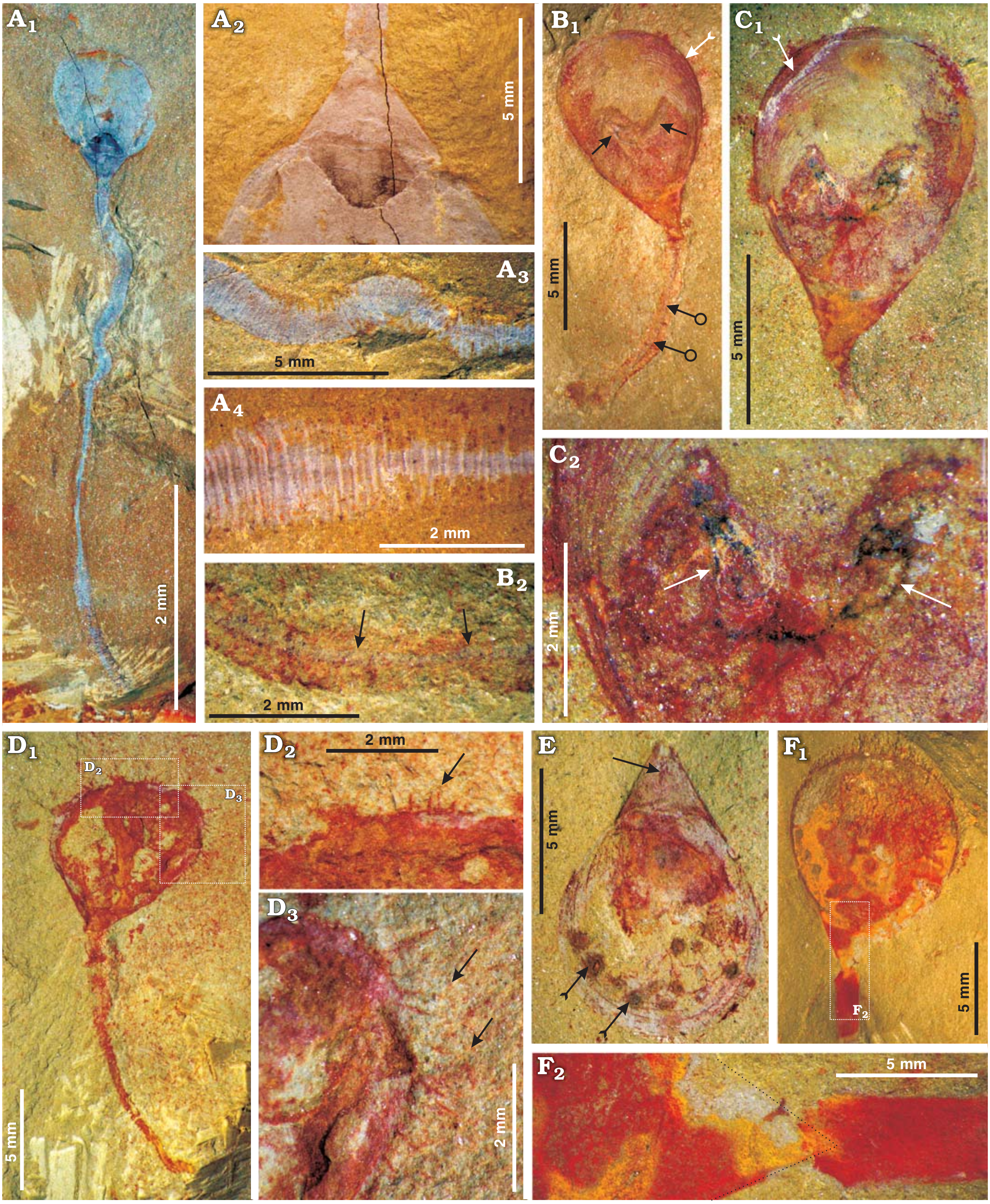

Fig. 2. Linguliform brachiopod *Acanthotretella decaius* sp. nov. from the Wulongqing Formation (*Palaeolenus* Zone), lower Cambrian (recently Series 2, Stage 4), China. **A**. Holotype, GKG CA-007 in general view (A_1); posterior details of the shell valves (A_2), showing the small body cavity posteromedially placed, the elongate subtriangular pseudointerarea and the proximate pedicle; details of the gentle S-shaped portion of pedicle in A_1 (A_3); close-up view of the pedicle annulations in A_1 (A_4). **B**. GKG CA-008A, a flattened specimen anterolaterally compressed in general view (B_1), showing the concentric growth

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specimens. Exterior of both valves was covered by long, spine-like and shell-penetrating setae. By contrast, the new material dealt with here exhibits an invariable shell contour, which might imply a higher degree of shell mineralisation. But this proposal is uncertain because of the difference in preservation between the Burgess Shale and Guanshan fauna. In the new Chinese specimen there is convincing evidence of spine-like setae comparable to those seen in the Canadian species (Holmer and Caron 2006). However, the pedicle differ somewhat between Burgess Shale and Guanshan species: it could be tightly folded and was thus more flexible in the middle Cambrian *Acanthotretella*.

Acanthotretella decaius sp. nov.

Figs. 2A–F, 3A–D.

Etymology: Latinised from Chinese Decai, excellent and brilliant, also acknowledges the Decai scholarship, sponsored by Professor Shu Degan in NWU for financial support of the study to excellent undergraduate and graduate students in NWU.

Type material: Holotype GKG CA-007 (Fig. 2A) composed of part (marked as A) and counterpart (B).

Type locality: Gaoloufang section (N 24°57’10’’; E 102°47’55’’) at Guangwei Village in Kunming of Yunnan Province (Fig. 1).

Type horizon: The lower part of the Wulongqing Formation (Series 2, Stage 4), *Palaeolenus* Zone, Canglangpuian Stage of South China (generally thought to correlate with the Botomian Stage of the early Cambrian in Siberia).

