

# Early Cambrian radiation of brachiopods: A perspective from South China

Zhifei Zhang<sup>a,\*</sup>, Sean P. Robson<sup>b</sup>, Christian Emig<sup>c</sup>, Degan Shu<sup>a</sup>

<sup>a</sup> Early Life Institute, State Key Laboratory of Continental Dynamics and Department of Geology, Northwest University, Xi'an, 710069, China

<sup>b</sup> The Manitoba Museum, 190 Rupert Avenue, Winnipeg, Manitoba, Canada R3B 0N2

<sup>c</sup> BrachNet, 20, Rue Chaix, 13007 Marseille, France

Received 30 April 2007; received in revised form 25 July 2007; accepted 1 August 2007

Available online 9 August 2007

## Abstract

Brachiopods, a group of benthic suspension-feeding marine invertebrates, made their first appearance in the Lower Cambrian. In the Yangtze Platform (South China), well-exposed Lower Cambrian stratigraphic succession represents shallow to deeper water environments. Strata from eastern Yunnan, southern Shaanxi and the Yangtze gorges areas of western Hubei Province, deposited in muddy-siltstone and carbonate lithofacies, contained an abundant variety of brachiopods, including all the representatives of the subphylum Linguliformea and the calcareous-shelled genera of *Kutorgina* and *Nisusia* from the subphylum Rhynchonelliformea. Thus the fossil assemblage bears witness to the first major phase of evolutionary radiation of brachiopods during the 'Cambrian explosion' interval of metazoans. Brachiopods from the celebrated Chengjiang fauna have exquisitely preserved soft-tissues, which reveal the body plans and evolutionary acquisition of morphological novelties of the early stocks, and also provide a good opportunity for testing the analogies with the stem groups from the extant representatives. These fossils have corroborated the view that brachiopods developed complex organization of tissues, and achieved considerable evolutionary success already by the onset of 'Cambrian Explosion'. Thus it is not improbable that a large part of this radiation occurred within, or only just before early Cambrian time. Studies of Chengjiang brachiopods suggest that attachment by a pedicle to the substrate was probably the most common relationship of Cambrian brachiopods with the substrate where they inhabited.

© 2007 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.

**Keywords:** Early Cambrian; Diversification; Brachiopods; Soft-tissue preservation; Character evolution

## 1. Introduction

Although substantially lower in diversity today, brachiopods were among the most abundant and diverse skeletal marine invertebrates throughout most the Paleozoic era. So far, well over 4500 genera have been described, a large proportion of which are known from fossil shell material in that their strongly biomineralized exoskeleton was prone to preservation. Traditionally, the Brachiopoda comprised two classes, Inarticulata and Articulata, but it is now generally accepted that the brachiopoda are divided into three subphyla, Linguliformea, Craniiformea and Rhynchonelliformea (Williams et al., 1996, 2000), despite some molecular studies repeatedly suggest that

the Phoronida should be considered as a shell-less Subphylum or Class (Cohen, 2000; Cohen and Weydmann, 2005). In many different palaeoenvironmental settings, brachiopods are well preserved and easily collected as fossils, therefore they play an important role in biostratigraphy, palaeobiogeography, palaeoecology, functional morphology and evolutionary palaeobiology (e.g.: Kondo et al., 2006). As a result, the early origin and early Palaeozoic diversification of brachiopods have been a subject of increasing interest in the last decade (e.g. Holmer and Popov, 1996; Popov et al., 1996; Holmer et al., 1997; Popov et al., 1997; Bassett et al., 1999; Holmer, 2001; Robson and Pratt, 2001; Holmer et al., 2002; Popov et al., 2002; Robson et al., 2003; Li and Holmer, 2004; Zhan et al., 2005; Skovsted and Holmer, 2005; Holmer and Caron, 2006). Despite intensive searches of late Pre-Cambrian strata in many parts of the world, no acknowledged fossil brachiopods have been found in strata earlier than the Lower Cambrian: all records of alleged Precambrian brachiopods are now highly doubtful (Holmer

\* Corresponding author. Early Life Institute and Department of Geology, Northwest University, 229#, Taibai Road, Xi'an, 710069, China. Tel.: +86 29 88303553; fax: +86 29 88302128.

E-mail addresses: [elizf@nwu.edu.cn](mailto:elizf@nwu.edu.cn), [zhangle@126.com](mailto:zhangle@126.com) (Z. Zhang).

and Popov, 1996). The unquestionable earliest known brachiopods together with the small shelly fossils occur in the lowermost of Cambrian (Holmer and Popov, 1996; Popov et al., 1996). Recent studies of brachiopods recovered from the Lower Cambrian of the Yangtze platform (South China) have substantially increased our understanding of the phylum (X.G. Zhang et al., 2003; Z.F. Zhang et al., 2003; Li and Holmer, 2004; Zhang et al., 2004a,b, 2005, 2006, 2007a,b,c). Of these, the reports of soft-tissue preservation of brachiopods (X.G. Zhang et al., 2003; Z.F. Zhang et al., 2003, 2004a,b, 2005, 2006, 2007a,b, c) are of key importance to understanding the body plans and palaeoecology of brachiopods in the Early Cambrian (Jin et al., 1991; Jin and Wang, 1992; Jin et al., 1993; Z.F. Zhang et al., 2005, 2006, 2007a), and thus has attracted considerable attention (Sutton et al., 2005; Holmer and Caron, 2006; Fang, 2006). The findings of soft tissues in brachiopods of South China demonstrate that the brachiopods had already achieved considerable evolutionary success already during the rapid radiation of metazoans (i.e. the Cambrian explosion interval), and that they became a numerically important component of marine benthic communities during that time (X.G. Zhang et al., 2003; Z.F. Zhang et al., 2003, 2004a,b, 2005, 2006, 2007a,b,c). It is crucial to the study of the Early Cambrian radiation of brachiopods to determine which lineages had emerged by that time, then the diversity of these lineages, and finally the evolutionary acquisition of the major morphological character states that characterize the taxonomic diversification of these lineages.

The main objective of this paper is to give an outlined summary of the Lower Cambrian diversification of brachiopods from the Yangtze Platform, and provide a perspective of the character-states of Early Cambrian brachiopods in the light of the available soft-tissue data from the Chengjiang Lagerstätte, South China. All the material illustrated herein was collected by the work-team of the Early Life Institute (prefix: ELI); and all

the specimens are deposited in the ELI, Northwest University, Xi'an, China.

## 2. The diversification of early Cambrian brachiopods in the Yangtze platform (South China)

The Yangtze Block in South China has figured in many recent reports related to the tectonic evolution of the South China Block (e.g., Ye et al., 2007; Zhou et al., 2007) and its correlation with adjacent crustal fragments (Oh, 2006; S.Z. Li et al., 2007). The Yangtze Platform was adjacent to Gondwana, and even a constituent part of this supercontinent at the temporal interval from at least Early Cambrian to late Early Devonian. This platform was most probably connected to the Great India–Australia region of the Gondwana margin (Li and Powell, 2001; S.H. Zhang, 2004). In this Platform, the latest Precambrian–Cambrian depositional sequences are finely developed and exposed. Within the Lower Cambrian, brachiopods have been broadly documented in different regions of the Yangtze Platform (Mansuy, 1912; Xie, 1988; Zeng, 1987; Shu, 1990; Jin et al., 1991; Jin and Wang, 1992; Jin et al., 1993; Li and Holmer, 2004). Detailed descriptions and taxonomic study of many of them, however, remain to be done. In this context, we concentrate on the diversification of the brachiopods in the Yangtze Platform, exemplified by the eastern Yunnan Province, the southern Shaanxi Province, and the Yangtze-gorge areas of western Hubei Province, South China (Fig. 1a). The Precambrian geological evolution of the Yangtze-gorges area, the history of sedimentation and chrono- and sequence stratigraphy have been investigated in various studies (e.g., Wang et al., 1999; Chen and Wang, 1999; Wang and Li, 2001, among several other workers). Of the three study provincial areas, Early Cambrian brachiopods are, however, well-documented only in the former two provinces (Rong, 1974; Jin and Wang,

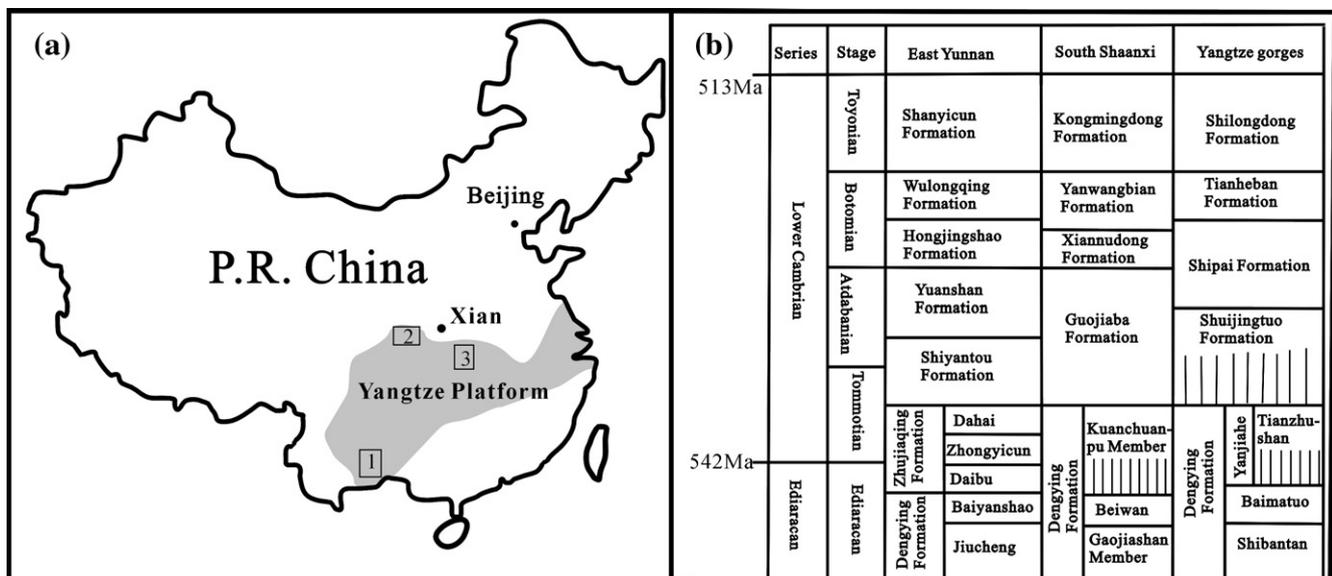


Fig. 1. (a) Geographic location of the eastern Yunnan (1), the southern Shaanxi (2), and the Yangtze gorges area in western Hubei province (3). (b) Stratigraphic nomenclature and correlation of the Early Cambrian of these three areas, adapted from Luo et al. (1994) and Zhu et al. (2005).

1992; Jin et al., 1993; Li and Holmer, 2004; Zhang et al., 2005, 2006, 2007a,b,c and references therein).

