RHYNCHONELLIFORMEAN BRACHIOPODS WITH SOFT-TISSUE PRESERVATION FROM THE EARLY CAMBRIAN CHENGJIANG LAGERSTÄTTE OF SOUTH CHINA

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Abstract: Cosmopolitan kutorginates, the most abundant Early Cambrian rhynchonelliformean brachiopods, became extinct at the end of the Middle Cambrian. Consequently, any information concerning the anatomy of this peculiar lineage of brachiopods has great phylogenetic significance with regard to their extant relatives for analogies with the stem-group clade. Such data have been supplied from fossils of which the soft parts have been preserved in exceptional detail. A new brachiopod, Kutorgina chengjiangensis sp. nov., from the Early Cambrian Chengjiang Lagerstätte of southern China, is described here. It is the first articulated brachiopod species collected from this deposit. The specimens preserve a set of soft-body parts, i.e. lophophore, digestive tract and pedicle, all previously poorly known in almost all Palaeozoic calcareous brachiopod taxa. The lophophore attains an early spirolophe stage, clearly homologous to that in the coeval lingulids. The digestive tract consists of a mouth, oesophagus, swollen stomach, intestine and a terminal anus. The pedicle protruding between the valves is stout and elongate, with annulated lamellae on the surface, and contains a putative celomic cavity. K. chengjiangensis displays the characteristics of the stem group of calcareous brachiopods, and illustrates anatomical similarities between Cambrian phosphatic- and calcareous-shelled brachiopods, thus corroborating that the Brachiopoda are a monophyletic group.

Key words: Early Cambrian, Chengjiang Lagerstätte, brachiopoda, lophophore, digestive tract, pedicle, soft-tissue preservation.

Although only minor members in present-day marine communities, brachiopods have an extensive fossil record, exhibiting morphological diversity and geological continuity that reflect their dominance in the marine benthos throughout the Palaeozoic era. Recent molecular studies suggest that the Phoronida should be assigned to the phylum Brachiopoda as a shell-less subphylum or class (Cohen 2000; Cohen and Weydmann 2005), but it is now generally argued that the Brachiopoda comprise three subphyla: Linguliformia, Craniformia and Rhynchoformia. The Rhynchoformia comprise five classes, of which only the Rhyynchonellata unquestionably have living relatives. Calcareous-shelled brachiopods, known since the Early Cambrian, soon became the largest group, dominant since Late Cambrian times. Nevertheless, fossils of this particular lineage are known almost exclusively from their shells. Consequently, anatomical knowledge of extinct taxa relies heavily on analogies with their extant relatives; yet these analogies have been untested conjectures as regards stem-group clades (Sutton et al. 2005). Information regarding these clades has been obtained recently from the fossil record, notably from those deposits with exceptional preservation of soft parts (Zhang, Z. F. et al. 2003, 2004a, b, 2005, 2006, 2007a, b; Zhang X. G. et al. 2003; Sutton et al. 2005; Holmer and Caron 2006).

Now perhaps surpassing in fame the classic Middle Cambrian Burgess Shale (Briggs et al. 1994), the Chengjiang Lagerstätte is an exceptional mudstone deposit acclaimed for yielding one of the earliest, most abundant and diverse faunas of soft-bodied organisms in the Phanerozoic (Shu et al. 2001, 2003, 2004, 2006; Hou et al. 2004). It preserves details of soft tissues in brachiopods with fine fidelity. The deposit yields an abundant variety
of inarticulated brachiopods, often with fine preservation of soft parts, notably lophophores, digestive tracts and mantle canal system, which are very rarely fossilized elsewhere. However in this Lagerstätte, rhynchonelliformean brachiopods are sparse, numerically overshadowed by their linguliformean cousins. Consequently, to date the rhynchonelliformeans in these Early Cambrian mud deposits have not been described.