Material.—Holotype plus GKG CA-001AB with marginal setae and pedicle (Fig 2D); GKG CA-002AB with setal remains (Fig 2E); GKG CA-003AB with setal fringes and pedicle (Fig 3F); GKG CA-004AB; GKG CA-005AB; GKG CA-006, a juvenile with some setal fringes and pedicle; GKG CA-008AB with fine preservation of lophophore and coelomic pedicle (Fig. 2B, C); GKG CA-009; GKG CA-010, a distorted specimen with proximal pedicle; GKG CA-011 and 012, shell valves, GKG CA-013AB with 4 individuals, of them 2 with setae and pedicles; GKG CA-014 with 2 individuals with preserved pedicle. Also, two of these individuals have a partially preserved gut, while the other shows faint lophophore imprints; GKG CA-015 with setal remains and a pedicle; GKG CA-016 with pedicle and inferred muscular scars.

Diagnosis.—Shell large with minor phosphatic mineralisation; surface with thin concentric fila; maximum width anterior of mid-valve; ventral pseudointerarea well developed, occupying about 1/3 of the sagittal valve length, probably apsacline lacking distinct flexure lines; elongate and thin pedicle, corresponding to around 15% of the maximum width of the shell; visceral areas of both valves, short, triangular, approximately extending anteriorly to 1/4 of dorsal valve length, and 1/3 of the sagittal ventral valve length.

Measurements.—See Table 1.

Description.—Shell biconvex and tear-shaped to sub-triangular in outline; the maximum sagittal length is 14 mm and the maximum width is 11.5 mm, at about the anterior third of shell length in one specimen. The ratio of shell length to width ranges from 1.22–1.67 (on average 1.38; see Table 1 for details of dimensions below). The ventral pseudointerarea is well developed, apsacline, occupying 37.7% of the sagittal length of the ventral valve, and 65.3% of shell width; the ventral pseudointerarea has a somewhat wide acute angle varying between 60–75°. The ornamentation consists of thin concentric growth lines (Figs. 2B$_1$, C$_1$, 3A, B), delineated by slender reddish fila. The concentric fila are so faint that they could be directly discerned exclusively on the anterolateral portion of some specimens (Fig. 2B$_1$, C$_1$). The ventral pseudointerarea is compressed as a triangular, flattened plate with reddish-brown tints. No flexure lines and transverse striations can be observed on the surface of the ventral pseudointerarea.

The setae of *Acanthotretella decaius* are most frequently preserved along the anterior and anterolateral margins (Fig. 2B–F), and poorly exposed in the posterior parts of the valves. Setae are preserved as reddish, delicate linear fringes or tints. In one specimen, the setae seemingly emerge upright to the anterior shell margin (Fig. 2D$_1$, D$_2$), but curve posteri-

Table 1. Statistics for *Acanthotretella decaius* sp. nov. based on GKG collection from the Guanshan fauna around Kunming, Yunnan Province, South China. See Fig. 5 for location of parameters.

	Lv	Lpi	Lvi	Lp	Wt	Wp	Wped	Lpi/Lv	Lv/Wt	Wp/Wt	apical angle [°]	Lped/Wt	Lp/Lv
Max	14	4	6	6	11.5	7.5	1.5	0.33	1.67	0.69	75	0.17	0.43
Min	7	1.2	3	2.6	5.3	3.6	0.6	0.17	1.21	0.6	60	0.11	0.33
Mean	11.25	3.13	5.22	4.25	8.23	5.4	1.2	0.27	1.38	0.65	64.5	0.14	0.38
SD	2.15	0.91	1.05	1.03	2.06	1.37	0.35	0.05	0.15	0.036	5.88	0.023	0.03
Count	6	6	6	6	6	6	4	6	6	6	6	4	6

line (tiled arrows) and the pedicle bending steeply downward into the sediment; note the paired lophophore imprints inside shell valves (simple arrows) and a longitudinal coelomic lumen in pedicle (circled arrows); details of the pedicle lumen (simple arrows) (B$_2$). **C**. GKG CA-008B, counterpart of B, showing the paired lophophore imprints in general view (C$_1$); details of lophophore imprints of C$_1$ (C$_2$). **D**. GKG CA-001A, an anterolaterally crushed specimen presumably in life position, with the pedicle steeply buried in sediment. An overview (D$_1$), boxes indicate the position of D$_2$ and D$_3$; detailed views of the marginal setae along the anterior and lateral margins (D$_2$, D$_3$). **E**. GKG CA-002B, posterior view of a dorso-ventrally compressed specimen; note the inferred pedicle tube (simple arrow) and some small rounded scars putatively allied with some epibionts (tailed arrows). **F**. GKG CA-003A, a dorso-ventrally compressed specimen in general view (F$_1$), note the marginal setae, sub-triangular pseudointerarea and proximal pedicle; close-up view of box marked in F$_1$ (F$_2$). See Fig. 4 for interpretations.