### 2.1. Eastern Yunnan Province

The Lower Cambrian and terminal Proterozoic stratigraphic successions are extremely developed and well exposed in eastern Yunnan Province, notably the areas near Kunming, Jinning, and Chengjiang. Consequently, a well-known candidate section for the global stratotype of the boundary between the Cambrian and Precambrian has been proposed at Meishucun Section in Jinning Country. According to the most recent biostratigraphic investigations in Yunnan (e.g. Zhu et al., 2005 and references therein), the depositional sequences from terminal Proterozoic to Early Cambrian comprise, in ascending order, the Ediacaran Dengying Formation, the Meishucunian (equivalent to the Tommotian of Siberia) Zhujiaping and Shiyantou Formations, the Qiongzhusian (Atdabanian) Yu'an-shan Formation, the Canglangpuian (Botomian) Hongjingshao and Wulongqing Formations, and the Longwangmian (Toyonian) Shanyicun Formation (Luo et al., 1999; Zhu et al., 2005). The Dengying Formation is composed of Donglongtan, Jiucheng and Baiyanshao Members (Zhu et al., 2005); the Zhujiaping Formation consists of Daibu, Zhongyicun and Dahai Members, the latter two of which bear an abundant variety of small-shelly fossils (Luo et al., 1984; Qian and Bengtson, 1989; Bengtson et al., 1990; Li and Xiao, 2004). The Lower Cambrian Yu'an-shan–Shanyicun Formations is a succession of muddy–siltstone–sandstone–siltstone deposition sequences, while the Longwangmian (Toyonian) Shanyicun Formation is represented by a set of carbonate deposition. The Yu'an-shan Formation contains the well-known Burgess Shale-type Chengjiang fauna (see Hou et al., 2004). Recently a new Burgess Shale-type fauna, called the Guanshan fauna (Luo et al., 1999), was recovered from the Lower Cambrian Canglangpuian Wulongqing Formation, including the primitive deuterostomes known as vetulicolians (Luo et al., 2005), an abundant variety of arthropods (Luo et al., 2006, 2007, Liu et al., 2006) and lingulate brachiopods not

yet described in details (Hu et al., 2007; Zhang et al., 2007b), some of which are definitely allied to the brachiopod genera *Lingulellotreta* and *Palaeobolus*.

The study of Cambrian brachiopods in eastern Yunnan can be traced back to Mansuy (1912), when 7 species of brachiopods were first reported, including *Acrothele mathewi eryx* Walcott, *Obolus demesis* Walcott, *O. chinensis* Walcott, *O. detritus* Mansuy, and two species, *Acrothele orbicularis*, *Lingulella yunnanensis*, firstly erected by Mansuy (1912). Sixty years later, Fang (1974) re-illustrated the brachiopods discovered by Mansuy (1912), and added two-species, *Kutorgina cingulata* and *Obolus? Meneghini* Walcott, to the assemblage of Early Cambrian brachiopods in eastern Yunnan Province. The same year, investigations of the Lower Cambrian brachiopods were made by Rong (1974), who reported the findings of three new species *Diandongia pista*, *Lingulellotreta malongensis* (Rong), *Lingulellotreta yunnanensis*, and two uncertain species *Acrothele* sp. and *Lingulella* sp. However, there was no further investigation and study of the brachiopods in eastern Yunnan until lingulids with soft-bodied preservation were found in the Lower Cambrian Chengjiang Lagerstätte (Jin et al., 1991; Jin and Wang, 1992; Jin et al., 1993). Meanwhile, the two species *L. malongensis* and '*Lingulella*' *chengjiangensis* was detailed described. Later, Luo et al. (1994) summarized the study of Early Cambrian brachiopods in East Yunnan, and illustrated by a plate of brachiopods, but no additional information was provided. Continuing excavation of the exceptional Chengjiang Lagerstätte revealed 8 species of brachiopods. They consist of *L. malongensis* Rong, 1974, "*Lingulella*" *chengjiangensis* Jin et al., 1991, *Longtancunella chengjiangensis* Hou et al., 1999, *Xianshanella haikouensis* Zhang and Han, 2004, the probable stem soft-shelled *Wangyuia chengjiangensis* Jin et al., 2004, *D. pista* Rong, 1974, the problematic brachiopod *Heliomedusa orientata* Sun et Hou 1987 (Jin and Wang, 1992; Holmer et al., 2003, 2004; Chen et al., 2007), and the cosmopolitan *Kutorgina* recently reported by Zhang et al. (2007c) as a representative of the Subphylum rhynchonelliformea in the unique muddy deposit. In addition, a single brachiopod specimen from Chengjiang is

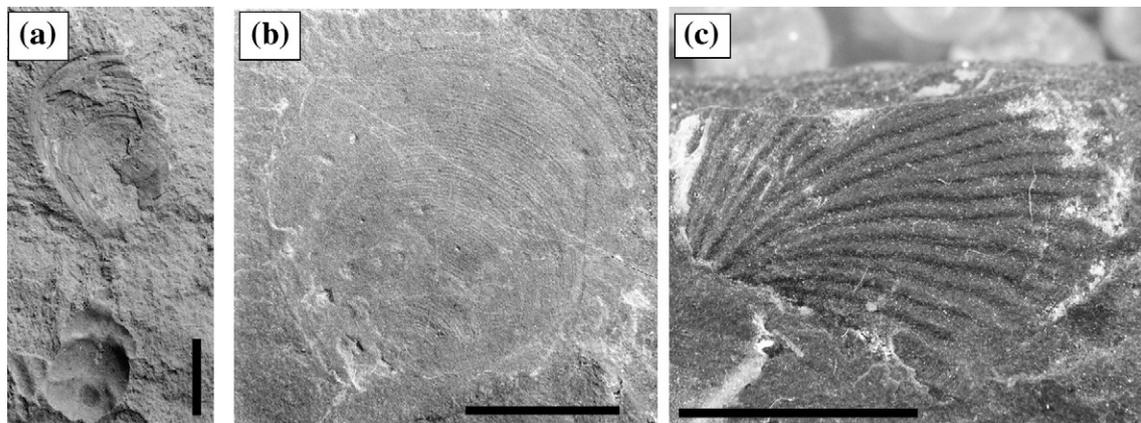


Fig. 2. Some fossil brachiopods from the Lower Cambrian Qiongzhusian Stage of eastern Yunnan and the Yangtze gorge area of Hubei province. (a) A lamellose brachiopod putatively allied to obolellids, with a pedicle attached on a trilobite. (b) ELI YBP-001B, a mold of shell of *Palaeobolus*. (c) ELI YBN-001, a mould of *Nisusia*. Scale bars 5 mm.

probably akin to the obolellids on the basis of its general shell contour and the lamellose surface shell ornamentation (Fig. 2a), but further confirmation awaits findings of additional data. To sum up, the brachiopod assemblage from the eastern Yunnan comprises 11 reported genera, of which only one is definitely assigned to the Subphylum Rhynchonelliformea, and the other ten to the Subphylum Linguliformea. It is accordingly presumed that the brachiopod assemblage recovered from eastern Yunnan could reflect the first radiation of Brachiopoda during metazoan macroevolution in South China (Fig. 3).

2.2. Southern Shaanxi Province

Recently, a diverse fauna of lingulate brachiopods has been made well available from the Early Cambrian (Qiongzhusian Stage) Guojiaba and Xiannüdong carbonates in southern Shaanxi Province (Fig. 1a and b) (Li and Holmer, 2004). The

assemblage consists of 8 species, assigned to 6 genera, including the Lingulelloretid *L. malongensis* (Rong), the obolid *Palaeobolus liantuensis* Zeng, *Eoobolus* aff. *Viridis* (Cobbold, 1921), *Eoobolus?* *shaanxiensis* Li and Holmer, and *Kyrshabaktella?* sp., the acrotheloid *Botsfordia minuta* Li and Holmer, as well as two primitive acrotretoid *Eohadrotreta zhenbaensis* Li et Holmer, and *E. zhujiangensis* Li et Holmer. Of these, *L. malongensis* is also known from the Lower Cambrian Yu'an-shan (equivalent to late Atdabanian stage) and Wulongqing (Botomian) Formations in eastern Yunnan Province, as well as from equivalent strata from Kazakhstan (Shabakty Group, Malyi Karatau). In addition, *Eoobolus* aff. *E. viridis* of the widespread family Eoobolidae, is also non-endemic in the Shaanxi lingulate assemblage (Li and Holmer, 2004). Similar species are known both from Avalonia (England and Newfoundland) and Australia (Ushatinskaya and Holmer, 2001) of Gondwana supercontinent.

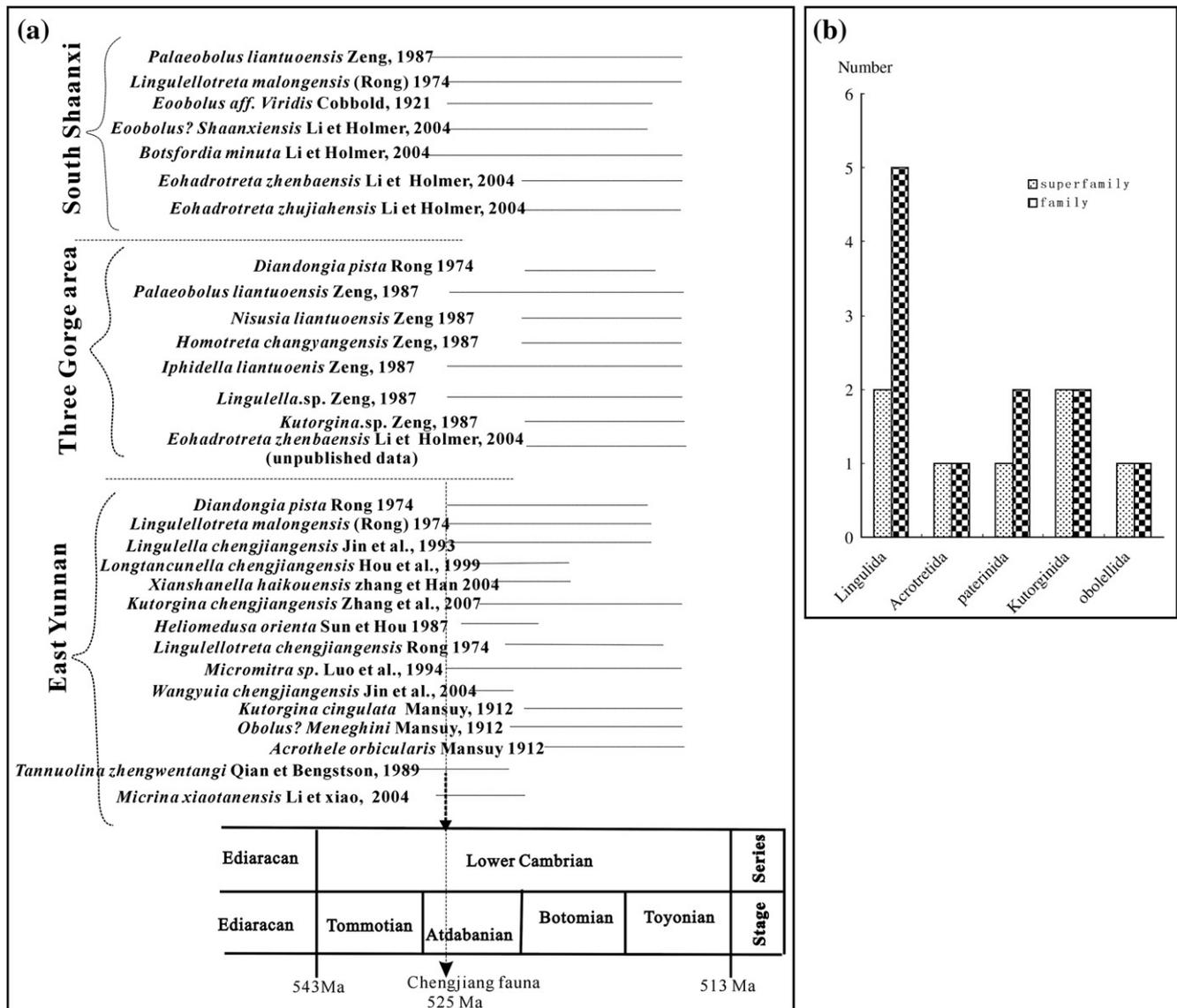


Fig. 3. (a) Fossil occurrence, and (b) a preliminary statistic for the Early Cambrian brachiopod diversification in the Yangtze Platform (South China).