Continuing excavations near Kunming, Yunnan (Text-fig. 1A–B), in south-western China have led to the discovery of many specimens of rhynchonelliformean brachiopods. The specimens are referred to Kutorgina and described as Kutorgina chengjiangensis sp. nov., based on the outline and morphology of the valves. As compared with the other kutorginate brachiopods of similar age without preserved soft parts from Greenland, Russia, Kazakhstan and Australia (Rowell 1977; Popov and Tikhonov 1990; Popov 1992; Popov et al. 1997; Popov and Williams 2000; Skovsted and Holmer 2005), our specimens show soft tissues, including pedicle, mantle canals, lophophore and digestive tract, as well as a marginal setal fringe. Although soft parts in Silurian articulated brachiopods from the Herefordshire (UK) Konservat-Lagerstätte have been reported recently (Sutton et al. 2005), no records of soft parts in Cambrian rhynchonelliformean brachiopods have been described previously. Thus, the c. 520–525 Ma fossils provide evidence about the state of anatomical characters of the rhynchonelliformean stock of brachiopods, a first step in elucidating the radiation of brachiopods during the Cambrian explosion and the evolution of their functional morphology.

MATERIAL AND PRESERVATION

The majority of the specimens were recovered from Jianshan Hill at Haikou (Text-fig. 1A–B), where the hitherto earliest-known agnathan Haikouichthys (Shu et al. 2003) and a variety of remarkable body plans of deuterostomes, including vetulicolians (Shu et al. 2001) and vetulocystids (Shu et al. 2004), as well as the most recently reported Early Cambrian vendobionts (Shu et al. 2006) have also been discovered. Ten specimens of the brachiopod were collected in the Shankoucun Section at Anning, about 30 km south-west of Kunming, Yunnan, and eight specimens in the Erjie section near Meishucun (Text-fig. 1A), where a candidate section for the global stratotype of the Precambrian/Cambrian boundary was proposed (Luo et al. 1984).

The strata containing these fossils belong to the Yu’anshan Member (Eoredlichia-Wudingaspis Zone), i.e. the
upper part of the Early Cambrian Heilinpu (formerly Qiongzhusi) Formation (Text-fig. 1B), exposed in a wide area around Kunming (Luo et al. 1999). The deposits, commonly regarded as late Atdabanian in age (Qian and Bengtson 1989; Bengtson et al. 1990; Zhu et al. 2001a), are considered to have accumulated in proximal offshore to lower shoreface environments disturbed by episodic storm events (Zhu et al. 2001b; Hu 2005). So far, more than 60 specimens of Kutorgina chengjiangensis have been collected from those localities by the work-team of the Early Life Institute (ELI) and are deposited in the ELI, Northwest University, Xi'an, China (designated ELI BK-001 to BK-062; part and counterparts indicated by suffixes A and B). Among them are 25 with more or less well-preserved pedicle remains (Text-figs 2A–C, G, 3A–F, 4D–H, 5A–C); six with partial or paired lophophoral imprints (Text-figs 2A–H, 5A–D), which in a few cases have a little relief and marginal setae (Text-fig. 4A–C); and five specimens have an exceptionally preserved digestive tract, dorsally curved, with a putative dorso-terminal anus located near the proximal end of a pedicle (Text-figs 2C, F–I, 3C–E).