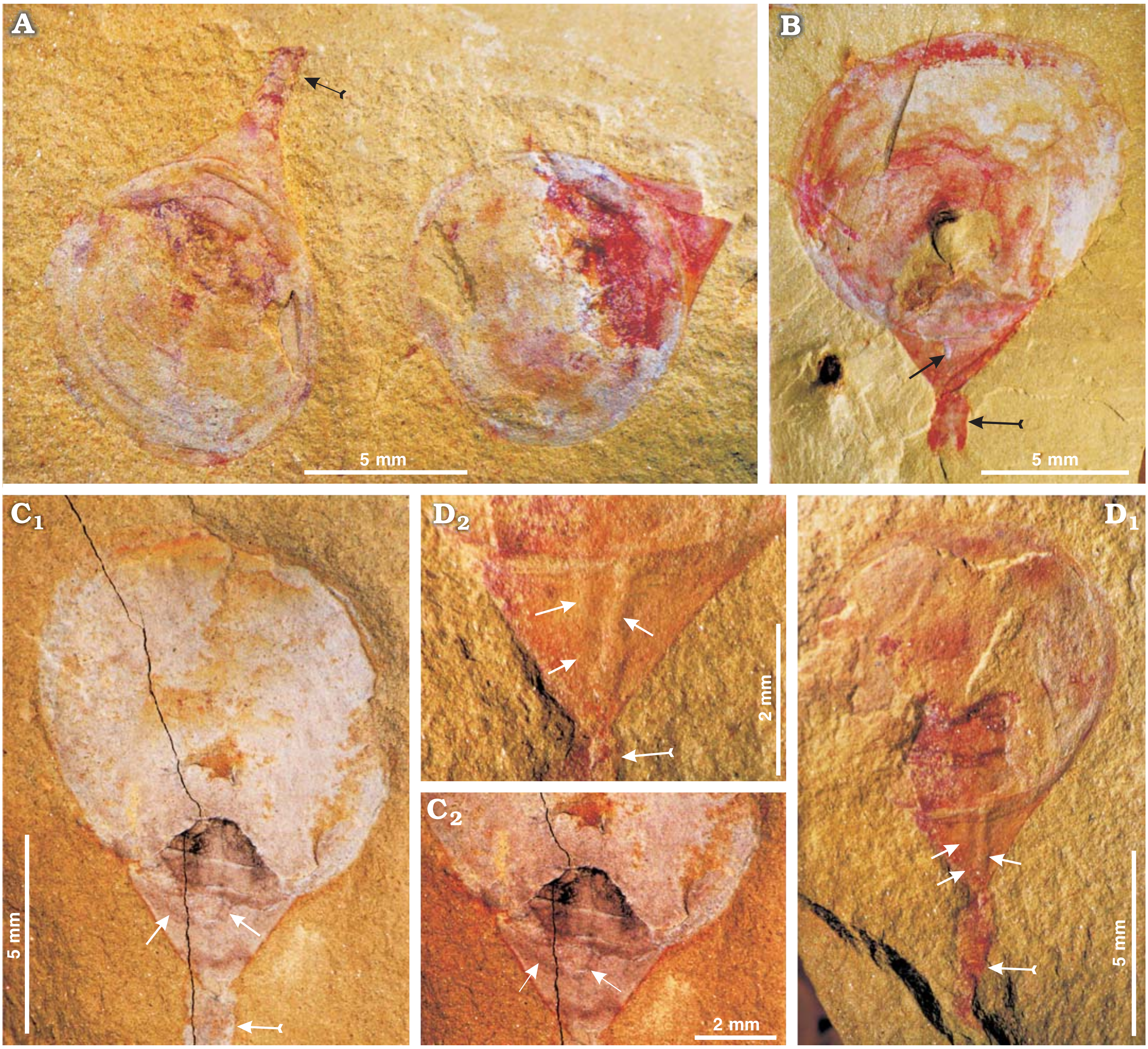

Fig. 3. Linguliform brachiopod *Acanthotretella decaius* sp. nov. from the early Cambrian Guanshan fauna, showing the proximal pedicles (tailed arrows) and gut remains (simple arrows), Yunnan, China. **A**. GKG CA-014, a muddy slab with two individuals preserved together. **B**–**D**. Photographs showing the U-shaped digestive tracts preserved as tubular imprints (simple arrows) with some relief. **B**. GKG CA-011B. **C**. GKG CA-007B. **D**. GKG CA-013(2). General view (C_1, D_1), close-up (C_2, D_2) of tubular relief of guts. See Fig. 4 for interpretations of C_1 and D_1.

orly along the lateral margins (Fig. 2D_3). The maximum setal length is 1.2 mm and they are about 80 μm thick.

A total of 12 individuals with the pedicle preserved were found. The pedicles vary in length and width between different specimens, but the pedicle is never preserved in its entire length. The observable maximum length of the pedicle is about 52 mm, which is more than 4 times the sagittal maximum length of the shell (Fig. 2A_1). The maximum width of the pedicles ranges between 0.6–1.5 mm, corresponding to an average of 15% of the maximum width of the shell. In the type specimen (Fig. 2A), the pedicle surface is ornamented with pronounced annulated rings, disposed at intervals of about 0.2 mm (Fig. 2A_3, A_4). However, no surface ornament could be recognised in the other specimens, probably due to preservational factors. In the centre of the pedicle (Fig. 2B_1), there is a dark longitudinal lineation, extending from the proximal to the distal part of the pedicle (Fig. 2B_2). It is here interpreted as the coelom of the pedicle. A terminal pedicle bulb, like that found in *Lingulelltreta malongensis* (Zhang et al. 2005: fig. 3O), is lacking and there is no direct evidence for benthic shell anchorage as seen in the Chengjiang taxa *Longtancunella* and *Xianshanella* (Zhang et al. 2006, 2007c,

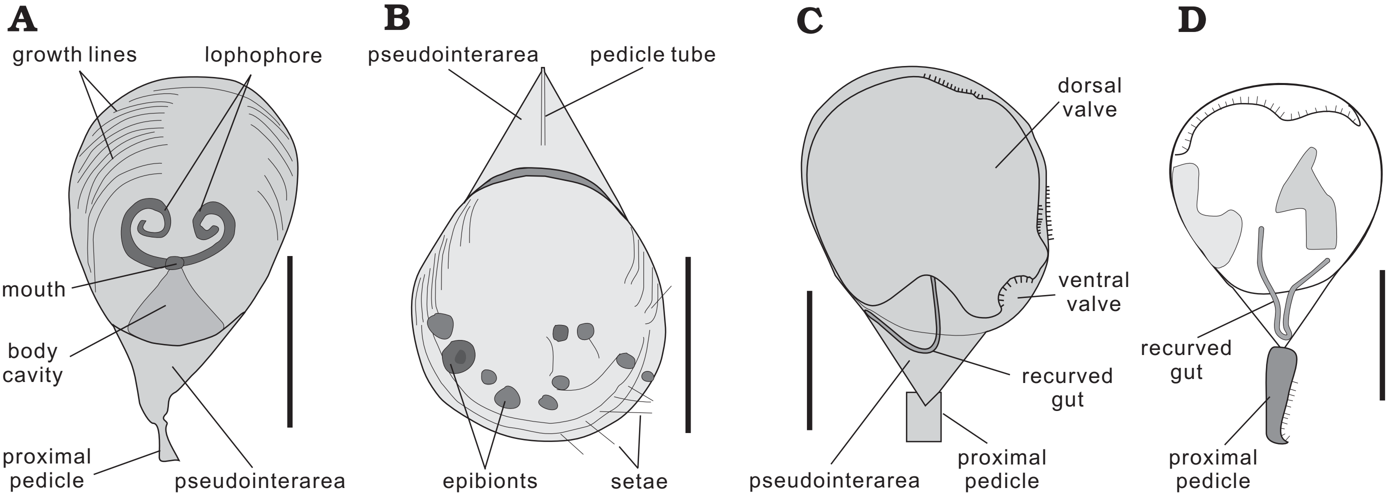

Fig. 4. Sketch drawings of the linguliform brachiopod *Acanthotretella decaius* sp. nov. illustrated in Fig. 2 and 3. **A**. Sketch of Fig. 2C$_1$ (GKG CA-008B). **B**. Sketch of Fig. 2 E(GKG CA-002B). **C**. Sketch of Fig. 3C$_1$(GKG CA-007B). **D**. Sketch of Fig. 3D$_1$(GKG CA-013(2)). Scale bars 5 mm.