### 2.3. The Three Gorge area of western Hubei Province

The Lower Cambrian and terminal Proterozoic stratigraphic successions are well exposed in the Three Gorge areas of Hubei Province (Fig. 1a), where the Early Cambrian strata consist of, in ascending order, the Yanjiahe/Tianzhushan Formations, Shuijingtuo Formation, Shipai, Tianheban, and Shilongdong Formations (Fig. 1b).

The known brachiopods from the Three Gorge area were mainly derived from the Shuijingtuo, Shipai, Tianheban Formations (Fig. 1b). The brachiopod assemblage is composed of *Palaeobolus liantuensis* (Fig. 2b), *Homotreta changyanensis*, *Iphidella liantuensis*, and *Nisusia liantuensis* (Fig. 2. c), and some specimens possibly belonging to *Lingulella*, *Kutorgina*, and *Obolella* (Zeng, 1987). Recently, several constituents of the Chengjiang brachiopod assemblage in Yunnan have been found in the Three Gorge area, notably the botsfordiid *D. pista*, which is widely distributed in the yellowish-green siltstone of the lower part of the Shipai Formation. In some specimens, the slim and labile pedicle was finely preserved (Zhang and Hua, 2005, 2006). In addition, several large individuals (also see: Fig. 2b) are putatively related to *Palaeobolus liantuensis*, also preserved as flattened impressions or composite molds in some cases with marginal setae or pedicles (Zhang and Hua, 2006). However, a detailed investigation of the brachiopods from this region remains to be done.

### 2.4. Remarks and discussion

Brachiopods, a group of benthic tentaculated suspension-feeding, bivalved invertebrates, were an important component of the Early Palaeozoic marine communities. Together with the Early Cambrian Meishucunian “Small Shelly Fossils” distributed worldwide, brachiopods occur in the lowermost Cambrian. They are, therefore, considered to be the result of the Cambrian Explosion and the outcome of repeated attempts at mineralization by early animals. The organophosphatic-shelled subphylum Linguliformea comprises two Classes, Lingulata and Paterinata, the former of which is composed of three orders, Lingulida, Acrotretida, and Siphonotretida, and the latter composed exclusively of the order Paterinida. In the Lower Cambrian of south China, the Order Lingulida is widely represented by the predominant linguloids, while the Order Acrotretida is less common, represented by a single genus of *Eohadrotreta* (Li and Holmer, 2004) (Fig. 3). Recently the senior author (Zhang, Z.) made available an important collection of a large number of acrotretid brachiopods from the Early Cambrian (Qiongzhusian Stage) upper Shuijingtuo Formation in the Yangtze gorges areas. This collection has not yet been prepared and studied in detail, but it is clear that they could be assigned to two different acrotretid genera (Our unpublished data). With regard to discinids, it is worth of noting that the Lower Cambrian brachiopod *H. orientalis*, which was first identified as a jellyfish (Sun and Hou 1987), later described as a representative of subphylum Craniiformea (Jin and Wang, 1992; Popov and Holmer, 2000), but most recently assigned to

Discinidae (Chen et al., 2007). Its affinity with discinids still remains controversial, mainly due to mixoperipheral and hemiperipheral growth respectively in ventral and dorsal valves with well-defined pseudointerarea (Fig. 4a–d). In addition, no fossil evidence could lend support for the presence of a pedicle in the postero-median region of the ventral valve. The only inferred cast of pedicle illustrated by Chen et al. (2007: Figs. 7. 5, 6) is most probably related to three dimensionally preserved visceral cavity (Fig. 4d), as this type of preservation of body cavity has been found in the contemporaneous lingulid brachiopods (see: Zhang et al., 2005: Fig. 1C). Anyway, the Class Lingulata has abundant Early Cambrian representatives dominated by their lingulid and acrotretid lineages.

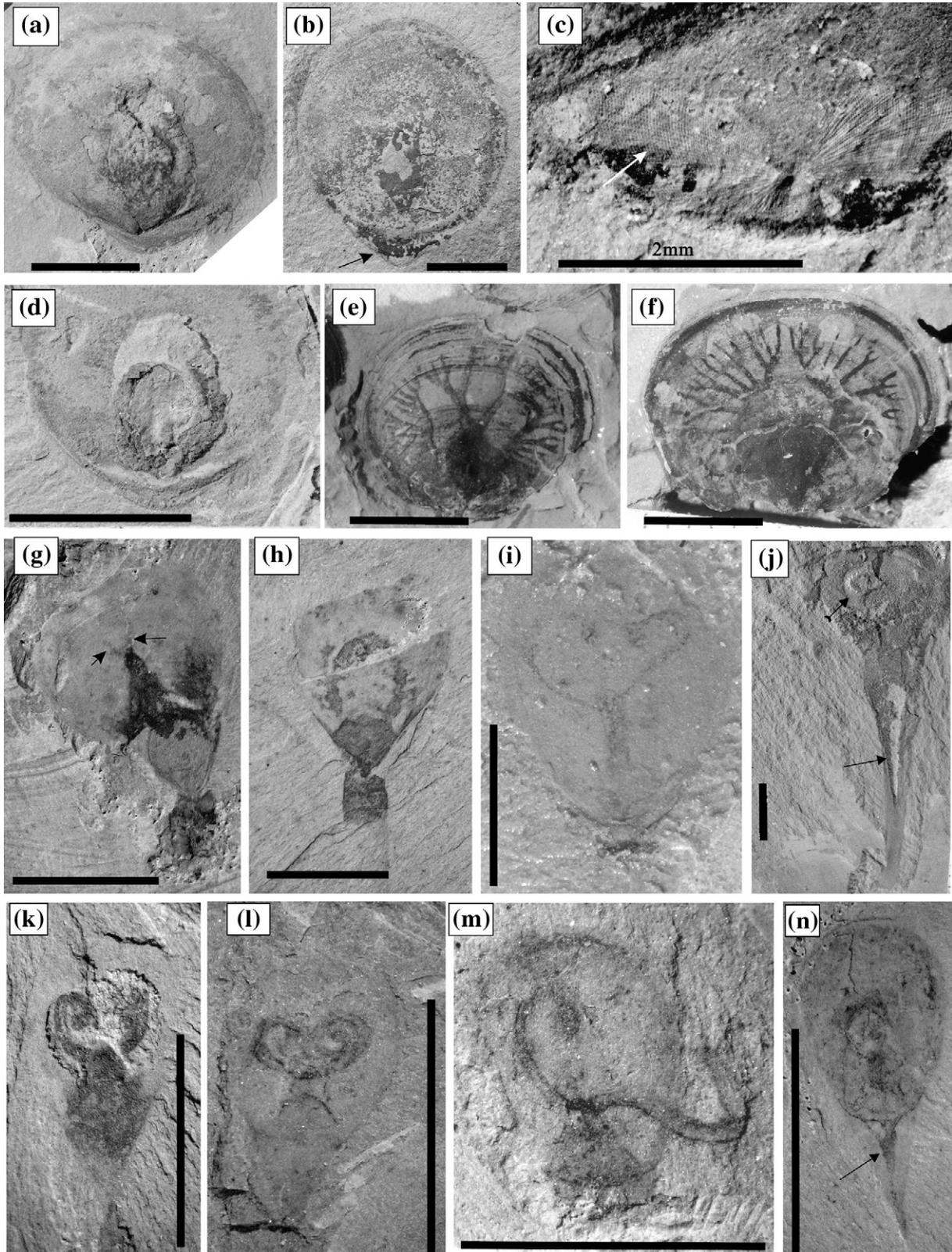
No acknowledged paterinid brachiopods were published and described in detail from the Lower Cambrian of the three regions of South China. Nonetheless, *Tianzhushanella ovata* of Tianzhushanellidae (Bengtson et al., 1990) is commonly referred to the Paterinida. The other eight genera reported by Liu (1979), including *Scambocris*, *Acidotocarena*, *Artimycetella*, *Protobolus*, *Plicatolingula*, *Dolichomocelypha*, *Psamathopalass*, *Heosomocelypha*, are in essence of importance to understanding the origin and body plan of the Lower Cambrian brachiopods because of their occurrence in the basal-most of Cambrian (Liu, 1979). Unfortunately, since then no additional study on these fossils was carried out. Now, some authors (Bengtson et al., 1990; Qian, 1999; Li et al., 2006) contended to classify them into a group of pseudobrachiopods, their convincing affinities with the phylum Brachiopoda, however, remain to be resolved. Nevertheless, the Class Paterinata has their possible representative as *Iphidella? liantuensis* (Zeng, 1987) in the Three Gorge area, Hubei, and one pre-representative as *Micromitra* sp. derived from the eastern Yunnan (Luo et al., 1994). The Class has also the Tommotian *Cryptotreta neguertchenensis* as representative in Siberia (Pelman, 1977), and *Askepasma* sp. in South Australia (Ushatinskaya and Holmer, 2001). This inconsistency of paterinid brachiopod taxa between Siberia, Australia, and South China awaits a pending detailed comparative study of the Early Cambrian brachiopods in these three Blocks.

The calcareous-shelled rhynchonelliformean brachiopods represented by *Kutorgina* and *Nisusia* occurred in the late Qiongzhusian Stage of the Yangtze platform, equivalent to late Atdabanian of Siberian Block. However, in the Siberian platform, the earliest calcareous-shelled brachiopods were referred to the order Obolellida that made its first appearance in the mid-Tommotian (Pelman et al., 1992; Geyer, 1994). This inconsistency of the earliest calcitic-shelled taxon of brachiopods between the Yangtze and Siberian platforms is therefore awaiting additional data to comparatively study, although we could owe this discrepancy to the differences of Early Cambrian paleogeographic locations of the two blocks.