Specimens of K. chengjiangensis commonly occur as dorsoventrally flattened moulds of valves (Text-figs 1–3), but the quality of the preservation of shells that have been replicated by clay minerals varies greatly. Soft-tissue preservation indicates that many of the complete shells represent carcasses buried alive, rather than accumulated valves. In many cases, they appear to be preserved as compressed composite dorsal/ventral moulds (Text-figs 2A–C, G, 3A–G, 4A–H, 5A–C, E). When removing the flattened dorsal valve, the ventral valve can be revealed (Text-fig. 4D–F). In specimen ELI BK-038A, the dorsal and ventral valves are more or less displaced owing to some factors of preservation (Text-figs 2B, E, 5C). In a few cases, the lateral profile of a shell can be observed (Text-fig. 4I). In specimen ELI BK-037A, B, the anterior part of the shell has been distinctly compressed (Text-fig. 4I). Intriguingly, when a mudstone containing the fossil brachiopod is cleaved, the split is usually along the flattened dorsal valve, the ventral valve can be revealed (Text-fig. 4D–F). In specimen ELI BK-038A, the anterior margin is rectimarginate; anterior margin rectimarginate; surface strongly lamellose peripherally, no visible prominent micro-ornamentation; ventral valve with a possible spiral impression seen through the compressed dorsoventrally flattened moulds of dorsal valves (Text-figs 2A–H, 5A–C, E). This arrangement could indicate in situ burial of the brachiopods in their original life position. As most of the pedicles were only partly visible after ‘crackout’ (Text-fig. 2A–C, G, 3A–F, 5A–C), mechanical preparation with fine needles and small brushes was necessary. The lophophores of K. chengjiangensis are visible either directly (Text-fig. 4A–B), as a result of cleavage approximately along the commissural plane, or as paired spiral impressions seen through the compressed dorsal valve as a result of post-depositional flattening (Text-figs 2A–H, 5A–D). The alimentary canals are also preserved as reddish-brown impressions on the internal moulds of dorsal valves (Text-figs 2C, F–I, 3C–E, 5B). The preservation of the setal fringe (Text-figs 3F–G, 5E) is weaker than those seen in Cambrian lingulid taxa (Zhang, Z. F. et al. 2005, 2006).

### SYSTEMATIC PALAEONTOLOGY

**Subphylum RHYNCHONELLIFORMEA** Williams, Carlson, Brunton, Holmer and Popov, 1996

**Class KUTORGINATA** Williams, Carlson, Brunton, Holmer and Popov, 1996

**Superfamily KUTOGINOIDEA** Schuchert, 1893

**Family KUTORGINIDAE** Schuchert, 1893

**Genus KUTORGINA** Billings, 1861

**Type species.** Kutorgina cingulata Billings, 1861, from the Lower Cambrian of Labrador, Canada.

**Diagnosis.** See Popov et al. 1997, p. 346.

**Kutorgina chengjiangensis** sp. nov.

Text-figures 2–5

**Derivation of name.** After the Chengjiang Lagerstätte, Yunnan Province, southern China, and implies soft-tissue preservation.

**Holotype and occurrence.** ELI BK-042 (Text-figs 2A, 5A), from the Yu’anshan Member (Eoredlichia-Wudingaspis Zone), Early Cambrian Heilinpu Formation, Yunnan, southern China.

**Diagnosis.** Shell strongly dorsiibiconvex, suboval or transversely oval in outline; anterior margin rectimarginate; surface strongly lamellose peripherally, no visible prominent micro-ornamentation; ventral valve with a possible...
apical foramen; dorsal valve with straight posterior margin and a moderate median fold developed anteriorly from mid-valve. Ventral interarea apsacline, dorsal interarea narrow; dorsal lateral mantle canal pinnate, and dorsal vascula media bifurcate at midline; muscle scars poorly impressed; lophophore a simple spiral lacking any support structures. Pedicle stout and elongate, with a centric coelomic cavity. Digestive tract composed of a mouth, oesophagus, enlarged stomach, intestine and a dorsoterminal functional anus.

