

Soft-tissue preservation in the Lower Cambrian linguloid brachiopod from South China

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The organization of the lophophore and the digestive system are recognized as two of the diagnostic characters in the definition of higher brachiopod taxa, and hence play a major role in their phylogenetic analysis, their structure, however, is very rarely fossilized. Here we describe and interpret specimens of the brachiopod *Lingulellotreta malongensis*, from the Lower Cambrian Chengjiang Lagerstätte (South China), one of the earliest known taxa of the Lingulellotretidae, in which lophophores and intact, U-shaped digestive tracts are extraordinarily well-preserved. The lophophore, with clearly preserved tentacles, corresponds to an early spirolophe developmental stage. The digestive tract consists of a mouth, esophagus, distended stomach, intestine and an anterior anus, and differs from that of the Chengjiang obolid *Lingulella chengjiangensis* by the presence of the dilated stomach and by the absence of a looped intestine as in *Lingula*. In addition, the relative sizes of the mantle and visceral cavities of *Lingulellotreta malongensis* also are described. These fossils demonstrate that by the Atdabanian brachiopods had already possessed advanced features, and suggest that a lophophore and a U-shaped intestine with an anterior anus are brachiopod plesiomorphies.

Key words: Linguloidea, lophophore, digestive tract, Lower Cambrian, Chengjiang Lagerstätte, China.

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Introduction

The Lower Cambrian Chengjiang Lagerstätte, Southwest China is exceptional, rivalling the Burgess Shale (Conway Morris 1998: 129–155), and provides another window into the Cambrian “explosion” (Zhang et al. 2001; Chen et al. 1996; Hou et al. 1999; Luo et al. 1999). It contains one of the earliest and most abundant known faunas of soft-bodied organisms in the Phanerozoic (Bergström 2000; Shu et al. 2001; Han et al. 2003), with especially detailed preservation of the evolutionary novelties of some early deuterostomes (Shu 2003; Shu et al. 2003a, b). Brachiopods are one of the numerically important groups in this extraordinarily preserved fauna, characterized by abundant pediculate forms (Jin et al. 1993; Zhang, Han, et al. 2003), of which *Lingulellotreta malongensis* Rong, 1974 (Holmer et al. 1997) is one of the most common (Jin et al. 1991, 1993). The palaeoecology of *L. malongensis* was initially investigated by Jin et al. (1991), when it was considered to be similar to that of modern lingulids. Later, a detailed morphological comparison of the pedicle of *L. malongensis* with that of Recent lingulids was published (Jin et al. 1993), and more recently, additional information on the morphology of the lingulellotretid species has been available (Holmer et al.

1997), including the details of the mantle canals and the principal muscle scars.

Whilst it is indisputable that molecular biology is dramatically increasing our understanding of brachiopod evolution (Cohen et al. 1998; Cohen 2000), evidence from fossils is still an indispensable component in elucidating the evolution and diversification of the phylum (Holmer et al. 2002; Conway Morris and Peel 1995; Skovsted and Holmer 2003). The lophophore and the digestive system have been considered as two of the diagnostic characters for phylogenetic analysis of higher taxa of Brachiopoda (Rowell 1982; Popov et al. 1993; Gorjansky and Popov 1986), but they rarely occur in the fossil state. In this paper, we concentrate on describing and interpreting specimens of the brachiopod *Lingulellotreta malongensis*, from the Lower Cambrian Chengjiang Lagerstätte (South China), one of the earliest known taxa of the Lingulellotretidae, in which lophophores with in some cases clearly preserved tentacles, and intact, U-shaped digestive tracts are extraordinarily well-preserved. These fossils provide direct evidences for the particular character-states of lophophore and gut characters in Cambrian (Atdabanian) representatives of particular lineages. They, therefore, are of key importance for our understanding of the early evolution of the phylum.



