

Evidence of lophophore diversity in Early Cambrian Brachiopoda

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The lophophore, an essential organ of the Brachiopoda, has been used widely in evolutionary and advanced phylogenetic studies, but is hitherto unknown in the fossil record. Here, the extraordinarily well-preserved lophophores of two inarticulated brachiopods *Lingulella chengjiangensis* and *Heliomedusa orientalis*, from the Lower Cambrian Chengjiang fauna (Yunnan, China) are described. These primitive lophophores, respectively, trocholophous and schizolophous, have some key characters that may be plesiomorphies inherited by their recent descendants. This discovery provides direct evidence regarding the taxonomy, ecosystems and early evolution of inarticulated brachiopods.

Keywords: inarticulated brachiopods; lophophore; Early Cambrian; China

1. INTRODUCTION

Brachiopods resemble bivalve molluscs in possessing a mantle and two mineralized valves. Based on the absence or presence of a hinge structure that permits articulation between the two valves, brachiopods are subdivided into two groups: inarticulates and articulates. Fossil inarticulated brachiopods appear in rocks of earliest Cambrian age (*ca.* 530 Myr ago), and their distant descendants are still living in modern oceans and have a cosmopolitan distribution. Most of these fossils are known from their shells, their soft parts will quickly decay after death. Only under certain extraordinary conditions are non-mineralized tissues preserved. A few examples of fossil pedicles have been reported from the Palaeozoic (Davidson 1874; Walcott 1888). However, many lingulate brachiopods with a long slender pedicle have been found recently in the Chengjiang fossil locality of the Lower Cambrian Qiongzhusi Formation (Yu'an-shan Member) in the Kunming and Chengjiang areas of southern China (Jin *et al.* 1993; Chen *et al.* 1996; Hou *et al.* 1999). At the same horizon 3D-preserved specimens of inarticulated brachiopods were buried with the commissural plane roughly parallel to the bedding surface of the mudstone. When a rock containing these fossil brachiopods is cracked open it splits either along the outer surface of the ventral or dorsal valve, or through the opening between the two valves. When this occurs a specimen may display details of structure within

the valves. The imprint of paired spiral structures and compressed, horseshoe-shaped structures preserved in three dimensions have been found in a few specimens of *Lingulella chengjiangensis* (figure 1) and *Heliomedusa orientalis* (figure 2), respectively. This is the first time that lophophores have been observed in Palaeozoic brachiopods; post-Palaeozoic records of soft-body preservation in brachiopods are very sparse and difficult to interpret.

2. PRESERVATION

The exceptional preservation of the Chengjiang fauna has attracted considerable attention (Babcock *et al.* 2001). Efforts have been focused on various process invoked for Burgess Shale-type fossil preservation (Butterfield 1995; Briggs 2001). However, the underlying mechanisms for the preservation of the Chengjiang fauna remain obscure. Nevertheless, particular preservation styles are associated with the extraordinary fossilization of lophophores. For instance, some of the lophophores appear to have been cemented by muddy sediment (figure 2*a,f*) and some appear to be well mineralized (figure 2*b*). Both styles can even be found in the same specimen (figure 2*c*). Clay has played an important role in the preservation of soft-bodied organisms (Butterfield 1990, 1995; Briggs *et al.* 1994; Briggs 2001). Curiously, the alimentary canal of the Chengjiang *Leanchoilia illecebrosa* and other arthropods is filled with mud (Bergström 2001), whereas the same taxon in the Burgess has no sediment in its gut (Butterfield 2002). Although both faunas are assumed by some authors to result from turbidity currents, taphonomic processes may be different. Probably, the peculiar muddy deposit during the burial process may account for the unique preservation of lophophores in the Chengjiang fauna.

3. NEW FOSSIL EVIDENCE

In the obolid *L. chengjiangensis*, the lophophore is represented by the imprint of a paired spiral structure with tentacles (figure 1). Similar imprints have been illustrated but were not identified in previous studies (Jin *et al.* 1993). This type is trocholophe–schizolophe, the simplest type, seen in the adult form of only one living species, the inarticulated discinid *Pelagodiscus atlanticus* and in some small articulated species (Emig 1992), but this type of lophophore appears in the latest larval stage of almost all the Brachiopoda. All the other extant inarticulated brachiopods share a spirolophous lophophore derived from the schizolophe type (Emig 1992).