TEXT-FIG. 2. Kutorgina chengjiangensis sp. nov. from the Chengjiang Lagerstätte, South China, showing lophophore imprints (single arrows) and digestive tract (tailed arrows). Scale bars represent 5 mm. A, D, holotype, ELI BK-042. A, general view of the holotype showing the lophophore imprints and the visceral region and pedicle (see also Text-fig. 5A). D, enlargement of the lophophore and visceral region. B, E, ELI BK-038A, laterally distorted specimen with conjoined and displaced valves. B, general view; note the proximal lophophore imprints and the proximal pedicle (see also Text-fig. 5C). E, close-up view of the lophophore. C, F, ELI BK-001. C, flattened specimen affected by lateral compression; note the imprints of paired brachial arms and digestive canal (see also Text-fig. 5B). F, details of the lophophore and gut. G–H, ELI BK-002A, flattened dorsal internal mould, showing the impression of the alimentary canal and lophophore. G, general (see also Text-fig. 5D), and H, enlarged views. I, ELI BK-003A, flattened dorsal internal mould, showing the remnants of the alimentary canal.
Description

Shell. Shell dorsobiconvex and subelliptical to subquadrate in outline; the maximum length is 15 mm and the maximum width of 17 mm occurs at about the anterior third of shell length in a different specimen. The ratio of shell length to width ranges from 0·72 to 0·97 (average 0·84; see ‘Dimensions’ below). Dorsal valve strongly convex with the maximum height at mid valve; ventral valve moderately convex with the highest point at about posterior quarter of the valve length (Text-fig. 4I–J). From the three-dimensional preservation of the ventral valve (Text-fig. 4I)

TEXT-FIG. 3. *Kutorgina chengjiangensis* sp. nov. from the Chengjiang Lagerstätte, South China, showing the pedicle (black arrows), putative pedicle cavity (white arrows), mantle canals (double-headed arrows) and possible dorsal-terminal anal openings (tailed arrows). Scale bars represent 5 mm. A, ELI BK-010, flattened specimen; note the pedicle extending downwards. B, ELI BK-051A, dorsal exterior with pedicle preserved and its presumed cavity replicated by pyrite. C, ELI BK-037B, crushed dorsal internal mould with a three-dimensional pedicle and linear lumen (white arrow); note the darkish scar of an anal opening. D–E, ELI BK-037A. D, general, and E, enlarged views of an anal opening and pedicle lumen (white arrow). F–G, ELI BK-036. F, general view of a flattened specimen with a flattened elongate pedicle, showing the dorsal vascula (see also Text-fig. 5E). G, close-up view of the mantle canals in F.
Visceral region and digestive tract. The visceral cavity appears in margin (Text-fig. 3B). The preservation of the lophophore varies among Lophophore. The visceral cavity appears in margin (Text-fig. 3B).

Pedicle. Pedicle protrudes between delthyrium and notothyrium and is always preserved as a flattened impression, usually bent steeply into the sediments (Text-figs 2A–C, G, 3A–F, 4D–H, 5). It arises from the posterior margin of the shell, continues as a stalk of constant diameter, is ornamented with transverse grooved annulations, and terminates in a flattened annulated disc. Distally the pedicle does not bear any of the root-like structures seen in many Recent articulates, and no other shell has been found to have anchorages as in Chengjiang lingulids (Zhang, Z. F. et al. 2006, 2007a). The maximum length of the pedicle is c. 13 mm, up to c. 31 mm in diameter in specimen ELI BK-037A, B (Text-fig. 4I). It appears to be much more robust than that of the Chengjiang lingulids (Jin et al. 1993; Zhang, Z. F. et al. 2005, 2006, 2007a, b). Its surface in some specimens shows pronounced concentric annular discs disposed at intervals of 0.6–1.0 mm. That this robust kutorginid pedicle was filled by connective tissue is uncertain, but it contains a putative coelomic cavity. This is suggested by a median darkish lineation (Text-fig. 3C–E), which is here interpreted as a coelomic lumen akin to the pedicle cavity seen in the fossil lingulids from the Chengjiang Lagerstätte. In specimen ELI BK-051A, this pedicle cavity seems to be preserved as a yellowish-brown pyrite string, extending some 5 mm posterior to the posterior shell margin (Text-fig. 3B).