2008, 2009) which could be due to the fact that no pedicle is preserved in its full length. The pedicles invariably arise from the circular foramen at the apex of the ventral valve, with the proximal pedicle end enclosing the tip of the ventral pseudointerarea. Nevertheless, at the posterior part of specimen GKG CA-002B, there is an inferred medial lineation, which is taken to represent a possible internal pedicle tube (Figs. 2E, 3B). The internal pedicle tube extends through a possible narrow external tube (Figs. 2E and 5), which is continuous with the coelomic lumen. In most cases, the pedicles are preserved as flattened impressions, parallel to the bedding plane or slightly bending into the sediments (Fig. 2A$_1$). By contrast, in specimen GKG CA-001(Fig. 2D$_1$), the pedicle appear to be relatively more steeply inserted into the sediments. This type of preservation may demonstrate that the brachiopod was buried in situ.

As seen in Fig. 2B$_1$, C the lophophore organisation of *Acanthotretella decaius* is only preserved in two slightly anterolaterally compressed specimens. It is represented by a pair of darkish imprints, extending from the antero-medial position of the visceral region, and then coils inward symmetrically about the valve midline (Figs. 2B$_1$, 2C, 4A). The mouth is presumed to be located at the base of the lophophore (Fig. 4A)

The visceral region forms a sub-triangular section (Fig. 2A$_1$, A$_2$), with an anterodorsal projection located in a posteromedial position of the dorsal valve. The projection does not extend to midlength of the ventral valve, and it reaches to approximately the posterior 1/3 of the dorsal valve length. There are no clearly defined muscle scars in any of the specimens and this absence has also been noted from the Chengjiang lingulids (Jin et al. 1993). Nevertheless, the digestive tract of *A. decaius* could be evidently detected in two specimens (Fig. 3C, D), where it forms a faint U-shaped tube with some relief, approximately 1 mm beyond the hinge line (Fig. 4C, D); the digestive tract is closely similar to that described from the Chengjiang lingulids (Zhang et al. 2004a, 2005, 2006, 2007a, c; Balthasar and Butterfield 2009).

Discussion and comparison

Shell morphology.—The flattened tear-shaped shell of *Acanthotretella decaius* is similar to both *Lingulella chengjiangensis* and *Lingulellotreta malongensis* from the Chengjiang fauna, as well as *Acanthotretella spinosa* and *Lingulella waptaensis* from the classic Burgess Shale fauna. The most remarkable aspect of *A. decaius* is the significantly larger size, attaining a maximum length of 14 mm (average 11.25 mm, see Table 1). Additionally, *A. decaius* has an elongate ventral pseudointerarea, extending far beyond the hinge line, whilst *Lingulella chengjiangensis* and *Lingulella waptaensis* have a short, triangular ventral linguloid pseudointerarea. This unique ventral pseudointerarea demonstrates that the Guanshan linguliform does not belong to *Lingulella*. Moreover, unlike species of *Lingulella*, the shell of the Guanshan linguliform was relatively thin and flexible, and although the shells are strongly compressed, they exhibit no brittle breakage and fractured deformation like that exhibited in *L. waptaensis* (Pettersson Stolk et al. 2010). By contrast, some brittle fractures or ruptures are distinctly exhibited in some calcareous-shelled and acrotheloid brachiopods from the Chengjiang fauna (Zhang et al. 2007b, 2010) and also discerned in some botsfordiid brachiopods from the Guanshan deposits (ZZ unpublished data).

The elongate shape of the ventral pseudointerarea (Figs. 2A$_1$, A$_2$, B$_1$, C, E, F, 3) is reminiscent of that of the Chengjiang *Lingulellotreta malongensis* as well as the Burgess shale *Acanthotretella spinosa*. However, *Lingulellotreta* is characterised by a large, suboval pedicle foramen that opens on the ventral linguloid pseudointerarea, in contrast to the minute and circular apical pedicle foramen and tube of *Acan-*

doi:10.4202/app.2009.1106

thotretella decaius which makes it unlikely that the Guanshan linguliform belongs within the family Lingulellotretidae. The gross shell outline and the morphology of the ventral pseudointerarea, with an apical foramen suggest a close phylogenetic affinity with the enigmatic brachiopod *A. spinosa*, recently described from the Burgess Shale fauna. More importantly, the close affinity to *Acanthotretella* is also supported by the similar apical angle of the ventral pseudointerarea and the relative size of the ventral pseudointerarea compared to the total shell dimensions (see Table 1). Moreover, the linguliform described here is similar to the Canadian form in that both of them have a small visceral area close to the hinge line, and bear an inferred interior pedicle tube, from which the pedicle emerges. Although no well-defined evidence of spine-like setae covering the shell surface is found in *A. decaius*, the brittleness and oblique extension of the setae away from the margin of the valve also support the assignment of these fossils to *Acanthotretella*. It is possible that the differences in setae morphology are due to preservational differences. The new Chinese species can be directly differentiated from the Canadian *A. spinosa* by its larger size, longer ventral pseudointerarea and the evidence for stable shell outline, probably implying a more strongly mineralised shell. The Guanshan linguliform is therefore recognised as a new species of *Acanthotretella*.

In addition, it should be mentioned that the fossils discussed here bear a general resemblance to *Lingulosacculus nuda* recently described from the early Cambrian Mural Formation of western Alberta (Balthasar and Butterfield 2009). However, *Lingulosacculus* differs from the Chinese form, primarily in that the shell of *L. nuda* is even larger and has a pronounced long pocket-shaped ventral pseudointerarea with a more acute apical angle (ca. 30°). Furthermore, there is compelling evidence for identifying *Lingulosacculus* as a member of the Lingulellotretidae, within the Order Lingulida (Balthasar and Butterfield 2009).