Fig. 1. The lophophore of *Lingulellotreta malongensis* from the Yu'an-shan Member of the Qiongzhusi (Chiungchussu) Formation, Lower Cambrian, China. **A.** ELI L-0014A, dorsal view of ventral interior, showing lophophore, with a series of definitive filaments, three-dimensionally preserved in a lamina of sediment between valves. **B.** ELI L-0033, showing paired imprints of brachia and depression of distinctive visceral cavity. **C.** ELI L-0052A, a specimen strongly compressed, showing lophophore with filaments. **D.** ELI L-0056A. **D₁**, parallel specimen with straight pedicle strongly compressed, and with paired spiral brachial imprints; **D₂**, details of the brachial imprints of **D₁**. **E.** ELI L-0073, a lateral oblique view of strongly compressed specimen, showing detail of a hollow brachial tube. **F.** ELI L-0101, lateral oblique view of the lophophore three-dimensionally preserved in sediment in valves. **G.** ELI L-0081, a parallel, possible juvenile specimen strongly compressed; note the relatively small brachia. Scale bars 2 mm. See Fig. 2 for some interpretations.

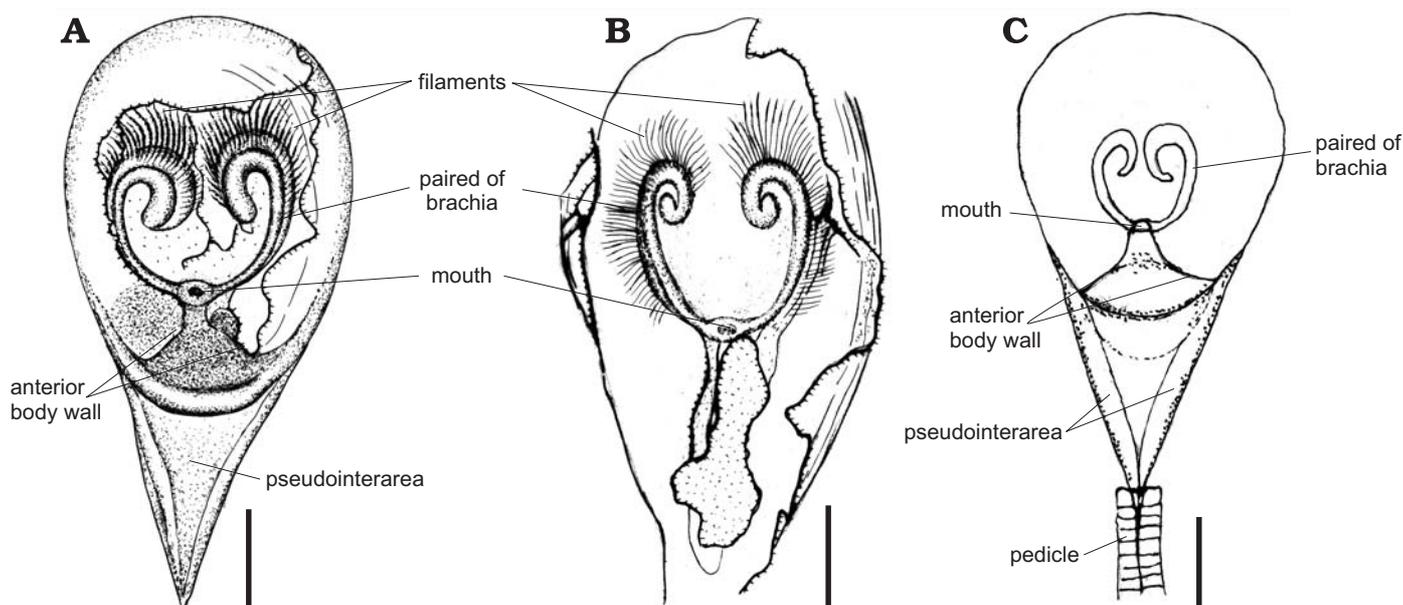


Fig. 2. Interpretative drawings of the interiors of *Lingulellotreta malongensis* shown in Fig. 1. **A.** Sketch of Fig. 1A. **B.** Sketch of Fig. 1C. **C.** Sketch of Fig. 1G. Scale bars 1 mm.