Visceral region and digestive tract. The visceral cavity appears in several specimens (Text-figs 2A–I, 5A) as a reddish-brown, recessed, pyriform imprint on the internal mould of the dorsal valve in a posteromedian position; it extends anteriorly over one-third of the valve length. The complete alimentary canal of K. chengjiangensis is revealed in Text-figure 2, and is completely shown in Text-figure 5B, D. The mouth is presumed to be located at the base of the lophophore. A postero-dorsally extending strand is interpreted as the oesophagus (Text-fig. 5B), an enlarged, dark-stained pouch represents the stomach, a narrow intestine is impressed as a dark red strand, and a putative dorso-posterior anus represented by a circular scar is located near the proximal end of the pedicle (Text-figs 2C, F–I, 3C–E).

Lophophore. The preservation of the lophophore varies among the specimens. The imprints of the paired brachial (lophophoral) arms in specimen ELI BK-042 run anterolaterally from the ante-rior of the median visceral area and bend inward (Text-fig. 5A) symmetrically to the midline; this disposition has been observed in many specimens (Text-figs 2A–H, 4A–C, 5A–D). In specimen ELI BK-016A–B, the lophophore appears three-dimensionally preserved inside the valve (Text-fig. 4A–C). As seen in Text-figure 4C, F, the brachial arms leave a pair of asymmetrical impressions with a faint colour contrast on the flattened dorsal valve as a result of laterally compressed preservation of the shell valves (Text-figs 2C, 5B). In addition, some specimens show only the proximal part of paired brachial imprints on a specimen that is strongly obliquely compressed (Text-figs 2B, E, 5C). The apparent flexibility shown by these paired imprints (Text-figs 2C, F, 5B) in the fossil state, and their less intricately spiralled configuration (Text-figs 2A, 4A, 5A) demonstrate that they are most likely allied with brachial arms rather than any type of lophophore support structures. The simple coiling of brachial imprints indicates that the lophophore of K. chengjiangensis has attained an early spiroloph development stage.

Although tentacles on a Cambrian lingulid lophophore are known from the Chengjiang deposits (Zhang X. G. et al. 2003; Zhang, Z. F. et al. 2004a, b, 2005), such structures cannot be confidently demonstrated in the available specimens. Continuing investigation of further material from these deposits may yield information bearing on this issue.

Mantle canals. The mantle canals of fossil brachiopods are commonly preserved as grooves and ridges more or less symmetrically disposed on either side of the longitudinal midline of the valves. The dorsal mantle canals of K. chengjiangensis are preserved as reddish-brown impressions on the internal mould of the dorsal valve (Text-fig. 3F–G). On the left side of one laterally compressed specimen (Text-figs 3F–G, 5E), three linear impressions arise from the anterior body wall at an anterolateral position, while on the right side they are weakly visible, presumably congruent with those on the left. The dorsal vascula media appears to be bifurcate. No information on the ventral mantle canals is detectable in our specimens.

Setae. Setae are a characteristic feature of all brachiopods. In the group, they show significant differences in length and width, as well as in their arrangement along the margin. All described Chengjiang lingulids bear setae. The poorly preserved setae of K. chengjiangensis are preserved as reddish linear impressions; they are spaced equidistantly, and radiate outward from the mantle margin with lengths of up to 1.7 mm (Text-fig. 4A–C).

Dimensions (in mm)

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<th>Max</th>
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<th>N</th>
<th>Mean</th>
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<tr>
<td>Valve length</td>
<td>15</td>
<td>6.44</td>
<td>15</td>
<td>9.7</td>
<td>2.38</td>
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<tr>
<td>Valve width</td>
<td>17</td>
<td>5.22</td>
<td>19</td>
<td>11.12</td>
<td>2.69</td>
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<tr>
<td>L/W ratio</td>
<td>0.97</td>
<td>0.72</td>
<td>15</td>
<td>0.84</td>
<td>0.082</td>
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Remarks. The Kutorginidae is one of the most common components of Cambrian calcareous-shelled brachiopod
faunas. The strong concentric growth lamellae and putative foramen in the fossils dealt with herein suggest that the organism is probably affiliated to the kutorginide brachiopods. Furthermore, species of *Kutorgina* are usually very variable in their morphology (Popov et al. 1997); thus, we refer these fossils provisionally to this genus.