Clearly, the brachiopod associations (Fig. 3) in the three regions of South China bear witness to the first major phase of evolutionary radiation, and it is not improbable that a large part of this radiation occurred within, or just before early Cambrian time (Benton and Ayala, 2003). Nonetheless, as organophosphatic-shelled lingulates dominate the brachiopod assemblage,

one may assume that the optimal acquisition of mineralized shells by brachiopods were phosphatic at the onset of Cambrian, which could be probably considered as a result of an evolutionary adaptation to the phosphorite-rich environment

settings during the temporal interval from terminal Proterozoic to Early Cambrian. But the problem of secreting a calcareous shell was also solved by the initial stage of the Cambrian, as demonstrated by the presence of the cosmopolitan kutorginid



brachiopods *Nisusia* and *Kutorgina* in the Lower Cambrian. Thus, it is likely that different mineralizations in brachiopods occurred more or less in parallel, while the underlying unmineralized diversification most probably occurred well before the Early Cambrian (e.g. Cohen, 2005). Although ambient seawater chemistry does not strongly influence skeletal mineralogy (Porter, 2007), the seawater chemical environment settings may, therefore, have played an important role in determining what type of mineralization of lineage blooming.

### 3. Evolutionary development of morphological character sets in Early Cambrian brachiopods

Although the Brachiopoda is well defined as a phylum, living species segregate into three groups differing fundamentally in their development, anatomy, and gross morphology. Brachiopods are known largely based on the fossil records of shells. Consequently, our knowledge of Palaeozoic brachiopod anatomy relies heavily on analogies with their extant relatives; yet these analogies have been untested regarding stem-group clades (Sutton et al., 2005; Zhang et al., 2007c). In the last 15 years, data has been increasingly recovered from Lagerstätte with exceptional preservation of non-biomineralized parts (Jin and Wang, 1992; Jin et al., 1993; Zhang et al., 2003a,b, 2004a,b, 2005; Sutton et al., 2005; Holmer and Caron, 2006; Zhang et al., 2006, 2007a,b,c). The most important new Cambrian findings are from the Chengjiang Lagerstätte, distributed in a wide area around Kunming, Yunnan (Luo et al., 1999). The mud-dominated deposits, commonly considered to correlate with the Late Atdabanian Stage of Siberia (Qian and Bengtson, 1989; Bengtson et al., 1990), contains abundant brachiopods including 7 phosphatic-shelled linguliformean species and only one rhynchonelliformean kutorginid species. The brachiopods from Chengjiang often exhibit preservation of soft parts, including pedicles, setae, mantle canals, lophophores, digestive tracts and well-defined visceral regions. Studies of these fossilized soft-tissue fossils are of utmost significance to identifying the character-state of internal tissues and organs in early brachiopods and for determining the plesiomorphic features, common to all inarticulated brachiopods, such as U-shaped intestines with an anteriorly placed anus, spiral lophophores, and the appearance of cartilaginous tissue in the pedicles of articulate. Thus the Chengjiang specimens are of great importance in understanding the differences between, and evolution of, soft tissues of phosphatic- and calcareous-shelled brachiopods,

some of which can be determined unambiguously by the well-preserved soft-bodied fossils.

#### 3.1. Setae

Setae can be found in Recent brachiopod species (except craniids), emerging from the setal follicles along the dorsal and ventral mantle margins. They probably function primarily as extended tactile sensors of the mantle edges (Rudwick, 1970), and are present in all brachiopods found in the Chengjiang Lagerstätte (Figs. 4a, b, 5a)(Jin and Wang, 1992; Zhang et al., 2005; 2006, 2007a,c; Chen et al., 2007) including the botsfordiid *D. pista* and the non-shelled stem group *W. chengjiangensis* (Jin et al., 2004) (Fig. 4j). The setae of different taxa show substantial differences in length and width, as well as in arrangement. The setae of the ventral valves of *X. haikouensis* look distinctly thicker and coarser than those of the dorsal valves (Zhang et al., 2006), but were presumably disposed equidistantly along the mantle edges of the valves. In *L. malongensis* and ‘*Lingulella*’ *chengjiangensis* as well as in *L. chengjiangensis*, the preserved marginal setae are thin, short, delicate linear fringes that emerge upright to the shell margin (Zhang et al., 2005, 2007a). The preservation of setae of the well-mineralized acrotheloid *D. pista* is fairly sparse. Two specimens indicate that the setae of this botsfordiid species are also thin and delicate, and spine-like, but inclined gently away from the anterior margin. With respect to the arrangement, the slim setae of *D. pista* bear a resemblance to those of *Heliomedusa orientalis* (Jin and Wang, 1992) putatively closely related to *Mickwitzia* (Holmer et al., 2004). Setal impressions of *H. orientalis* are recognizable in most the specimens in our collections. They are either preserved as linear impressions or rod-shaped structures in three dimensions (Figs. 4a and 5a). In addition, the setae of the Kutorgina specimens, recovered from the Chengjiang deposits, were similar to the coeval lingulids in gross arrangement (Zhang et al., 2007c). However, the disposition of setae along the mantle edge differs between Early Cambrian and Recent lingulids: while the setae of living lingulids are disposed in three pseudosiphons at the anterior mantle margin (two inhalant and one median exhalant apertures) (Emig, 2000, 2003), the setae of the fossil lingulids were fringed equidistantly along the mantle edge. Hence, it is assumed that the evenly fringed setae along the entire mantle edge could be the ground state of setae of stock lingulids (Zhang et al., 2005, 2006, 2007a), and that the three-pseudosiphon formation of setae found in Recent lingulids is proposed to be an apomorphy derived as an adaptation to an infaunal lifestyle (Zhang et al., 2005).

Fig. 4. (a)–(d) *Heliomedusa orientalis* from the Lower Cambrian Chengjiang Lagerstätte. (a) ELI BH-674B, a composite mould of dorsal and ventral valves; note the dorsal and ventral pseudointerarea. (b) ELI BH-714, Ventral valve showing the pseudointerarea with some transverse linear surface ornaments (arrow). (c) ELI BH-641B, Details of ventral pseudointerarea; note the oblique diamond-like ornaments. (d) ELI BH-61A, showing a three-dimensionally preserved visceral region of *Heliomedusa orientalis* preserved with muscular scars, equivalent to the pedicle cast in Chen et al., 2007 (Figs. 7, 5, 6). (e)–(f) *Diondonesia pista*, showing the dorsal and ventral mantle canals with distributaries peripherally diverged by dichotomy. (e) ELI D-103A, (f) ELI D-077. (g)–(i) ‘*Lingulella chengjiangensis*’. (g) ELI C-440, showing the bifurcate vascula media. (h) ELI C-441, baculate vascula lateria with distributaries; (i) ELI C-087, showing the lophophore imprints. (j) an undescribed soft-shelled lingulid-like brachiopod; note the lophophore imprint (tailed arrows) and posteriorly extended body cavity (single arrow) beyond the hinge line. (k)–(n). *Lingulellotretra malongensis* (k)–(m), showing typical coiled paired arms. (k) ELI L-500. (l) ELI L-50. (m) ELI L-503, note the atypical extension of brachial tube in the right. (n) ELI L-440, showing the posteriorly extended cone-shaped body cavity (arrow) covered by the pseudointerarea. Scale bars 5 mm except for 2 mm in (c). See Fig. 5 for some interpretations.

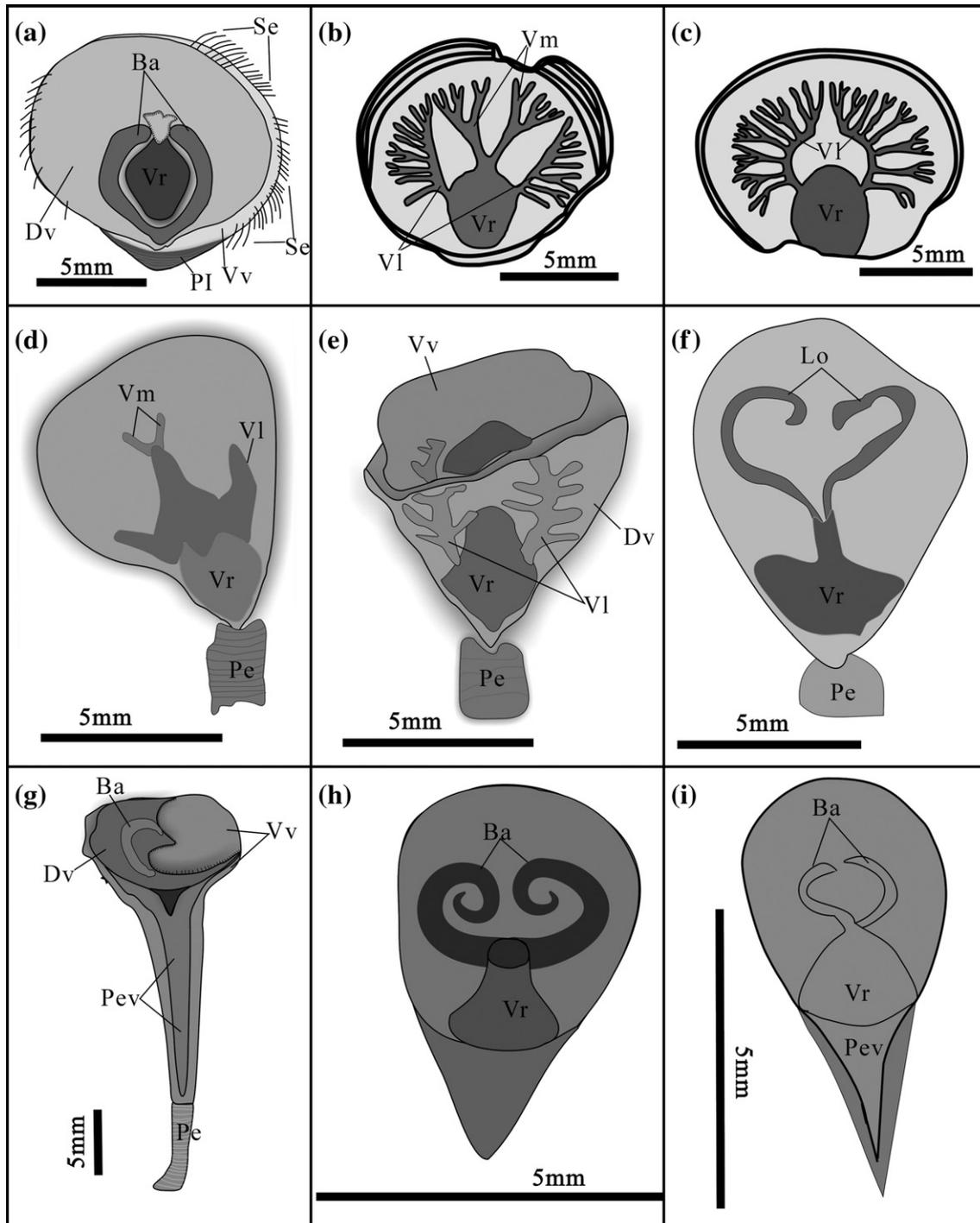


Fig. 5. Interpretative drawings of some specimens illustrated in Fig. 4. (a) Sketch of Fig. 4a. (b) Sketch of Fig. 4e. (c) Sketch of Fig. 4f. (d) Sketch of Fig. 4g. (e) Sketch of Fig. 4h. (f) Sketch of Fig. 4i. (g) Sketch of Fig. 4j. (h) Sketch of Fig. 4l. (i) Sketch of Fig. 4n. Abbreviations: Dv, dorsal valve; Vv, ventral valve; Se, setae; Vr, visceral region; Ba, brachial arms; PI, pseudointerarea; Vm, vascula media; Vl, vascula lateralia; Lo, lophophore; Pe, pedicle; Pev, posterior extension of body cavity.