Material and methods

The materials in this work were recovered from the grayish-green and grayish-yellow mudstone of Yu'an-shan Member (*Eoredlichia* Zone), Qiongzhusi Formation, Lower Cambrian at Haikou, Kunming, South China. Details of the localities and stratigraphy were given in Jin et al (1993) and Zhang et al. (2001). Up to 400 specimens of *L. malongensis* have been collected from these localities by the work team of Early Life Institute. Detailed descriptions and diagnostic features of the genera and species were given in Holmer et al. (1997) and Jin et al. (1993). Most specimens are preserved as reddish brown casts or moulds, in strikingly contrast to the surrounding yellowish-green mudstone. More than 40 of the collected specimens show a lophophore well enough for observation of details. Lophophores are visible either directly, as a result of cleavage approximately along the plane of the commissure (Fig. 1A, F), or as paired spiral impressions seen through the flattened dorsal valve as a result of post-mortem flattening (Fig. 1B–E, G; see also some interpretative drawings in Fig. 2). The alimentary canals are preserved three-dimensionally by muddy sediment “in-fill” (Fig. 4A, B), as also seen in the guts of many other Chengjiang animals, such as arthropod *Naraoia* (Vannier and Chen 2002), the vetulicolian *Didazoon* and *Vetulicola* (Shu et al. 2001). There are 8 specimens in our collections, with a partially or completely preserved gut. The exceptional preservation of soft-tissues suggests that these animals must have been either buried alive, or killed immediately before burial. The rapid entombment of undecayed material is probably of key importance in the unique Chengjiang preservation, although early phosphatic mineralization and subsequent replacement by the

clay minerals may also have played a taphonomic role in a way analogous to the Burgess Shale (Orr et al. 1998; Butterfield 2000).

The specimens were observed by means of the Olympus Zoom Stereo Microscope and photographed with Nikon camera mounted on photomicrographic system, with different illuminations for particular views when high contrast images are required. Measurements were made with a microscope micrometer for specimens smaller than about 10 mm. All the specimens illustrated in this work are deposited in the Early Life Institute, Northwest University, Xi'an, Shaanxi Province, China, abbreviated ELI.

Systematic palaeontology

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulellotretidae, Koneva and Popov, 1983

Genus *Lingulellotreta* Koneva (in Gorjansky and Koneva), 1983

Lingulellotreta malongensis Rong, 1974.

Lingulepis malongensis Rong; Rong 1974: 114, pl. 44: 27, 32.

Lingulepis malongensis Rong; Jin et al. 1993: 794, figs. 5.1, 5.6, 5.7, 8.1–8.4, 9.4.

Lingulepis malongensis Rong; Luo et al. 1994: pl. 37, figs. 11–14.

Lingulepis malongensis Rong; Chen et al. 1996: 135, figs. 165–167.

Lingulellotreta malongensis; Homer et al. 1997: figs. 4.1–4.14.

Lingulellotreta malongensis Rong; Holmer and Popov 2000: 72, figs. 1a–d.

Lophophore.—The shells of *Lingulellotreta malongensis* are small, pedicle valve ranging from 2.28–8.09 mm long

(see Table 1), the average length is 6.32 mm. The pseudo-interarea of pedicle valve extends anteriorly to 30–40% of valve length. Inside the shell (No: ELI L-0014A), an undulant, transverse reddish brown strand correlates with the position of the anterior body wall (Figs. 1A, 2A). It divides the space inside the shell into two parts, the anterior portion putatively representing mantle cavity (about 80% of the volume/length), and a posterior 20% representing viscera. In the mantle cavity, the lophophore appears as imprints of a pair of ear-shaped spiral brachial arms, disposed symmetrically about the midline (Figs. 1, 2). They extend antero-laterally, then converge inward. The brachial arms are markedly hollow or tubiform, delineated by a pair of parallel curved threads in reddish brown (Fig. 1E, D₂), which are probable marginal doublures of the tubular brachial axes. The brachial arms are sometimes impressed in the internal mould of the dorsal valve (Figs. 1B–D, E, G, 2B, C), or in some specimens are directly exposed in a lamina of sediment filling the mantle cavity (Figs. 1A, F, 2A). It is within such a lamina of sediment that filaments of the lophophore are three-dimensionally preserved, (Figs. 1A, 2A). The filaments project along the spiral brachial axes, bowing antero-laterally (Figs. 1A, C, 2A, B). On a single brachium, about 23–34 tentacles can be counted (Figs. 1A, C, 2A, B). They are arranged apparently in a single palisade, are elongate and coarse, and distinctly visible in the hitherto known four specimens (e.g., Figs. 1A, C, 2A, B, 4A). In the other specimens (Fig. 1B, D–F, G) only impressions of brachial axes were seen. At the base of a pair of brachia, a circular mark occurring in some specimens (Figs. 1A–D, G, 2A–C), could represent the position of the mouth. In more than 40 specimens with preserved lophophore impressions, no trace of any skeletal lophophore support was evident. It is, therefore, assumed that the lophophores of these linguloids were supported alone by a hydrostatic skeleton as in Recent lingulids.