*Kutorgina chengjiangensis* differs from the other four described species of the genus in its relatively large size, in having a much more strongly convex dorsal valve and a moderately developed ventral valve, as well as in terms of a lack of any discernible micro-ornamentation on the shell surface. In contrast, the four previously described species have a strongly convex ventral valve and a moderately developed dorsal valve with fine micro-ornamentation. *K. reticulata* was first described by Poulsen (1932, p. 29) from the Ella Island Formation of north-east Greenland. It is distinguished from the other species of the genus by the supposedly unique micro-ornamentation of hexagonal pustules. *K. cingulata* Billings, 1861 is similar to *K. catenata* Koneva, 1979 from the Lower Cambrian of Kazakhstan and Kirgizia in having a granular micro-ornamentation (Popov et al. 1997), but is distinguished from it in having a ventral sulcus, a well-defined notothyrial platform, and strongly developed ridges bounding the inner sides of the grooves in the dorsal pseudointerarea. The fourth species is *K. perugata* Walcott, 1905 (Walcott 1912; Rowell 1977). Its valves are ornamented with minute rhomboid granules. In addition, *Trematosia undulata* (Cooper, 1976), from the Early Cambrian Nimra Formation of southern Negev, Israel, was also considered to have an affinity with *Kutorgina* because of its lamellose shell, minute apical foramen, broadly triangular, convex pseudodeltidium and poorly defined propareas on an apsacrine ventral interarea (Popov et al. 1997).

**DISCUSSION AND COMPARISON**

Although lophophores are known from Cambrian linguliforme and Silurian articulated brachiopods, we present here the first detailed description of the lophophores of Cambrian articulated brachiopods. Intriguingly, *K. chengjiangensis* has a relatively large mantle cavity and a small visceral cavity, whilst the brachial arms discussed here are less intricately coiled or spiraled, and occupy a little of the mantle cavity. The simple spirals of the lophophores perhaps indicate that the feeding currents they produced were relatively weaker and perhaps less effective in providing for gas exchange. Thus, it is a prerequisite that Cambrian brachiopods possessed a relatively larger mantle space for gas exchange than extant forms, as the transport of oxygen in brachiopods into the body tissues takes place predominantly through the epithelia of the lophophore and mantle lobe (Williams et al. 1997). In addition, the Cambrian atmospheric/environmental oxygen concentration was rather lower, approximately 15 per cent of current O\(_2\) levels (Holland 1994). Therefore, the higher ratio of the mantle cavity to body cavity of Early Cambrian brachiopods appears to be reasonable for oxygen demand. In this respect, the calcareous-shelled brachiopod is similar to its coeval lingulid cousins (Zhang, Z. F. et al. 2004a, 2005, 2006, 2007a, b), probably reflecting similar environmental constraints. It is clear that *K. chengjiangensis* bears no trace of any skeletal lophophore support. The coiled lophophore corresponds to an early spirolophe developmental stage. Therefore, it is assumed that the lophophores of Cambrian kutorginids were supported by a hydrostatic skeleton as in Recent lingulides. This lophophore shows significant similarities with those of Cambrian–Recent lingulids (Emig 1992; Zhang X. G. et al. 2003; Zhang, Z. F. et al. 2004a) in both a comparable configuration that comprises a pair of spirals arranged symmetrically about a midline, and in the absence of any skeletal support. These similarities support the view that lophophores in phosphatic- and calcareous-shelled brachiopods are homologous. The finding of the lophophore in calcareous-shelled brachiopods, in conjunction with the description of Cambrian lophophores in various lingulid taxa (Zhang X. G. et al. 2003; Zhang, Z. F. et al. 2004a, b, 2005, 2006, 2007a, b) demonstrate that an
early spirouloph has been the most common lophophore configuration since the onset of Cambrian times. The lophophores of Cambrian lingulids, e.g. Lingulella chengjiangensis and Lingulelloreta malongensis (Zhang, Z. F. et al. 2004a, b, 2005), include trochocephes, schizolophes and the less intricately coiled spiroulophes. This development of lophophores is mirrored in the ontogeny of Recent lingulids. Thus, the early stages of spiroulophous lophophore ontogeny and development appear to be plesiomorphic characters inherited from an ancestral form.