Soft-part anatomy.—*Acanthotretella* was previously only known from the Burgess Shale. The discovery of *Acanthotretella decaius* from the lower Cambrian (Series 2, Stage 4) Wulongqing Formation (Guanshan Fauna) represents a significant extension of their geological range of this enigmatic brachiopod. The fossils described here provide the oldest direct evidence of the disposition of the lophophore and digestive tract in *Acanthotretella*, here assigned to the class Siphonotretida.

In most specimens of *Acanthotretella decaius*, the pedicle is straight or gently arched, and in the type specimen (GKG CA-007; Fig. 2A$_3$) the middle part of the pedicle only exhibits a gentle S-shaped contortion. This type of straight pedicle shapes are distinctly different from those exhibited in the Burgess Shale specimens of *Acanthotretella spinosa* and *Lingulella waptaensis*, where the pedicle may be tightly folded and even self-entangled (Holmer and Caron 2006) (see also above). Moreover, the pedicle of *A. decaius* is relatively thick as compared with that of *A. spinosa* and *L. waptaensis*.

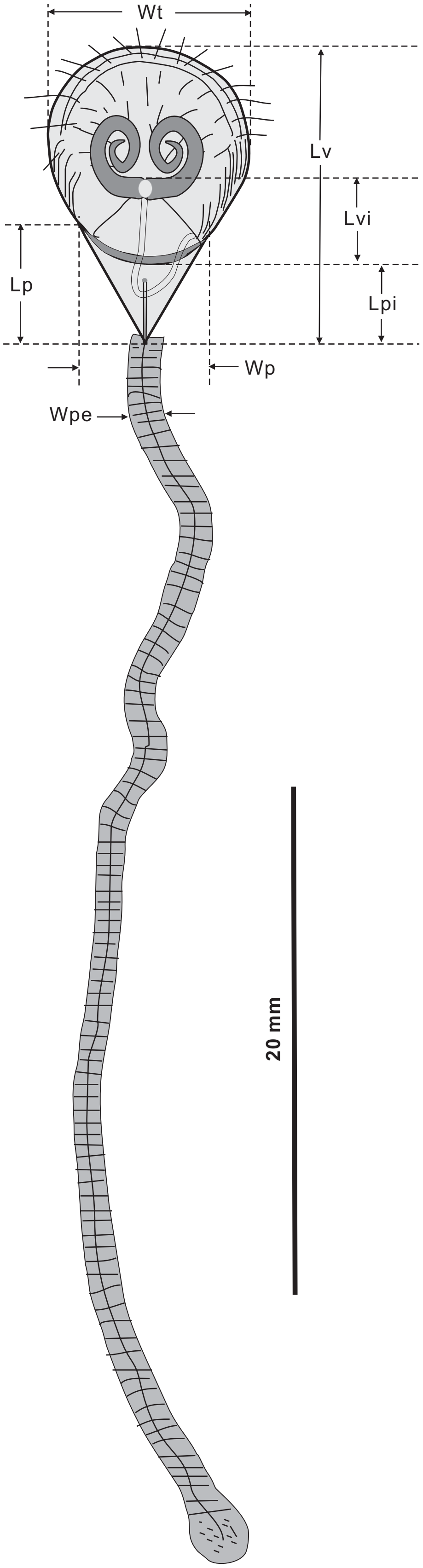

Fig. 5. Reconstruction of *Acanthotretella decaius* sp. nov. based on GKG CA-007,GKG CA-008, GKG CA-002B, showing disposition of lophophore, small visceral cavity and location of measurements indicated in Table 1.

Setae represent another of the most commonly preserved soft parts in Burgess shale-type preservation of brachiopods (Zhang et al. 2005, 2006, 2007b, c, 2008, 2009; Holmer and Caron 2006; Pettersson Stolk et al. 2010). As mentioned above, the setae of *Acanthotretella decaius* are also preserved in 7 specimens (Fig. 2B–F). Most frequently, they occur along the anterior and anterolateral margins, and are poorly exposed in the posterior parts of the valves. Despite this, the overall morphology of the setae and their preservation suggest some kind of brittleness. With respect to the preservation and arrangement along the mantle edge, the setae of *A. decaius* are different from those seen in *Lingulellotreta malongensis* and *Lingulella chengjiangensis* (see also below) which are short and equidistantly distributed along the shell valve (see Zhang et al. 2005: fig. 2D–G).

Autoecology.—Whilst it is clear that the shapes and ornamentation of linguliform shells are important sources of clues in trying to reconstruct brachiopod palaeoecology (e.g., Savazzi 1986; Holmer 1989, 1991), reports of soft-tissue preservations are an indispensable component in elucidating the lifestyle of brachiopods (Zhang et al. 2004a, 2005, 2008). The linguliform described herein exhibits a subcircular shell shape and a long and slender pedicle, more than 4 times as long as the shell. Like the Chengjiang *Lingulella chengjiangensis* and *Lingulellotreta malongensis* (Zhang et al. 2004a, 2005), the new Guanshan species also have a small, posteriorly placed visceral cavity, which would preclude development of widespread muscle insertions, a necessary prerequisite for mobility of the valves, and it is thus unlikely to have had a burrowing mode of life similar to that of Recent lingulid species (e.g., Thayer and Steele-Petrovic 1975). It is most likely to have had an epifaunal lifestyle with the valves suspended above the sea floor to avoid turbulence at the sediment-water boundary. An epifaual life mode is also endorsed by the preservational mode of the Guanshan linguliforms. The valves and the main part of the pedicles are invariably preserved inside the homogeneous muddy sediments, possibly as a result of storm-induced burial (Babcock and Zhang 2001). Although the pedicles of *Acanthotretella decaius* do not extend parallel to the same bedding planes as the valves, but bend slightly or steeply downward into the event-related sediment (Fig. 2D), they never penetrate the storm-induced muddy beds into the underlying layer. In a few cases, the shell surface of the linguliforms examined here are overgrown with some small, rounded or oval organisms (Figs. 2E, 4B), which may provide a direct support for an epifaunal life mode (see also Zhang et al. 2005, 2008, 2010).

Phylogenetic implications.—Previously, all well-defined records of exceptional preservation of brachiopod soft anatomy were known exclusively from the Chengjiang Fauna and the majority of them only represented linguloid brachiopods. This paper is the first described record from outside of Chengjiang, and it provides another window into the morphology and character evolution of the feeding organ in the oldest known possible member of the Siphonotretida lineage.