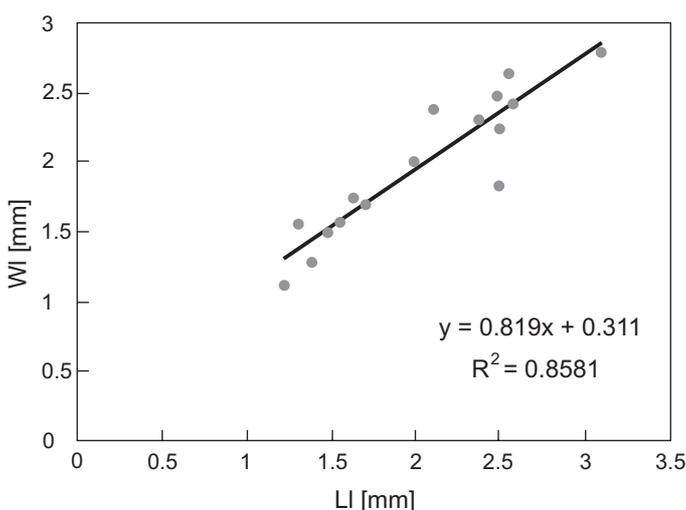


Fig. 3. Plots of maximum length (LI)/maximum width (WI) between the paired brachia of *Lingulellotreta malongensis* based on ELI collection from the Early Cambrian Chengjiang fauna at Haikou, Kunming, South China. See Fig. 5 for location of measurement.

Table 1. Statistics for *Lingulellotreta malongensis* based on ELI collection from the chengjiang fauna at Haikou, Yunnan, South China. See Fig. 5 for location of parameters.

	L	Ls	Lb	Ws	LI	WI	Lb:Ls
Count	64	55	47	57	18	18	43
Min	2.28	1.46	0.39	2.2	1.22	1.12	0.22
Max	8.09	5.5	3.65	4.36	3.1	2.8	1.12
Mean	6.32	4.2	1.4	3.22	1.97	1.92	0.33
SD	1.03	0.65	0.45	0.48	0.56	0.43	0.13

The digestive system.—The configuration of the alimentary canal of *L. malongensis* is completely revealed in one informative specimen (Fig. 4A, B). It is marked by a recurved, “mud-filled” tube, showing considerable relief (Fig. 4A, B). Mouth is represented by a circular mark at the base of the lophophore (Figs. 1, 2, 4A), which is followed by a short esophagus (Fig. 4A). This leads posteriorly into a pouchlike distended stomach (Fig. 4A). A transverse belt-like impression across the stomach could represent the gastroparietal band (Fig. 4A). Several protuberances with considerable relief at or near the posterior part of the stomach are interpreted as digestive diverticula (Fig. 4A). Beyond the stomach the digestive canal continues as a narrow intestine filled with muddy sediment and extending posteriorly. Then, it recurves in front of the posterior body wall, and extends forwards toward the right anterior body wall, finally terminates in an anal opening some distance postero-lateral to the mouth (Fig. 4A, B).

Comparison

The lophophore of modern *Lingula* is a spirulophe with the two spires directed inwards, each being an inhalant spire carrying unfiltered water, which is strained and exhaled medially. The apices of the spirals converge toward one another and are generally oriented dorsally (Cohen et al 2003). The lophophore is held up purely by the hydrostatic pressure of fluid in the great brachial canal (Williams et al. 2000; Clarkson 1998).