The trocholeloph-schizolopho-early spirouloph development of the lophophore has been universal throughout the history of the phylum (Emig 1992; Zhang, Z. F. et al. 2004b). The spirouloph is the final stage of development among the Linguliformes and the Craniiformes, while in the Rhynchonelliformes, three stages have evolved from the schizolopho stage, respectively: the spirouloph, the more efficient plectolopho (Rudwick 1970; Emig 1992) and the lobate psycholopho (Rudwick 1970; Grant 1972).

In brachiopods the presence or absence of an anus was formerly taken to be a difference of the highest importance, differentiating 'inarticulate' from 'articulate' brachiopods. Although, as discussed above, alimentary canals are known from Cambrian linguliformean brachiopods, there is no direct fossil evidence that a digestive tract was present in articulate stocks. The only putative fossil evidence from rhynchonelliformean brachiopods was deduced from the silicified kutorginid Nisusia sulcata of the Middle Cambrian of the Marjum Limestone of western Utah, USA. Because of some silicified, sausage-like objects protruding posteriorly through the gap between shell valves of Nisusia sulcata (Rowell and Caruso 1985; Popov and Williams 2000), which were misinterpreted as faecal material or coprolites, Rowell and Caruso (1985) concluded that Nisusia possessed a functional anus. However, these sausage-like objects bore markedly transverse grooves on their surface, and the maximum observed length was up to 6 mm (Rowell and Caruso 1985; Cohen et al. 2003). Their gross form and the way they emerged from between the delthyrium and notothyrium suggest that they represent pedicles. Indeed, Cohen et al. (2003) postulated that the sausage-like structures identified as faecal material could represent a pedicle, and this is corroborated by the finding of the pedicle in the material described here. The pedicle of K. chengjiangensis has a general resemblance to the sausage-like, transversely grooved projections illustrated by Rowell and Caruso (1985). Therefore, fossil evidence bearing on an opening digestive tract at an anus in articulate stocks no longer appears to be tenable.

The fossils described here provide the oldest direct evidence of the disposition of the digestive tract in carbonate-shelled brachiopods. In K. chengjiangensis it is undoubtedly directed posteriorly from a mouth within the lophophore, and is presumed to terminate in a functional anus located near the proximal end of the pedicle. Although the possibility of a blind ending may not be completely eliminated because of the location of the end of the intestine in the fossils, it is obvious that there is a circular scar on the internal mould of the dorsal valve and ferruginous matter scattered along the posterior dorsal margin. In addition, the imprint of the digestive canal with a low relief unequivocally terminates at a darkish rounded opening situated anterior to the posterior valve margin. The weight of evidence reviewed above leads us to reject the possibility of a blind-ending intestine, and conversely argues for the existence of a dorsoposterior anus in kutorginides, as in Recent craniids.

All extant rhynchonelliformean taxa have been described with a blind-ending intestine. Consequently, the occurrence of an anus in kutorginids allows us to state that in the Brachiopoda this is a plesiomorphic character inherited from an ancestral group common to both linguliformean and craniiformean taxa, all of which have a functional anus; the organization of the alimentary canal of linguliformean brachiopods is known from the Cambrian. Thus, the blind intestine among the Rhynchonelliformes must be regarded as an apomorphous evolutionary novelty.