It is beyond doubt that the lophophore revealed here is spirolophous, and the digestive tract depicted in *Acanthotretella decaius* is U-shaped with an inferred anus. So far, there are at least five genera of lingulid brachiopods from the lower Cambrian of South China in which a U-shaped digestive tract with an anterior anus and a lophophore have been observed (Zhang et al. 2008 and reference therein; also see Balthasar and Butterfield 2009). The lophophore and digestive tract in *A. decaius* have strong similarities with those found in the Chengjiang lingulids (Zhang et al. 2004a, 2006, 2007a). The similarities in the configuration of the lophophore, the digestive tract and pedicle anatomy in *Acanthotretella* to that of the lingulid lineage demonstrate that a spirolophous lophophore and a U-shaped gut are synplesiomorphies of lingulids and siphonotretids.

It should be mentioned that the organisation of the lophophore in *Heliomedusa orienta* from the Chengjiang fauna is distinctive in that its paired lophophoral arms arched posteriorly, a condition which is otherwise completely unknown from all fossil or living brachiopods (Williams et al. 2000). Moreover, the posteriorly pointed lophophoral arms of *Heliomedusa* are not only fringed with laterofrontal tentacles, but also ciliated with short tentacles, presumably facilitating transport of mucous-bound nutrient particles to the mouth. This brachiopod genus is therefore proposed as a brachiopod stem group (Zhang et al. 2009), together with the mickwitziids (Holmer and Popov 2007). Together with earlier reports of lophophores in Cambrian brachiopods (Zhang et al. 2008 and reference therein), the material illustrated here, therefore, shows that lophophores of Cambrian brachiopods, although morphologically diversified, are dominated by spirolophous forms.

The flattened preservation and the absence of evidence of brittle breakage indicate that the integuments were flexible and had a highly organic composition, with only a minor mineral component. The partial and uneven occurrence of the concentric growth lines on their surface may suggest varying rigidity of the shell and possibly that the mineral component was concentrated mainly to the primary layer. When compared to the linguliform brachiopods *Diandongia* and *Eoobolus* from the Guanshan fauna (ZZ unpublished data), shell valves of *Acanthotretella decaius* are comparably more flattened and deformed. However, the entire outline of the shell is invariably preserved in all specimens of *A. decaius*. In contrast, the valves of *Acanthotretella spinosa* from the Burgess Shale exhibit a different type of preservation: the valves of the Burgess species are mostly preserved as a thin film that was seemingly softer and more easily deformable than both the pedicle and the spine-like setae covering the shell surface. In some specimens of *A. spinosa* from the Burgess Shale, most of the anterior part of the shell has been lost and only the pedicle and posterior sections of shell are well preserved (Holmer and Caron 2006: fig. 4A, E).

The record of non-mineralised to poorly mineralised Cambrian brachiopods is expanding (Jin et al. 2004; Holmer and Caron 2006; Zhang et al. 2007a, c, 2008; Balthasar and Butterfield 2009), and as discussed by Balthasar and Butterfield

(2009) it is possible to regard the lack of mineralisation as a derived condition for the Brachiopoda. Similarly, the shell of the lower Cambrian *Acanthotretella decaius* show evidence of being comparatively more rigid and mineralised than the younger, middle Cambrian *Acanthotretella spinosa*, which is here interpreted as an example of secondary loss of mineralisation (cf. Balthasar and Butterfield 2009). This model would also be more consistent with the recent suggestions that the strongly organo-phosphatic tommotiids belong within the stem of the Brachiopoda, implying that this type of mineralisation is primitive (Williams and Holmer 2002; Holmer et al. 2002, 2006, 2008; Skovsted and Holmer 2003; Balthasar 2004, 2008; Skovsted et al. 2008, 2009; Balthasar et al. 2009).

Acknowledgements

We thank John Peel (Uppsala University, Uppsala, Sweden) for linguistic help and Qingtao Chen (Kunming University, Kunming, China) for field assistance, and Juanping Zhai (NWU) for help with preparation and photograph of these fossils. Thanks are also due to Sean Robson (The Manitoba Museum, Winnipeg, Canada) and Uwe Balthasar (University of Glasgow, United Kingdom) for their critical review of an earlier and final version. This work represents a contribution to the projects funded by NSFC (G. 40772020, 40702005, 40830208), the National 973 Programme (2006CB806401) and the most special fund from the State Key Laboratory of Continental Dynamics, NWU. The manuscript has been completed by ZZ during tenure of postdoctoral fellowship at the Uppsala University, supervised by Lars E. Holmer. Grants to ZZ from a Foundation for the Author of National Excellent Doctoral Dissertation of P.R. China (FANEDD), Fok Ying Tung Education Foundation (G 121016), and from the China Scholarship Council (CSC) for a one-year-research stay at the Uppsala University are acknowledged. LEH and CBS acknowledge support from the Swedish Research Council (VR).

Reference

Babcock, L.L. and Zhang, W.T. 2001. Stratigraphy, paleontology, and depositional setting of the Chengjiang Lagerstätte (Lower Cambrian), Yunnan, China. *Palaeoworld* 13: 66–86.

Balthasar, U. 2004. Shell structure, ontogeny, and affinities of the Lower Cambrian bivalved problematic fossil *Mickwitzia muralensis* Walcott, 1913. *Lethaia* 37: 381–400. http://dx.doi.org/10.1080/00241160410002090

Balthasar, U. 2008. *Mummpikia nuda* gen. nov. and the origin of calcitic-shelled brachiopods. *Palaeontology* 51: 263–279. http://dx.doi.org/10.1111/j.1475-4983.2008.00754.x

Balthasar, U. and Butterfield, N.J. 2009. Early Cambrian "soft-shelled" brachiopods as possible stem-group phoronids. *Acta Palaeontologica Polonica* 54: 307–314. http://dx.doi.org/10.4202/app.2008.0042

Balthasar, U., Skovsted, C.B., Holmer, L.E., and Brock, G.A. 2009. Homologous skeletal secretion in tommotiids and brachiopods. *Geology* 37: 1143–1146. http://dx.doi.org/10.1130/G30323A.1

Holmer, L.E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Vastergotland and Dalarna, Sweden. *Fossils and Strata* 26: 1–172.

Holmer, L.E. 1991. The taxonomy and shell characteristics of a new elkaniid brachiopod from the Ashgill of Sweden. *Palaeontology* 34: 195–204.