The general shape of the lophophore of *L. malongensis* is analogous to that of Recent lingulids. The fossil lingulellotretid lophophore appears to share the following features with living lingulids: (1) A comparable configuration that comprises a pair of spirals, arranged symmetrically about a mouth; (2) absence of any skeletal support; and (3) a single palisade of tentacular filaments. However, the fossil lophophore differs from the extant forms in: (1) the proportion of the total shell length/volume that it occupies, and (2) the brachial arms appear to be less intricately coiled than in living lingulids.

As in the other lingulids, the digestive tract of *L. malongensis* is U-shaped, opening at the mouth and terminating

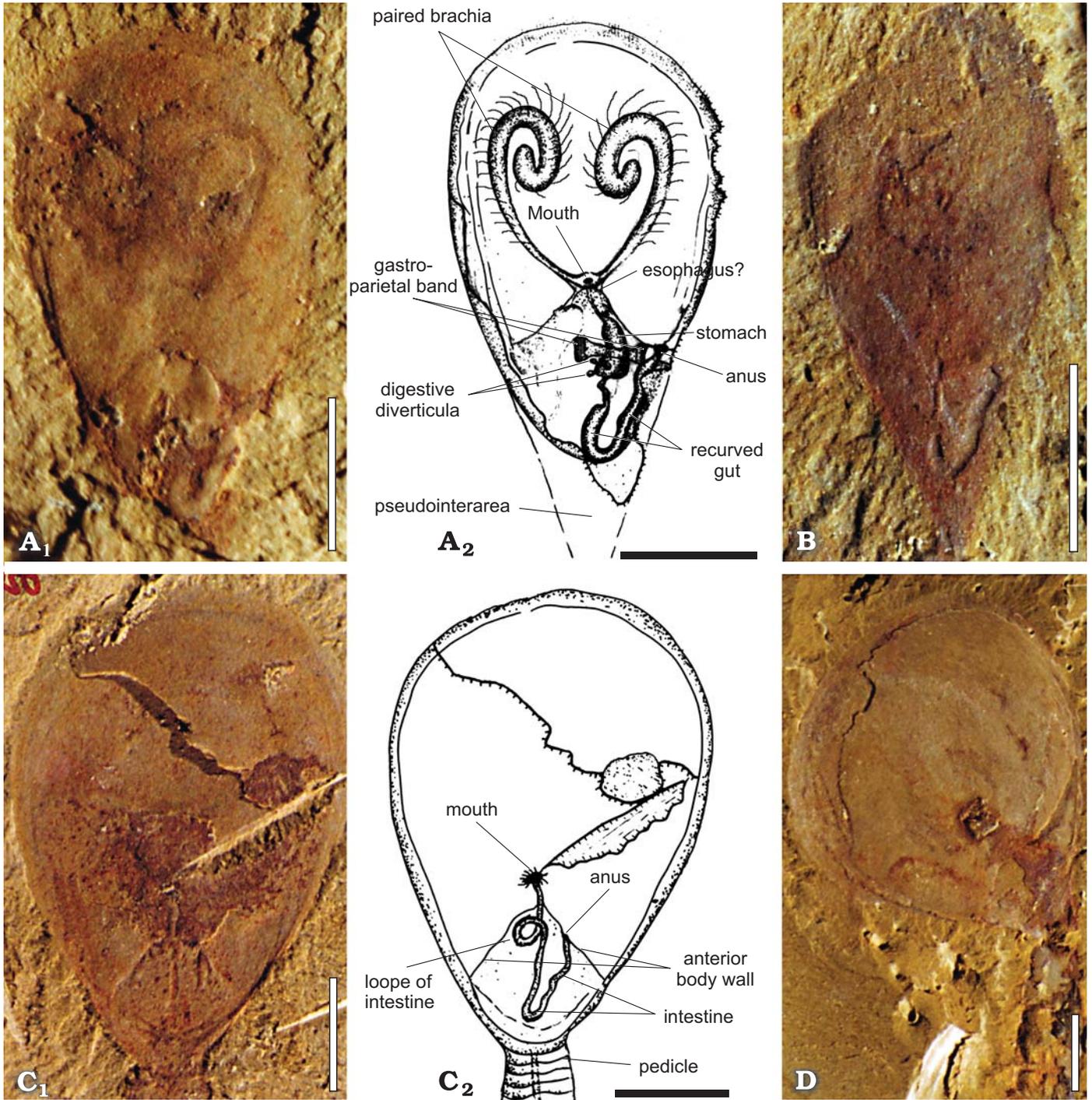


Fig. 4. Two linguloid brachiopods, *Lingulelloreta malongensis* and *Lingulella chengjiangensis*, from the Yu'an-shan Member of the Qiongzhusi (Chiung-chussu) Formation, Lower Cambrian, South China. **A.** *Lingulelloreta malongensis*, ELL L-0017. **A₁**, photograph of the dorsally and right laterally compressed specimen, showing the interiors, including the digestive system and paired imprints of brachia; **A₂**, explanatory drawing of the same. **B.** ELI L-0091A, a parallel specimen of *Lingulelloreta malongensis*, note the faint brachial contour and digestive tract with considerable relief. **C.