### 3.2. Mantle canal systems

Mantle canals are tubular branching extensions of the body cavity. Within them the coelomic fluid circulates, used mainly for respiration. The vascular systems are commonly preserved as grooves and ridges on fossil brachiopod valves. However, the mantle canals in the Chengjiang brachiopods are exclusively impressed as reddish or reddish-brown imprints on the interior

mold of both valves (Figs. 4e–h and 5b–e). Investigations of these different taxa of brachiopods (Zhang et al., 2003a, 2005, 2006, 2007a,c) demonstrate that the vascular markings in Cambrian brachiopods are more variable and intricate in arrangement than previously thought. Evidently, the circulatory canal systems in the ventral mantles of *L. chengjiangensis* (Zhang et al., 2007a) and *X. haikouensis* (Zhang et al., 2006) and both ventral and dorsal mantles of *W. chengjiangensis* (Jin

et al., 2004) conform to the pinnate condition. The mantle canal systems of most of the Chengjiang lingulids, however, consists of a single pair of ventral *vascula lateralia* and two pairs in the dorsal mantle (Figs. 4e–h and 5b–e): one pair of dorsal *vascula lateralia* occupy a similar position to the single pair in the ventral mantle and a second pair of *vascula media* originates from the dorsoanterior projection of the body cavity, as exemplified by the earliest known lingulelloretid *L. malongensis*, the possible obolid ‘*Lingulella*’ *chengjiangensis*, and, notably, the acrotheloid *D. pista* (Figs. 4e–h and 5b–e). The *vascula lateralia* of both valves curve forward from a lateral position on the anterior body wall, subparallel with the shell margin; the *vascula media* directly diverge anteriorly from the anterior body wall near the midline (Figs. 4g–h and 5d–e). In some specimens of the three Chengjiang lingulids (Fig. 4e–h and 5b–e), numerous minor canals branch from either side of the main lateral trunks. In some superbly preserved adult specimens of *D. pista*, pallial sinus trunks give off branches peripherally by dichotomy so that the fourth-order distributaries are distinctly recognizable (Figs. 4e–f and 5b–c). In the juvenile specimens, the mantle canal systems of both valves are, however, baculate, and exhibit progressive bifurcate branching in immature individuals (Zhang et al., 2003a). It is thus presumed that the bifurcate pattern of vascular system is derivation of the baculate mantle sinus (Figs. 4e–f and 5b–c).

More importantly, the dorsal mantle canals in kutorginids, one of the most primitive types of articulated brachiopods, are revealed in the Chengjiang fauna. They also consisted of a pair of *vascula lateralia* and a bifurcate *vascula media* (Zhang et al., 2007c). But whether they are strictly homologous with the vascular markings in the contemporary lingulids discussed above is still a matter of opinion. However, it is apparent that one ventral and two dorsal pairs of canals represent the commonest pattern of mantle canals in Cambrian brachiopods. Thereafter, the Ordovician *Pseudolingula* (Holmer, 1990; Popov et al., 1994) and *Dignomia* (Emig and Herrera, 2006), the Paleo-Mesozoic *Lingularia* (Biernat and Emig, 1993; Emig, 2003) and the Tertiary to present *Lingula* and *Glottidia* (Emig, 2000; Emig et al., 2007) have a fundamentally different mantle canal systems: the *vascula media* are absent and the *vascula lateralia* in both valves become anteriorly subparallel. The arrangement of the mantle canals is closely associated with the in- and exhalant water currents (Emig, 1992). Consequently, the inhalant and exhalant currents of Cambrian lingulids more likely differ from the three apertures of the Lingulides in vertically burrow-dwelling life with the central for the exhalant current and the outer two for the inhalant currents (Emig, 2000; 2003). Accordingly, the occurrence of the sub-parallel *vascula lateralia* and the “loss” of *vascula media* could reflect the beginning of burrow-dwelling life of lingulids. Thus, the presence of dorsal *vascula media* is the ground state of the vascular system in lingulid stocks, and a lack of dorsal *vascula media* and an increase in the length of the lateral mantle canals, from an ‘asymmetrical’ positioning of the termination of the canal tips up to termination at the same distal level may presume to be novelties adapted to an infaunal lifestyle (Emig, 1992, 2003).

### 3.3. Lophophore and digestive system

The organization of the lophophore and the digestive system are recognized as two of the diagnostic characters in the definition of the higher brachiopod taxa, and hence play a major role in their phylogenetic analysis. Exceptional preservation of the lophophore and alimentary canals is most unusual, and nearly all the Cambrian records come from the Chengjiang Lagerstätte (X.G. Zhang et al., 2003; Zhang et al., 2004a,b, 2005, 2006; Holmer and Caron, 2006; Zhang et al., 2007a,b,c; Chen et al., 2007). All brachiopods from the Chengjiang Fauna, except for *D. pista*, have preserved imprints of a simply coiled spirolophe in adult forms (Figs. 4i–n and 5f–i), including the non-shelled lingulid *W. chengjiangensis* undescribed in details (Figs. 4j and 5g). In addition, the lophophores of *Lingulella chengjiangensis*, as well as those of *L. malongensis*, also encompass the forms at the trocholophe, and schizolophe developmental stage (Zhang et al., 2004b). All this ontogeny of lophophores is mirrored in the ontogeny of the lophophores of Recent lingulids (Emig, 1992). Lophophore ontogeny in Cambrian lingulids is therefore homologous to that of extant lingulids, and has remained fairly constant over 530 million years. Thus, the early stages of lophophoral ontogeny and development in adult forms appear to be plesiomorphic characters inherited from an ancestral form (Emig, 1992; Zhang et al., 2004a,b, 2005, 2006). It is apparent that there is a single palisade of tentacles along each of the lophophoral arms (Fig. 4m). More intriguingly, the lophophores of the cosmopolitan kutorginids are similar to those of the Cambrian to Recent lingulids in both a comparable configuration and a hydrostatic support mechanism. The findings of comparable lophophores in both calcareous- and phosphatic-shelled brachiopods demonstrate that an early spirolophe was the most common configuration of lophophores at least from the beginning of the Cambrian.

The digestive tracts of Cambrian brachiopods have been previously found preserved in at least 5 taxa of brachiopods, i.e. *L. malongensis*, ‘*Lingulella*’ *chengjiangensis*, *X. haikouensis* and *L. chengjiangensis*, notably the calcareous *Kutorgina chengjiangensis* (see: Zhang et al., 2007c). The chitinophosphatic-shelled species have a horizontally curved gut with an open anus, while the calcareous-shelled *K. chengjiangensis* has a postero-dorsally extending intestine with a putative anus placed posteriomedially. The presence of an open anus, common in Cambrian brachiopods (including organophosphatic- and calcareous-shelled brachiopods) suggests that this trait is a plesiomorphic state inherited from a lophophorate precursor. Consequently, the blind intestine found in the extant rhynchonelliformeans likely represent an apomorphy, which had not arisen by the onset of the Cambrian. This proposal has yet to be tested by finding preserved intestines in the other Cambrian calcareous brachiopods, such as the Obolellidae.

### 3.4. Pedicle

Most of the brachiopods are attached to or in the substrate by a pedicle. The pedicles of articulated and non-articulated

brachiopods, however, are only analogous organs, differing in their origin and morphology. The pedicle of non-articulated brachiopods develops as an outgrowth of the posterior body wall and thus is associated with the ventral valve only. In contrast, the pedicle rudiment of articulated brachiopods is continuous with the mantle rudiment, which produces both the ventral and dorsal valves, and therefore the adult pedicle is continuous with the body wall of both valves (Williams et al., 2000), however generally emerging through a foramen on the ventral valve. In addition, the form of the pedicles varies considerably in different taxa. There are at least two pedicle types and each was probably variable: stout plenipedunculate structures (conventional fleshy stalk) and rhizopedunculate forms where the pedicle is divided into a number of threads or rootlets. Pedicle variation allows pedunculate brachiopods considerable flexibility in their choice of substrate. Plenipedunculate structures could attach firmly to a variety of hard substrates, whereas rhizopedunculates could root into soft sediment.

Records of Cambrian pedicles mainly come from the Chengjiang Lagerstätte (Jin et al., 1993; Z.F. Zhang et al., 2003, 2005, 2006, 2007a,c). Recently, some impressions of pedicles were reported from the classic Burgess Shale (Holmer and Caron, 2006), and the Early Cambrian Shipai Formation in Three Gorge area in western Hubei Province of South China (Zhang and Hua, 2005; 2006). The pedicles of Cambrian lingulids vary widely in gross morphology (Fig. 6). In the Chengjiang fauna, both ‘*Lingulella*’ *chengjiangensis* and *L. malongensis* bear an elongate and relatively slim pedicles (Fig. 5a–c), which can be up to 5–7 times its relative shell length. *L. malongensis* bears a bulb-like termination at its distal end (Zhang et al., 2005: Fig. 3. O) (Fig. 6a), while the pedicle of ‘*Lingulella*’ *chengjiangensis* seemingly tapers in its distal part (Jin et al., 1993). Differing in morphology from the pedicles of ‘*Lingulella*’ *chengjiangensis* and *L. malongensis*, those of *L. chengjiangensis* and *X. haikouensis* are relatively shorter and thicker (Zhang et al., 2006, 2007a) (Fig. 6e–g). Nevertheless, the pedicle of *X. haikouensis* is approximately up to 28 mm, more than 1.5 times as long as the valve length, and around 2.1–2.5 mm in width (Fig. 6g). Despite the differences in the pedicles of the Chengjiang lingulids, they share a general similarity in exterior wrinkles developed on the pedicle surfaces. Another similarity between these lingulids except for *L. chengjiangensis* is the presence of a coelomic cavity in the pedicle center (Fig. 6a–g). By contrast, the pedicles of the bostfordiid *D. pista* are distinctly slim and delicate, and lack of visible annulations on the exterior surface (Fig. 6j and k). Recently, a central coelomic lumen was found in *D. pista* (Z.F. Zhang et al., 2003), represented by a parallel band of ferruginous matter, occupying approximately one-third of the pedicle width (Fig. 6k). It is worthy of note that the pedicles of *L. chengjiangensis* and *X. haikouensis* arise from between the valves (Fig. 6e–g), but the pedicles in ‘*Lingulella*’ *chengjiangensis* and *L. malongensis* is apparently associated only with the ventral valves with the proximal part enclosing the tips of the ventral valve (Figs. 4g–k and 6b–d). The bostfordiid *D. pista* (Z.F. Zhang et al., 2003), however, bears a slim pedicle apparently

extending posteriorly from the triangular pedicle groove (Fig. 6i). The undescribed *W. chengjiangensis* bears a pedicle equal in diameter to the tip of the pseudointerarea (Fig. 4j, also see: Zhang et al., 2007b). Intriguingly, the spinose stem group brachiopod *Acanthotretella spinosa* from the Middle Cambrian Burgess Shale (Holmer and Caron, 2006) has a pedicle emerging from the ventral apical foramen through a narrow external pedicle tube. The findings of the lingulid pedicles from the exceptional Cambrian deposits, therefore, demonstrate that the lingulid pedicles varied considerably in location relative to their valves. Although Cambrian lingulid pedicles were much like those of Recent lingulids in anatomy and structure (Jin et al., 1993), they are much more variable in morphology. Therefore, the abundant variety of pedicle records affords little support for the view that all fossil inarticulates possessed the type of pedicles characteristic of their few living survivors.