Holmer, L.E. and Caron, J.B. 2006. A soft-shelled spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologia* 87: 273–290. http://dx.doi.org/10.1111/j.1463-6395.2006.00241.x

Holmer, L.E. and Popov, L.E. 1996. Early Paleozoic radiation and classification of organo-phosphatic brachiopods. *In*: P. Copper and J. Jin (eds.), Brachiopods. *Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2–5. September 1995*, 117–121. A.A. Balkema, Rotterdam.

Holmer, L.E. and Popov, L.E. 2000. Lingulata. *In*: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H2, Brachiopoda*, 30–146. Geological Society of America, Boulder, and University of Kansas Press, Lawrence.

Holmer, L.E. and Popov, L.E. 2007. Organophosphatic bivalved stem-group brachiopods. *In*: P.A. Selden (ed.), *Treatise on Invertebrate Paleontology, Part H6, Brachiopoda,* 2580–2590. Geological Society of America, Boulder, and University of Kansas Press, Lawrence.

Holmer, L.E., Popov, L.E., Koneva, S.P., and Rong, J.Y. 1997. Early Cambrian Lingulellotreta (Lingulata, Brachiopoda) from South Kazakhstan (Malyi Karatau Range) and South China (eastern Yunnan). *Journal of Paleontology* 71: 577–584.

Holmer, L.E., Skovsted, C.B., and Brock, G.A. 2006. First record of canaliform shell structure from the Lower Cambrian paterinate brachiopod Askepasma from South Australia. *Memoirs of the Association of Australian Palaeontologist* 32: 1–5.

Holmer, L.E., Skovsted, C.B., and Williams, A. 2002. A stem group brachiopod from the Lower Cambrian: support for a *Micrina* (halkieriid) ancestry. *Palaeontology* 45: 875–882. http://dx.doi.org/10.1111/1475-4983.00265

Holmer, L.E., Skovsted, C.B., Brock, G.A., Valentine, J.L., and Paterson, J.R. 2008. The Early Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod: *Biology Letters* 4: 724–728. http://dx.doi.org/10.1098/rsbl.2008.0277

Hou, X.G., Aldridge, R.J., Bergström, J., Siveter, D.J., and Feng, X.H. 2004. *The Cambrian Fossils of Chengjiang, China: the Flowering of Early Animal Life*. 233 pp. Blackwell Publishing, Oxford.

Hu, S.X., Luo, H.L., and Liu, Q. 2009. *The Early Cambrian Guanshan Fauna—A New Burgess Shale Type Fossil Lagerstätte from Yunnan, SW China.* Abstract of the International Conference on the Cambrian Explosion, Banff, Alberta, August 3–8, 2009, 77–78.

Hu, S.X., Li, Y., Luo, H.L., Fu, X.P., You, T., Pang, J.Y., Liu, Q., and Steiner, M. 2008. New record of Palaeoscolecids from the Early Cambrian of Yunnan, China. *Acta Geologica Sinica* 82 (2): 244–248.

Hu, S.X., Luo, H.L., Hou, S.G., and Erdtmann, B.D. 2007. Eocrinoid echinoderms from the Lower Cambrian Guanshan Fauna in Wuding, Yunnan, China. *Chinese Science Bulletin* 52 (5): 717–719. http://dx.doi.org/10.1007/s11434-007-0083-6

Jin, Y.G., Hou, X.G, and Wang, H.Y. 1993. Lower Cambrian pediculate lingulids from Yunnan, China. *Journal of Paleontology* 67 (5): 788–798.

Jin, Y.G., Yang, J., Cao, C.Q., Wang, H.F., and Chen, A.L. 2004. *An Agglutinated Brachiopod-like Fossil from the Lower Cambrian of China. Sina-German Symposium, 25–28th September 2004*, 40–41. Nanjing, China.

Jin, Y.G., Wang, H.Y., and Wang, W. 1991. Palaeoecological aspects of brachiopods from Chiungchussu Formation of Early Cambrian age, Eastern Yunnan, China. *In*: Y.G. Jin., J.G. Wang, and S.H. Xu (eds.), *Palaeoecology of China, Vol. 1*, 25–47. Nanjing University Press, Nanjing.

Liu, Q., Luo, H.L., Chen, L.Z., and Hu, S.X. 2006. *Panlongia*, A new trilobitomorph genus from the Lower Cambrian, Kunming, Yunnan. *Acta Palaeontologica Sinica* 45: 384–392.

Luo, H.L., Li, Y., Hu, S., Fu, X., Hou, S., Liu, X., Li, F., Pan, J., and Liu, Q. 2008. *Early Cambrian Malong Fauna and Guanshan Fauna from Eastern Yunnan, China* [in Chinese with English summary], 94–98. Yunnan Science and Technology Press, Kunming.

Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Chen, L.Z., You, T., and Liu, Q. 2005. New Vetulicoliids from the Lower Cambrian Guanshan Fauna, Kunming. *Acta Geologica Sinica* 79: 1–6.

Luo, H.L., Hu, S.X., Chen, L.Z., Zhang, S.S., and Tao, Y.H. 1999. *Early Cambrian Chengjiang Fauna From Kunming Region, China* [in Chinese with English summary]. 129 pp. Yunnan Science and Technology Press, Kunming.

Luo, H.L., Jiang, Z.W., and Tang, L.D. 1994. *Stratotype Section for Lower Cambrian Stages in China* [in Chinese with English summary]. 183 pp. Yunnan Science and Technology Press, Kunming.

Pettersson Stolk, S., Holmer, L.E., and Caron, J.-B. 2010. First record of the brachiopod *Lingulella waptaensis* with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologica* 91: 150–162. http://dx.doi.org/10.1111/j.1463-6395.2009.00394.x

Popov, L.E., Bassett, M.G., Holmer, L.E., and Pour, M.G. 2009. Early ontogeny and soft tissue preservation in siphonotretide brachiopods: New data from the Cambrin–Ordovician of Iran. *Gondwana Research* 16: 151–161. http://dx.doi.org/10.1016/j.gr.2009.01.009

Popov, L.E., Holmer, L.E., and Bassett, M. 1996. Radiation of the earliest calcareous brachiopods. *In*: P. Copper and J. Jin (eds.), *Brachiopods. Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2–5 September 1995*, 209–213. A.A. Balkema, Rotterdam.