** *Lingulella chengjiangensis*, ELI C-0029. **C₁**, photograph (dorsal view) of dorsal interior, showing the digestive tract with an anterior anus, and with impression of visceral cavity; **C₂**, explanatory drawing of the same. **D.** *Lingulella chengjiangensis*, ELI C-0027, anterodorsally compressed specimen, showing the position of the mouth. Scale bars 2 mm.

with an anteriorly placed anus. The obolid *Lingulella chengjiangensis* (Jin et al. 1991, 1993) is another of the most common linguloid brachiopods in Chengjiang Lagerstätte and the U-shaped digestive tract of this brachiopod is

also well revealed in several exceptional specimens (Fig. 4C, D) where it appears as a continuous, mud-infilled narrow tube, medially located inside the posterior 1/3 of shell (Fig. 4C). As a whole, the arrangement of the digestive tract

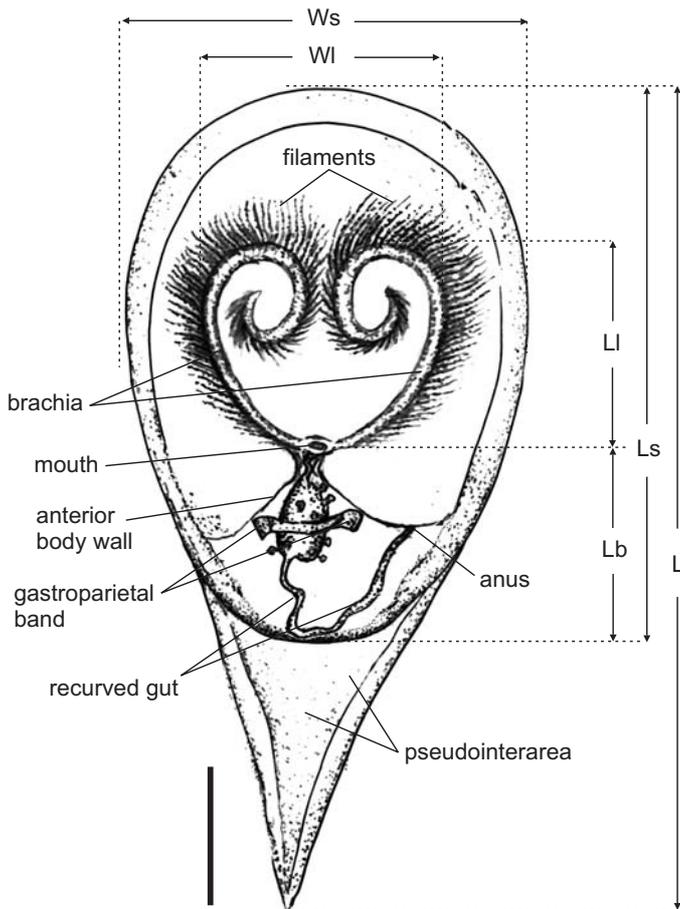


Fig. 5. *Lingulellotreta malongensis* from the Chengjiang Fauna, reconstruction of the internal morphology based on ELI L-0014 and ELI L-0017, showing disposition of lophophore and digestive tract, and location of measurements indicated in Table. 1. Abbreviations: L, length of the shell; Lb, length of the body; LI, length of the lophophore; Ls, length of the dorsal valve; WI, width of the lophophore; Ws, width of the shell. Scale bar 1 mm.