At the present day, the pedicles of brachiopods are most commonly attached to some hard substrate, such as pebble, a rock surface, or a piece of shell or coral (Rudwick, 1970) except for the burrowing *Lingula* and *Glottidia*, which use a sticky mucous secretion to attach the distal part of their long pedicle to the sand at the rear-end of a deep vertical burrow. Similarly, the pedicles of Cambrian brachiopods can also be separated into two large morphological groups, depending on the size and length of the pedicle and the nature of the substrate to which the brachiopods were attached: 1) thin, long pedicle with only the distal termination embedded into soft sediments; 2) massive pedicles of medium length with its distal end attached to hard shells of other animals. The pedicles of ‘*Lingulella*’ *chengjiangensis*, *L. malongensis* and *W. chengjiangensis* appear to be grouped into the first types. The three fossil lingulid genera, with small, slightly mineralized shell valves, could probably ascend above turbulence at the sediment–water interface, like kites, tethered by long, thin pedicles. In contrast, *L. chengjiangensis* and *X. haikouensis*, together with the rhynchonelliformean brachiopod *K. chengjiangensis* recently reported by Zhang et al. (2007c), possess the second type of pedicles (Fig. 6h). They appear to be an epibenthic, fixosessile, suspension-feeder, attached by their stout and massive pedicles. The invariable attachment of *Longtancunella*, *Xianshanella* and *Kutorgina* to hard shells in mud seafloors (Zhu et al., 2001), on the one hand, suggests the capability of Cambrian brachiopods to select suitable substrates (Fig. 6) which is emphasized by clustered occurrence of *Longtancunella* and *Xianshanella* (Fig. 6j) (Zhang et al., 2006, 2007a), while on the other hand demonstrates that the chemical resorption capabilities could be achieved by the Lower Cambrian stocks (Fig. 6e–h). Thus it is presumed that this resorption facility have been inherited by the extant rhynchonelliformean descendants.

An intriguing question concerns the pedicle of the acrotheloid *D. pista*. The brachiopod pedicle was fairly thin and elongate (Fig. 6i–k) so as to hardly provide any support for elevation of this well-mineralized shell far away the seafloor. In addition, the shell valves of *D. pista* were ordinarily attached by some other epifaunal animals, notably the coeval brachiopod *Longtancunella* (Fig. 6j). It is, therefore, presumed that this brachiopod most probably have a semi-infaunal lifestyle with

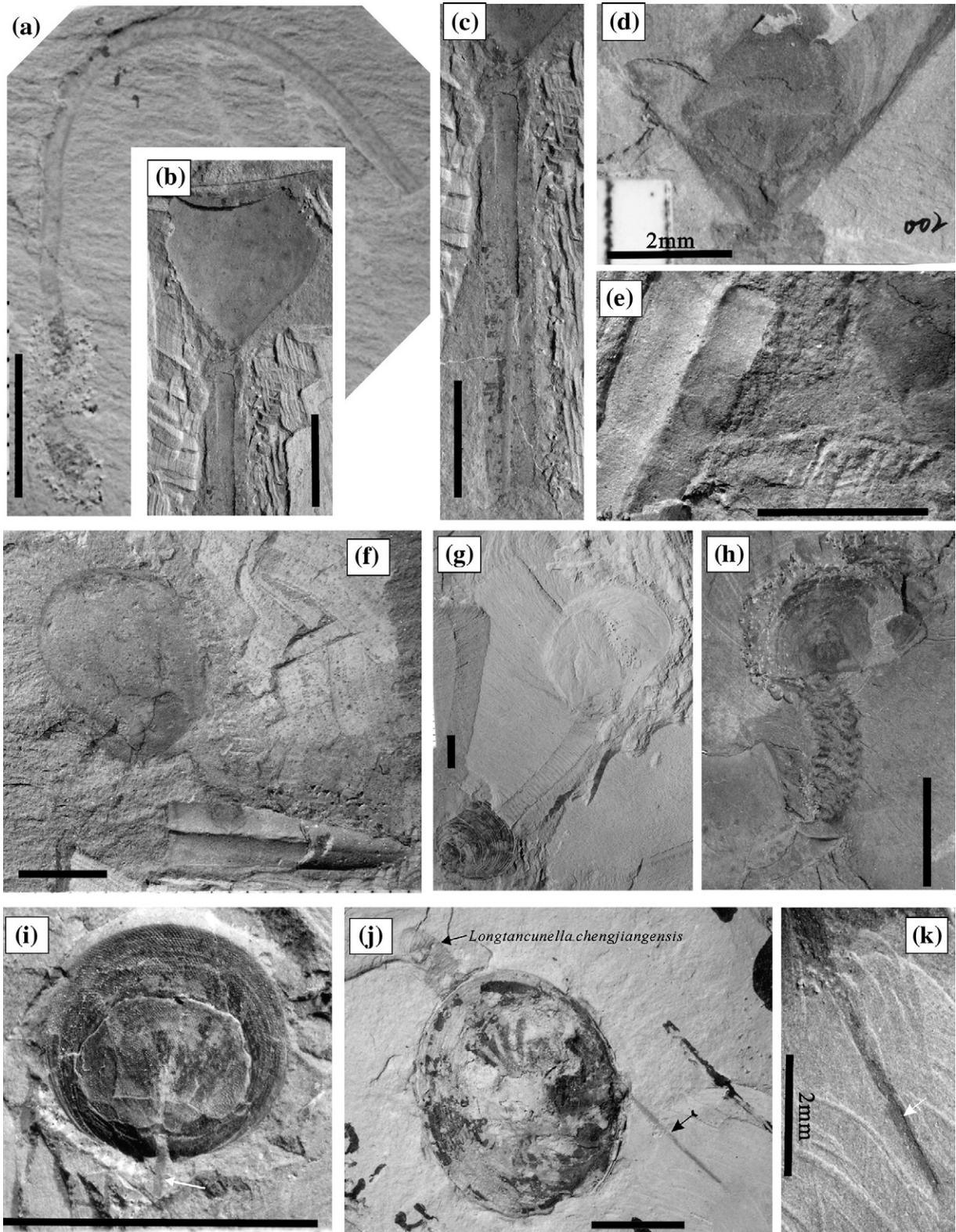


Fig. 6. The morphological variations of pedicles of the Early Cambrian Chengjiang brachiopods. Scale bars 5 mm except for those indicated. (a) ELI L-0085B, elongate pedicle of *Lingulellotreta malongensis* with grain-encrusted bulb-like termination. (b)–(d) '*Lingulella*' *chengjiangensis*; (b)–(c) ELI C-00450, showing the pedicle and a tube-like coelomic cavity. (d). ELI C-0044, showing the shell tip enclosed by the proximal pedicle. (e)–(f) ELI –BL041, *Longtancunella chengjiangensis* attached by a pedicle on the hyolith shell; note the semicircular trace of putative chemical resorption. (g) ELI-BX 017A, *Xianshanella haikouensis* attached by a massive pedicle on the shell of *Diandongia pista*. (h) ELI-BK 066, *Kutorgina* attached by a stout pedicle on the gena of a trilobite. (i)–(k) *Diandongia pista* Rong, 1974. (i) ELI D-0375, pedicle (white arrow) protruding from the triangular pedicle groove. (j)–(k) ELI D-61A. (j) showing an elongate and slim pedicle (tailed arrow); note another stout pedicle (single arrow), putatively belonging to *Longtancunella chengjiangensis*, attached on the antero-lateral margin of the shell of *D. pista*. (k) close-up view of the central lumen of *D. pista*, delineated by a thin-laminated ferruginous matter.

only the pedicle buried in deep sediments for this brachiopod to provide anchorage (Fig. 6j) (also see: Z.F. Zhang et al., 2003), and the ventral valve tilted lying onto the seafloor where they inhabited.

### 3.5. Significance and discussion

The soft-bodied fossils from China give new insights in the evolutionary acquisition of morphological novelties and the character states of Early Cambrian brachiopods. The preserved soft-tissues clearly demonstrate that Cambrian brachiopods had acquired a fully developed organization of organs and organ systems. Some tissue organization or organ systems, e.g. mantle canals, pedicle, had diversified and showed a series of variations in morphological style. In contrast, the organization of adult lophophore at that time exhibited exclusively an early spirolophore developmental stage in the light of the fossil evidences preserved in various Chengjiang lingulid taxa (Zhang et al., 2004a, b, 2005, 2006, 2007a,b) and one species of calcareous-shelled brachiopods (Zhang et al., 2007c) in the unique deposits. Consequently, it is assumed that an early spirolophore has been the most common configuration of the lophophore, and perhaps the most evolved form in the Cambrian times. Compared studies of the interiors of the Chengjiang lingulid fossils and modern lingulids do little to support the widespread notion that the morpho-anatomy of this lingulid lineage has remained remarkably constant since at least the early Palaeozoic (Zhang et al., 2005). In this respect, it is strikingly worthy to be emphasized that the soft-tissue configuration in the Early Cambrian lineages could not unambiguously deduced directly from that of their Recent descendants (Zhang et al., 2007b). As in the Chengjiang lingulid/lotretid brachiopods, there exist a more or less long posterior extension of body cavity behind shell hinge-line or umbo (Figs. 4n and 5i), presumably covered by extended pseudointerarea. This posteriorly extended body cavity beyond the hinge line subtended by the pseudodelthyrium was distinctively invaded and occupied by the posterior portion of U-shaped digestive tract (Zhang et al., 2007b). This case was deduced to exist also in the contemporary soft-shelled, even naked mantle-folded brachiopod *W. chengjiangensis* Jin et al., 2004, from the Chengjiang mudstone deposits (Figs. 4j and 5g). The nature of *W. chengjiangensis* is well endorsed by the internal paired coiled lophophore (Figs. 4j and 5g), pinnate mantle canals in dorsal and ventral mantle folds (Figs. 4j and 5g), as well as the presence of setae along mantle margin (ELI unpublished data). The brachiopod nature was also supported by an elongate coelomatic pedicle, which has convincing morphological homologies with that occurred in Recent lingulids. However, the shell of *W. chengjiangensis* seems likely to be unmineralized or unhardened due in part to their ordinary preservation as composite mould agglutinated by detrital grains, and partly to the common occurrence of compressed marginal wrinkles of posterior ventral valve in many specimens (Zhang et al., 2007b). Moreover, the shell valves could be randomly preserved, either laterally or dorsoventrally, and nearly all could be flattened in a same bedding plane, but do not show any signs of brittle breakage. The

weight of evidence above leads us to infer that the animals are very unlikely to have a mineralized integument to enclose the body. Therefore, the soft-shelled brachiopods, if correctly interpreted, demonstrate that there must have existed unmineralized precursor creatures of fully developed tissues, organs and organ systems long predating the Cambrian explosion. Furthermore, the posteriorly extended body cavity in the unmineralized brachiopod *W. chengjiangensis* is reminiscent of that of living phoronids in chitinous tube, and thus could argue for the proposal that brachiopod+phoronid clade may be evolved from a common stem group of lophotrochozoan progenitor that was not armoured (Cohen, 2005). Therefore, one may argue that the brachiopods developed a mineralized shell posterior to the divergence of brachiopod–phoronid from the common ancestor lineage. If so, brachiopods acquired a mineralized shell at least twice, even three times.