Rong, J.Y. 1974. Cambrian brachiopods. *In*: Nanjing Institute of Geology, Academia Sinica (ed.), *Handbook of Palaeontology and Stratigraphy of Southwest China*, 113–114. Sciences Press, Beijing.

Savazzi, E. 1986. Burrowing sculptures and life habits in Paleozoic lingulacean brachiopods. *Paleobiology* 12: 46–63.

Skovsted, C.B. and Holmer, L.E. 2003. The Early Cambrian (Botomian) stem group brachiopod *Mickwitzia* from Greenland. *Acta Palaeontologica Polonica* 48: 1–20.

Skovsted, C.B., Brock, G.A., Paterson, J.R., Holmer, L.E., and Budd, G.E. 2008. The scleritome of *Eccentrotheca* from the Lower Cambrian of South Australia: lophophorate affinities and implications for tommotiid phylogeny. *Geology* 36: 171–174. http://dx.doi.org/10.1130/G24385A.1

Skovsted, C.B., Holmer, L.E., Larsson, C.M., Hogstrom, A.E.S., Brock, G.A., Topper, T.P., Balthasar, U., Petterson Stolk, S., and Paterson, J.R. 2009. The scleritome of *Paterimitra*: an Early Cambrian stem group brachiopod from South Australia. *Proceedings of Royal Society, Series B* 276: 1651–1656. http://dx.doi.org/10.1098/rspb.2008.1655

Thayer, C.W. and Steele-Petrovich, H.M. 1975. Burrowing of the lingulid brachiopod *Glottidia pyramidata*: its ecologic and paleoecologic significance. *Lethaia* 8: 209–221. http://dx.doi.org/10.1111/j.1502-3931.1975.tb00925.x

Williams, A. and Holmer, L.E. 2002. Shell structure and inferred growth, functions and affinities of the sclerites of the problematic *Micrina*. *Palaeontology* 45: 848–873. http://dx.doi.org/10.1111/1475-4983.00264

Williams, A., Holmer, L.E., and Cusack, M. 2004. Chemico-structure of the organophosphatic shell of siphonotretide brachiopods. *Palaeontology* 47: 1313–1337. http://dx.doi.org/10.1111/j.0031-0239.2004.00404.x

Williams, A., James, M.A., Emig, C.C., Mackay, S., and Rhodes, M.C. 2000. Anatomy. *In*: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda*, 7–188. Geological Society of America, Boulder and University of Kansas, Lawrence.

Zhang, X.L. and Hua, H. 2005. Soft-bodied fossils from the Shipai Formation, Lower Cambrian of the Three Gorge area, South China. *Geological Magazine* 142: 699–709. http://dx.doi.org/10.1017/S0016756805000518

Zhang, Z.F., Han, J., Wang, Y., Emig, C.C., and Shu, D.G. 2010. Epibionts on the lingulate brachiopod *Diandongia* from the Early Cambrian Chengjiang Lagerstatte, South China. *Proceedings of Royal Society of London Proceedings, Series B* 277: 175–181. http://dx.doi.org/1098/rspb.2009.0618.

Zhang, Z.F., Han, J., Zhang, X.L., Liu, J.N. and Shu, D.G. 2004a. Soft tissue preservation in the Lower Cambrian linguloid brachiopod from South China. *Acta Palaeontologica Polonica* 49: 259–266.

Zhang, Z.F., Han, J., Zhang, X.L., Liu, J.N., and Shu, D.G. 2007a. Note on the gut preserved in the Lower Cambrian *Lingulellotreta* (Lingulata, Brachiopoda) from South China. *Acta Zoologica* (Stockholm) 88: 65–70. http://dx.doi.org/10.1111/j.1463-6395.2007.00252.x

Zhang, Z.F., Li, G.X., Emig, C.C., Han, J., Holmer, L.E., and Shu, D.G. 2009. Architecture and function of the lophophore in the problematic brachiopod *Heliomedusa orienta* (Early Cambrian, South China). *Geobios* 42: 649–661. http://dx.doi.org/10.1016/j.geobios.2009.04.001

Zhang, Z.F., Robson, S.P., Emig, C.C., and Shu, D.G. 2008. Early Cambrian radiation of brachiopods: A perspective from South China. *Gondwana Research* 14: 241–254. http://dx.doi.org/10.1016/j.gr.2007.08.001

Zhang, Z.F., Shu D.G., Emig, C.C., Zhang, X.L., Han, J., Liu, J.N., Li, Y., and Guo, J.F. 2007b. Rhynchonelliformean brachiopods with soft-tissue preservation from the Lower Cambrian Chengjiang Lagerstätte of South China. *Palaeontology* 50: 1391–1402. http://dx.doi.org/10.1111/j.1475-4983.2007.00725.x

Zhang, Z.F., Han, J., Zhang, X.L., Liu, J.N., and Shu, D.G. 2003. Pediculate brachiopod *Diandongia pista* from the Lower Cambrian of South China. *Acta Geologica Sinica (English Edition)* 77: 288–293.

Zhang, Z.F., Shu, D.G., Han, J., and Liu, J.N. 2004b. New data on the lophophore anatomy of Early Cambrian linguloids from the Chengjiang Lagerstätte, Southwest China. *Notebooks on Geology, Letter* 1: 1–7.

Zhang, Z.F., Shu, D.G., Han, J., and Liu, J.N. 2005. morpho-anatomical differences of the Early Cambrian Chengjiang and Recent linguloids and their implications. *Acta Zoologica* 86: 277–288. http://dx.doi.org/10.1111/j.1463-6395.2005.00211.x

Zhang, Z.F., Shu, D.G., Han, J., and Liu, J.N. 2006. New data on the rare Chengjiang (Lower Cambrian, South China) linguloid brachiopod *Xianshanella haikouensis*. *Journal of Paleontology* 80: 203–211. http://dx.doi.org/10.1666/0022-3360(2006)080%5B0203:NDOTRC%5D2.0.CO;2

Zhang, Z.F., Shu, D.G., Han, J., and Liu, J.N. 2007c. A gregarious lingulid brachiopod *Longtancunella chengjiangensis* from the Lower Cambrian, South China. *Lethaia* 40: 11–18.

doi:10.4202/app.2009.1106