The Kutorginidae and Nisusidae, being alike in possessing an extremely primitive articulation that lacks teeth (Popov and Tikhonov 1990; Popov et al. 1997), were considered to be related and thus to belong to the same order, Kutorginida. Studies of the articulation of Kutorgina and Nisusia (Rowell and Caruso 1985; Popov and Tikhonov 1990) suggested that kutorginids may represent one of the most primitive types of articulate brachiopods (Popov et al. 1997). The distinctive features of the kutorginate stocks are the possession of a large convex pseudodeltidium and the presence of a minute supra-apical foramen. The traditional view is that this supra-apical opening is the pedicle foramen, an aperture for the egress of the pedicle. However, the fossils figured here demonstrate that K. chengjiangensis has a massive, stout pedicle to provide a reliable anchor. Nevertheless, it is difficult to imagine such a massive pedicle could emerge through such a minute supra-apical opening that was well illustrated in the type species Kutorgina cingulata (see Popov et al. 1997; pl. 1, figs 1–12). Therefore, we conclude that the small supra-apical opening was not the aperture for pedicle egress in kutorginates. This conclusion is consistent with silicified three-dimensional specimens of Nisusia from the Middle Cambrian of western Utah (Rowell and Caruso 1985; Popov and Williams 2000) in which the silicified pedicles, originally misinterpreted as faecal material (see above), distinctly protruded posteriorly through the gap defined by the notothyrium and the dorsal surface of the pseudodeltidium (see Rowell and Caruso 1985,
Furthermore, the small, supra-apical opening was evidently recognizable in the western Utah material. The cases reviewed above therefore argue against the traditional view that the supra-apical opening is the pedicle foramen. Crucial in this respect is how to interpret and understand the function of the minute apical opening in the kutorginite lineages. It is probably difficulties in reconstructing this function that led Rowell and Caruso (1985, p. 1234) to reject the identification of the sausage-like projection in their material as the pedicle. One possibility is that this opening may represent a rudiment of a hydrodynamic shell-opening mechanism (Popov 1992).

Almost all brachiopods are attached to the substratum by a pedicle, but the pedicles of articulated and inarticulated brachiopods differ in structure, function and embryonic origin (Williams et al. 1997). The pedicle of inarticulated brachiopods develops as an outgrowth of the posterior body wall and is associated only with the ventral valve, whereas the pedicle of articulated brachiopods is correlated with the body wall of both valves because their pedicle rudiment is continuous with the mantle rudiment that produces both the ventral and the dorsal valves. It is not at all clear how this difference should be interpreted phylogenetically. When compared with pedicles of Cambrian lingulids (Jin et al. 1993; Zhang, Z. F. et al. 2005, 2006, 2007a; Holmer and Caron 2006), the pedicle of *K. chengjiangensis* is markedly stout and stiff, possibly filled with connective tissue and containing a cecolic cavity; thus it is rather similar to those of Recent lingulids (Williams et al. 1997). Although some pedicles in extant rhynchonellate brachiopods are as robust as that of *K. chengjiangensis*, they are shorter (Richardson 2000). Many of them bear holdfast papillae with distal rootlets that are absent in *K. chengjiangensis*. By contrast, the pedicle of the Cambrian species is relatively larger, lacks distal rootlets and has a median cecolic cavity. Although it was not possible to determine the presence or not of the pedicle lumen in other fossil articulate (Sutton et al. 2005) the pedicle of *K. chengjiangensis* resembles that of Silurian articulated brachiopods in gross morphology and surface ornamentation with concentric laminae or subtransverse ridges. The similarities in the configuration of the lophophore, the digestive tract and pedicle anatomy in the Cambrian rhynchonelliforme brachiopods to that of the linguliformean branch give additional support for the monophyly of the Brachiopoda (Hyman 1959; Rowell 1982; Emig 1997), which has been corroborated recently from molecular perspectives (see Cohen et al. 1998; Passamanek and Halanych 2006).

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**REFERENCES**


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