### Acknowledgements

This work represents a contribution to the China–Japan Cooperative Program on “Evolution of Early Life and Environments from Snowball to the Phanerozoic Earth: Records in South China”, and to the programs funded by the National Natural Science Foundation of China (Grant 40332016, 40702005 and 40602003), National Basic Research Program of China (Grant 2006CB806401), the Program for Changjiang Scholars and Innovative Research Team in University (PCSIRT), the Research Fund for the Doctoral Program of Higher Education (to Z. Zhang). We are glad to express heartfelt thanks to B.L. Cohen (Glasgow) for the constructive comments and interesting discussion, and to an anonymous referee for advice. The first author (Z. Zhang) would like to express many thanks to Drs. X.L. Zhang, J. Han, J.N. Liu, J.F. Guo, Q. Ou in the work team of ELI, Northwest University (Xi’an) for their ongoing fruitful cooperation on the Lower Cambrian of China, and to Drs. G. X. Li (Nanjing) and S. X. Hu (Kunming) for some advice. Thanks are also due to H. X. Guo and Y. C. Yao for their help with fieldwork, J. P. Zhai, M. R. Cheng for preparation of the fossils.

### References

- Bassett, M.G., Popov, L.E., Holmer, L.E., 1999. Organophosphatic brachiopods: patterns of biodiversification and extinction in the early Palaeozoic. *Geobios* 32, 145–163.
- Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A., Runnegar, B.N., 1990. Early Cambrian fossils from South Australia. *Memoir of the Association of Australasian Palaeontologists* 9, 1–364.
- Benton, M.J., Ayala, F.J., 2003. Dating the tree of life. *Science* 300, 1698–1700.
- Biernat, G., Emig, C.C., 1993. Anatomical distinctions of the Mesozoic lingulid brachiopods. *Acta Palaeontologica Polonica* 38, 1–20.
- Chen, X., Wang, X., 1999. Early Palaeozoic chrono- and sequence-stratigraphy in the Yangtze Gorges Area, China with an approach of palaeobiogeography. *Gondwana Research* 2, 627–633.
- Chen, J.Y., Huang, D.Y., Chuang, S.H., 2007. Reinterpretation of the Lower Cambrian brachiopod *Heliomedusa orientalis* Sun and Hou, 1987 as a discinid. *Journal of Paleontology* 81, 38–47.
- Cobbold, E.S., 1921. The Cambrian horizons of Comley (Shropshire) and their Brachiopods, Pteropoda, gastropoda etc. *Journal of the Geological Society (London)* 76, 325–386.

- Cohen, B.L., 2000. Monophyly of brachiopods and phoronids, reconciliation of molecular evidence with Linnaean classification (the subphylum Phoroniformea nov.). *Proceedings of the Royal Society of London. Series B*, 267, pp. 225–231.
- Cohen, B.L., 2005. Not armour, but biomechanics, ecological opportunity and increased fecundity as keys to the origin and expansion of the mineralized benthic metazoan fauna. *Biological Journal of the Linnean Society* 85, 483–490.
- Cohen, B.L., Weydmann, A., 2005. Molecular evidence that phoronids are a subtaxon of brachiopods (Brachiopoda, Phoronata) and that genetic divergence of metazoan phyla began long before the early Cambrian. *Organisms Diversity and Evolution* 5, 253–273.
- Emig, C., 1992. Functional disposition of the lophophore in living Brachiopods. *Lethaia* 25, 291–302.
- Emig, C.C., 2000. Ecology of inarticulated brachiopods. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda. Vol. 1, Geological Society of America. Boulder and University of Kansas Press, Lawrence*, pp. 473–495.
- Emig, C.C., 2003. Proof that *Lingula* (Brachiopoda) is not a living-fossil, and emended diagnoses of the Family Lingulidae. *Carnets de Géologie/Notebooks on Geology, Maintenon, Letter 2003/01(CG2003\_L01\_CCE)*, 8p., 7figs., 1 tab.
- Emig, C.C., Herrera, Z., 2006. *Dignomia munsterii* (Brachiopoda, Lingulata) from the Ordovician of Bolivia, with redescription of the genus. *Geodiversitas* 28, 227–237.
- Emig, C.C., Bitner, M.A., Cahuzac, B., 2007. First record of *Lingula* (Brachiopoda) from the Miocene of France, with diagnosis of *L. dregeri*. *Comptes rendus Palevol* 6, 261–267.
- Fang, R.S., 1974. The Geological Bureau of Yunnan Province. Pictures of Fossils from Yunnan. Science Press, Beijing, pp. 285–470.
- Fang, Z.J., 2006. An introduction to Ordovician bivalves of southern China, with a discussion of the early evolution of the Bivalvia. *Geological Journal* 41, 303.
- Geyer, G., 1994. A new obolellid brachiopod from the Lower Cambrian of Morocco. *Journal of paleontology* 68, 995–1002.
- Holmer, L.E., 1990. The systematic position of *Pseudolingula Mickwitz* and related lingulacean brachiopods. In: Mackinnon, Lee, Campbell (Eds.), *Brachiopods Through Time*. Balkema, Rotterdam, pp. 15–21.
- Holmer, L.E., 2001. Phylogeny and classification: Linguliformea and Craniiformea. In: Carson, S., Sandy, M. (Eds.), *Brachiopods Ancient and Modern: A tribute to G. Arthur Cooper*. Palaeontological Society Special Publications, vol. 7, pp. 11–26.
- Holmer, L.E., Caron, J.B., 2006. A soft-shelled spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologica* 87, 273–290.
- Holmer, L.E., Popov, L.E., 1996. Early Paleozoic radiation and classification of organo-phosphatic brachiopods. In: Copper, P., Jin, J. (Eds.), *Brachiopods. Proceedings of the Third International Brachiopod Congress Sudbury/Ontario/Canada/2–5 September 1995*, pp. 117–121.
- Holmer, L.E., Li, G.X., Zhu, M.Y., 2003. The systematic position of the Lower Cambrian brachiopod *Heliomedusa* Sun and Hou. Abstracts, Palaeontological Association 47th Annual Meeting. Department of Geology, University of Leicester. December 14–17.
- Holmer, L.E., Popov, L.E., Koneva, S.P., Rong, J.Y., 1997. Early Cambrian Lingulelloretta (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., Williams, A., 2002. A stem group brachiopod from the Lower Cambrian: support for a *Micrina* (Halkieriid) ancestry. *Palaentology* 45, 875–882.
- Holmer, L.E., Streng, M., Skovsted, C.B., Babcock, L.E., 2004. Exceptional preservation in the stem group brachiopod *Mickwitzia* from the Early Cambrian of Nevada. *GFF* 126, 112.
- Hou, X.G., Bergström, J., Wang, H.F., Feng, X.H., Chen, A.L., 1999. The Chengjiang Fauna: exceptionally well-preserved animals from 530 million years ago. Yunnan Science and Technology Press, Kunming, p. 80 (In Chinese with English summary).
- Hou, X.G., Aldridge, R.J., Bergstrom, J., David, J.S., Derek, J.S., Feng, X.H., 2004. The Cambrian fossils of Chengjiang, China: the Flowering of Early Animal Life. Blackwell Publishing Company, Oxford. 233pp.
- Hu, S.X., Luo, H.L., Hou, S.G., Erdtmann, B.D., 2007. Eocrinoid echinoderms from the Lower Cambrian Guanshan Fauna in Wuding, Yunnan, China. *Chinese Science Bulletin* 52 (5), 717–719.
- Jin, Y.G., Wang, H.Y., 1992. Revision of the Lower Cambrian brachiopod *Heliomedusa* Sun & Hou, 1987. *Lethaia* 25, 35–49.
- Jin, Y.G., Wang, H.Y., Wang, W., 1991. Palaeoecological aspects of brachiopods from Chiungchussu Formation of Early Cambrian age, Eastern Yunnan, China. In: Jin, Y.G., Wang, H.Y. (Eds.), *Palaeoecology of China*. Nanjing University Press, Nanjing, China, pp. 25–47.
- Jin, Y.G., Hou, X.G., Wang, H.Y., 1993. Lower Cambrian pediculate lingulids from Yunnan, China. *Journal of Paleontology* 67, 788–798.
- Jin, Y.G., Yang, J., Cao, C.Q., Wang, H.F., Chen, A.L., 2004. An agglutinated brachiopod-like fossil from the Lower Cambrian of China. Sino-German Symposium, 25–28 September 2004, Nanjing.
- Kondo, Y., Kozai, T., Kikuchi, N., Sugawara, S., 2006. Ecologic and taxonomic diversification in the Mesozoic brackish-water bivalve faunas in Japan, with emphasis on infaunalization of heterodonts. *Gondwana Research* 10, 316–327.
- Li, G.X., Holmer, L.E., 2004. Early Cambrian lingulate brachiopods from the Shaanxi Province, China. *GFF* 126, 193–211.
- Li, Z.X., Powell, C.M., 2001. An outline of the palaeogeographic evolution of the Australasian region since the beginning of the Neoproterozoic. *Earth-Science Reviews* 53, 237–277.
- Li, G.X., Xiao, S.H., 2004. Tannuolina and Micrina (Tannuolinidae) from the Lower Cambrian of eastern Yunnan, South China, and their scleritome reconstruction. *Journal of Paleontology* 78, 900–913.
- Li, G.X., Steiner, M., Qian, Y., Zhu, M.Y., Erdtmann, B.D., 2006. Explosive Radiation of Early Cambrian skeletal faunas in South China. In: Rong J.Y., Fang, Z.J., Zhong, H., Zhan, R.B., Wang, X., Yuan, X.L. (Eds.), *Originations, Radiations and Biodiversity changes-evidences from the Chinese fossil record*. Beijing: Science Press. Pp. 41–57, 831–834. (in Chinese with English abstract).
- Li, S.Z., Kusky, T.M., Wang, L., Zhang, G., Lai, S., Liu, X., Dong, S., Zhao, G., 2007. Collision leading to multiple-stage large-scale extrusion in the Qinling orogen: Insights from the Mianlue suture. *Gondwana Research* 12, 121–143.
- Liu, D.Y., 1979. Earliest Cambrian brachiopods from southwest China. *Acta Palaeontologica Sinica* 18, 505–511 (in Chinese with English abstract).
- Liu, Q., Luo, H.L., Chen, L.Z., Hu, S.X., 2006. *Panlongia*, a new trilobitomorpha genus from the Lower Cambrian, Kunming, Yunnan. *Acta Palaeontologica Sinica* 45, 384–392 (In Chinese with English abstract).
- Luo, H.L., Jiang, Z.W., Wu, X.C., Song, X.L., Qu, Y.L., Xing, Y.S., Liu, G.Z., Zhang, S.S., Tao, Y.H., 1984. Sinian–Cambrian Boundary Stratotype Section at Meishucun, Jinning, China. People’s Publishing House, Yunnan, pp. 1–154 (In Chinese with English summary).
- Luo, H.L., Jiang, Z.W., Tang, L.D., 1994. Stratotype Section for Lower Cambrian Stages in China. Yunnan Science and Technology Press, Kunming, China. 183 p. (In Chinese with English summary).
- Luo, H.L., Hu, S.X., Chen, L.Z., Zhang, S.S., Tao, Y.H., 1999. Early Cambrian Chengjiang Fauna From Kunming Region, China. Yunnan Science and Technology Press, Kunming, China. 129 pp. (In Chinese with English summary).
- Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Chen, L.Z., You, T., Liu, Q., 2005. New vetulicolliids from the Lower Cambrian Guanshan Fauna, Kunming. *Acta Geologica Sinica* 79, 1–5 (English Edition).
- Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Chen, L.Z., You, T., Pang, J.Y., Liu, Q., 2006. New Bivalved arthropods from the Early Cambrian Guanshan Fauna in the Kunming and Wuding area. *Acta Palaeontologica Sinica* 45, 460–472 (In Chinese with English abstract).
- Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Hou, S.G., You, T., Pang, J.Y., Liu, Q., 2007. A new arthropod, *Guangweicaris* Luo, Fu et Hu gen. nov. from the Early Cambrian Guanshan Fauna, Kunming, China. *Acta Geologica Sinica* 81, 1–7 (English Edition).
- Mansuy, H., 1912. Etude géologique du Yunnan orienta. Pt. 2. Paléontologie. *Mémoires du Service géologique de l’Indochine* 6, 1–146.
- Oh, C.W., 2006. A new concept on tectonic correlation between Korea, China and Japan: histories from the late Proterozoic to Cretaceous. *Gondwana Research* 9, 47–61.