of *Lingulellotreta malongensis* resembles that in *Lingulella chengjiangensis*, both displaying U-shaped. But the former differs from the latter in absence of a free loop of intestine to the left, and in presence of a distended stomach. The alimentary canal of *Lingulella chengjiangensis* is similar to that of Recent *Lingula* (see Williams 2000: fig. 90.2, 6), except that the intestine loop is much smaller in the latter. By contrast, the digestive tract of *L. malongensis* is relatively simple, turning right from the stomach toward the lateral body wall, terminating at an anus on the right body wall, somewhat similar to that of *Discinisca* (see Williams 2000: fig. 90.1, 5).

Discussion

In the study of brachiopods the presence or absence of an anus was formerly taken to be a difference of the highest importance differentiating inarticulate and articulate brachiopods. But it is hard to tell whether the anus has always been

characteristic of the inarticulates in that the gut leaves no trace in fossil brachiopods. These fossils demonstrate that a U-shaped digestive tract and an anterior anus were present in the Early Cambrian in at least two inarticulate brachiopods. We argue that these character-states are likely to be plesiomorphies, inherited by the Recent lingulids and discinids from a common stem ancestor especially in view of molecular evidence, which has demonstrated the monophyly of Brachiopoda (Cohen et al. 1998). It follows that the absence of an anterior anus in articulate brachiopods represents a loss. Similarly, the recurved gut of inarticulate and the lophophore with a single palisade of filaments are likely to be plesiomorphies of the Brachiopoda. However, a comparison of the interiors of the fossil linguloids and the modern lingulids suggests that the morphology of the linguloids has not remained remarkably constant at least since the early Paleozoic, and probably argues for the contrary claim that some authors recently presumed (Emig 2003; Biernat and Emig 1993). Some detectable differences include the fairly small, and posteriorly situated visceral cavities, and in the simpler coiling of the lophophore. The visceral cavity in the fossil linguloids accounts for roughly the posterior 20–30% of the space inside shell (Figs. 1, 2; Table 1), which would preclude development of the widespread muscle insertions, a necessary prerequisite for the mobile valves associated with burrowing. Thus such a posterior and small body cavity may restrict the mobility of the valves, and may be unlikely to be adaptation to burrowing. Additionally, the pseudointerarea of *Lingulellotreta malongensis* is elongate and large, projecting far from the rear margin of the valves (Figs. 1, 2). Such projections appear to be unfavorable to burrowing, and may have prevented movement of valves and entry into the substrate occurs in Recent *Glottidia* (Emig 2000; Thayer and Steele-Petrovich 1975). Furthermore, the current patterns and the disposition of setae of the Early Cambrian linguloids could be strikingly different from the modern *Lingula* with three “pseudosiphons” (in preparation by our team). Thus it appears likely that the animals examined here were either planktonic juvenile or, given their relative large size, epibenthic forms, unable to burrow. The relatively simple lophophore of these fossil lingulids may also indicate that their feeding currents were relatively weak and perhaps less effective in providing for gas exchange. This accords with the probable lower oxygen demand of an epifaunal brachiopod when compared with an infaunal one of the same size. The fact that the fossil lingulid shell valves and the main part of the pedicle are invariably preserved on the same bedding plane (Fig. 1D, F, G) may also be an indirect evidence for epifaunal life.

The fossils described here from the Early Cambrian (Atdabanian) provide the oldest direct evidence of the form of the lophophore and the disposition of the digestive tract in fossil brachiopods. These findings demonstrate that the inarticulate brachiopods were quite advanced by the Mid-Lower Cambrian, implying that much morphological evolution had occurred before that time. Furthermore, the diversity of the

lophophores (Zhang, Hou, and Emig 2003) and the variety in the arrangements of the recurved guts of the different taxa strongly indicates that the inarticulate brachiopods had already diversified by the beginning of the Cambrian. If so, the oldest relatives or stem groups of the brachiopods presumably lived in the late Proterozoic, or even earlier. In this context, fewer readers will need to be reminded that no fossil Brachiopoda from the Precambrian are known.

Acknowledgements

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