- Pelman, Y., 1977. Ranne I srednekembriiskije bezzamkovyie brachiopody Sibirskoj Platformy [Early and Middle Cambrian inarticulate brachiopods of the Siberian Plate]. Trudy Instituta Geologii Geofiziki, Sibirskogo otdelenija 36, 1–168.
- Pelman, Y.L., Aksarina, N.A., Koneva, S.P., 1992. The earliest brachiopods of North Eurasia territory. Novosibirsk: Complex Institute of Geology, Geophysics and Mineralog Russian Academy of Sciences.
- Popov, L.E., Holmer, L.E., 2000. Craniopsida. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology. Brachiopoda (revised). Geological Society of America and University of Kansas Press, Lawrence, pp. 164–168.
- Popov, L.Y., Blodgett, R.B., Anderson, A.V., 1994. First occurrence of the genus Bicarinata (Brachiopoda, inarticulate) from the Middle Devonian in North America (Alaska). Journal of Paleontology 68, 1214–1218.
- Popov, L.E., Holmer, L.E., Bassett, M., 1996. Radiation of the Earliest Calcareous brachiopods. In: Copper, P., Jin, J. (Eds.), Brachiopods. Proceedings of the Third International Brachiopod Congress Sudbury/Ontario/Canada/2–5 September 1995, pp. 209–213.
- Popov, L.E., Rowell, A.J., Peel, J.S., 1997. Early Cambrian brachiopods from North Greenland. Palaeontology 40, 337–354.
- Popov, L.E., Holmer, L.E., Miller, J., 2002. Lingulate brachiopods from the Cambrian–Ordovician boundary beds of Utah. Journal of Paleontology 76, 211–228.
- Porter, S.M., 2007. Seawater chemistry and Early Carbonate biomineralization. Science 316, 1302.
- Qian, Y., 1999. Taxonomy and Biostratigraphy of Small Shelly Fossils in China. Science Press, Beijing, pp. 1–247 (In Chinese with English abstract).
- Qian, Y., Bengtson, S., 1989. Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. Fossils and Strata 24, 1–156.
- Robson, S.P., Pratt, B.R., 2001. Cambrian and Ordovician linguliform brachiopods from the Shallow Bay Formation (Cow Head Group), western Newfoundland. Journal of Paleontology 75, 241–260.
- Robson, S.P., Nowlan, G.S., Pratt, B.R., 2003. Middle to Upper Cambrian linguliform brachiopods from the Deadwood Formation of subsurface Alberta and Saskatchewan, Canada. Journal of Paleontology 77, 201–211.
- Rong, J.Y., 1974. Cambrian brachiopods. Nanjing Institute of Geology and Palaeontology, Academia Sinica, Handbook of Palaeontology and Stratigraphy of Southwest China. Science Press, Beijing, pp. 113–114.
- Rudwick, M.J.S., 1970. Living and Fossil Brachiopods. Hutchinson and Co. Ltd, London. 199p.
- Shu, D.G., 1990. Cambrian to Ordovician bradoriids from western Zhejiang, western Hunan, and southern Shaanxi. Northwest University Press, Xi'an, pp. 1–95.
- Skovsted, C.B., Holmer, L.E., 2005. Early Cambrian brachiopods from north-east Greenland. Paleontology 48, 325–345.
- Sutton, M.D., Briggs, D.E.G., Siveter, D.J., Siveter, D.J., 2005. Silurian brachiopods with soft-tissue preservation. Nature 436, 1013–1015.
- Ushatinskaya, G.T., Holmer, L.E., 2001. Brachiopoda. In: Alexander, E.M., Jago, J.B.I., Rozanov, A.Y., Zhuravlev, A.Y. (Eds.), The Early Cambrian Biostratigraphy of the Stansbury Basin, South Australia. Russian Academy of Sciences, Transactions of the Palaeontological Institute, vol. 282, pp. 120–132.
- Wang, J., Li, Z.-X., 2001. Sequence stratigraphy and evolution of the Neoproterozoic marginal basins along Southeastern Yangtze Craton, South China. Gondwana Research 4, 17–26.
- Wang, X., Ma, D., Chen, X., 1999. Precambrian geological Evolution in the Yangtze Gorges Area, China. Gondwana Research 2, 621–626.
- Williams, A., Carlson, S.J., Howard, C., Brunton, C., Holmer, L.E., Popov, L., 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London, Series B 351, 1171–1193.
- Williams, A., James, M.A., Emig, C.C., Mackay, S., Rhodes, M.C., 2000. Anatomy. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda. Geological Society of America and University of Kansas Press, Lawrence, pp. 7–188.
- Xie, Y., 1988. Small shelly fossils in Qiongzhusi Stage of Lower Cambrian in Zhenba Country, Shaanxi Province. Journal of Chengdu College of Geology 15, 21–29.
- Ye, M.-F., Li, X.-H., Li, W.-X., Liu, Y., Li, Z.-X., 2007. SHRIMP zircon U–Pb geochronological and whole-rock geochemical evidence for an early Neoproterozoic Sibaoan magmatic arc along the southeastern margin of the Yangtze Block. Gondwana Research 12, 144–156.
- Zeng, Q., 1987. Brachiopoda. Biostratigraphy of the Yangtze Gorge Area, Part 2. Early Palaeozoic Era. Geological Publishing House, Beijing, pp. 209–245.
- Zhan, R.B., Rong, J.Y., Cheng, J.H., Chen, H.F., 2005. Early-Mid Ordovician brachiopod diversification in South China. Science in China Ser., D Earth Sciences 48, 662–675.
- Zhang, S.H., 2004. South China's Gondwana connection in the Paleozoic: Paleomagnetic evidence. Progress in Natural Science 14, 85–90.
- Zhang, Z.F., Han, J., 2004. A new linguliform brachiopod from the Chengjiang Lagerstätte. Journal of Northwest University (Natural Science edition) 34, 449–452.
- Zhang, X.L., Hua, H., 2005. Soft-bodied fossils from the Shipai Formation, Lower Cambrian of the Three Gorge area, South China. Geological magazine 142, 699–709.
- Zhang, X.L., Hua, H., 2006. Soft-bodied fossils from the Shipai Formation, Lower Cambrian of the Three Gorges area, South China. Abstracts of the 2nd International Palaeontological Congress June 17–21, 2006, Beijing, China. 313pp.
- Zhang, X.G., Hou, X.G., Emig, C.C., 2003a. Evidence of lophophore diversity in Early Cambrian. Proceedings of the Royal Society of London B (Sup.) S1–S4.
- Zhang, Z.F., Han, J., Zhang, X.L., Liu, J.N., Shu, D.G., 2003b. Pediculate brachiopod *Diandongia pista* from the Lower Cambrian of South China. Acta Geologica Sinica 77, 288–293 (English Edition).
- Zhang, Z.F., Han, J., Zhang, X.L., Liu, J.N., 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., Shu, D.G., Han, J., Liu, J.N., 2004b. New data on the lophophore anatomy of Early Cambrian linguloids from the Chengjiang Lagerstätte, Southwest China. Carnets de Géologie – Notebooks on Geology, Letter 2004/04 (CG2004.L04), 7p., 2figs.
- Zhang, Z.F., Shu, D.G., Han, J., Liu, J.N., 2005. Morpho-anatomical differences of the Early Cambrian Chengjiang and Recent linguloids and their implications. Acta Zoologica 277–288.
- Zhang, Z.F., Shu, D.G., Han, J., Liu, J.N., 2006. New data on the rare Chengjiang (Lower Cambrian, South China) linguloid brachiopod *Xianshanella haikouensis*. Journal of Paleontology 80, 203–211.
- Zhang, Z.F., Shu, D.G., Han, J., Liu, J.N., 2007a. A gregarious lingulid brachiopod *Longtancunella chengjiangensis* from the Lower Cambrian, South China. Lethaia 40, 11–18.
- Zhang, Z.F., Han, J., Zhang, X.L., Liu, J.N., Shu, D.G., 2007b. Note on the gut preserved in the Lower Cambrian *Lingulelloreta* (Lingulata, Brachiopoda) from South China. Acta Zoologica (Stockholm) 88, 65–70.
- Zhang, Z.F., Shu D.G., Emig, C.C., Zhang, X.L., Han, J., Liu, J.N., Li, Y., Guo, J.F., in press. Rhynchonelliform brachiopods with soft-tissue preservation from the Lower Cambrian Chengjiang Lagerstätte of South China. Palaeontology. doi:10.1111/j.1475-4983.2007.00725.x.
- Zhou, J., Li, X.-H., Ge, W., Li, Z.-X., 2007. Age and origin of middle Neoproterozoic mafic magmatism in southern Yangtze Block and relevance to the break-up of Rodinia. Gondwana Research 12, 181–197.
- Zhu, M.Y., Zhang, J.M., Li, G.X., 2001. Sedimentary environments of the Early Cambrian Chengjiang biota: sedimentology of the Yu'an shan Formation in Chengjiang county, Eastern Yunnan. Acta Palaeontologica Sinica 40 (Sup), 80–105.
- Zhu, Y., Li, G.X., Hu, S.X., Zhao, F.C., 2005. Ediacaran–Cambrian boundary stratigraphy at Meishucun, Jinning County, and fossil quarries of the Early Cambrian Chengjiang Biota near Haikou, Kunming city Yunnan China. In: Peng, S.C., Babcock, L.E., Zhu, M.Y. (Eds.), Cambrian System of China and Korea. University of Science and Technology of China Press, pp. 30–36.