In the craniopsid *H. orientalis* all of the characteristics of the lophophore are comparable with those of extant forms, including paired arms (brachia) and tentacles with delicate cilia. In particular, the microstructure is essentially identical to that of modern ones. The type of lophophore appears to be as in *L. chengjiangensis*. The lophophore occupies a large portion of the mantle cavity even after strong compaction (figure 2*a*). This is a remarkable feature and is clearly distinguishable from the imprints of shallow grooves or low ridges left by mantle canals on the inner surface of both valves. With both rear ends of the lophophoral arms in contact with the dorsal valve, the lophophore is firmly located within the valves. If broken, it may shift its position to some extent (figure 2*b*): this means that the lophophore is a free organ between the valves, and its disposition is similar to that of extant

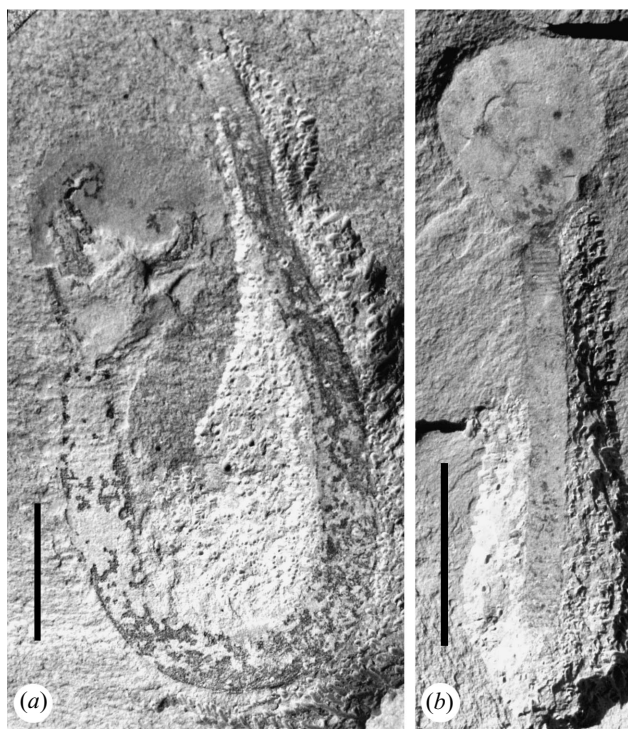


Figure 1. *Lingulella chengjiangensis* from the Lower Cambrian Qiongzhusi Formation in Chengjiang, Yunnan Province. (a) RCCBYU10201; the pedicle is curved, and paired spiral lophophores with fine tentacles are shown. (b) RCCBYU10202; the pedicle is almost straight, the paired lophophores were preserved as imprints. Scale bars, 5 mm.

craniid species (Emig 1992). The tentacles are parallel to each other. However, the pliable tentacles may be preserved in other ways, combining and crossing (figure 2d), and indistinguishable from mantle canals. Also, small bifurcate branches may be seen at the distal end of the mantle canals. These structures are not part of the lophophore. The absence of the 'mantle canals' on the ventral valve of *H. orientata* (see Jin & Wang 1992) is additional evidence supporting the view that the structure described is the lophophore. Note that the authors of that study remarked on this unusual absence and considered its possible significance with regard to a lophophore by making a reconstruction (Jin & Wang 1992, fig. 12). The variable size of these specimens indicates that they represent a series of developmental stages. With growth, more tentacles are added to the arm, which, however, remains schizolophe according to the available data (figure 3).

4. EVOLUTIONARY IMPLICATIONS

The early inarticulated brachiopods are a prominent worldwide component of Lower Cambrian shelly fossil assemblages. Nevertheless, previous studies report very little about the soft-bodied lophophores. As an indication of their presence, the lophophore supports the brachidium, which, although unknown in the inarticulated brachiopods, has evolved into various morphological types (Emig 1992). The relatively simple structure of the Cambrian lophophore is primitive, a trend shared by at least all the lingulate and craniate brachiopods. Anatomically, the well-preserved lophophores from the Early Cambrian Chengjiang brachiopods demonstrate that the

lophophoral suspension-feeding apparatus has been achieved in the Early Cambrian and thus is really a basic phylogenetic character of the group and fundamental to their ecological requirements as in the other lophophorate group, the Phoronida. However, inarticulated brachiopods are much less conservative than previous authors presumed (Biernat & Emig 1993); even their habitats appear to have changed very little. The Cambrian obolid *Lingulella* was infaunal, living in burrows (Jin *et al.* 1993). The basic functions of the lophophore are to pump water, to collect food and to exchange oxygen, as it does in extant lingulide brachiopods; the lophophore seems not to have evolved but it occupies less space in the shell (Biernat & Emig 1993). That may imply more efficient pumping by the lophophore and an increase in spiral coiling in accordance with changes in ecological factors after the Early Cambrian.

Heliomedusa orientata, which lacks a pedicle, is considered to have adapted to an epifaunal habit with its ventral valve lying free on the sea floor. The well-developed setae along the mantle margin of both valves are consistent with this mode of life (Jin & Wang 1992). The lophophore of *H. orientata* is larger than that of *L. chengjiangensis*. This may indicate that an epifaunal habit required more energy and oxygen for metabolism and activity than that required for an infaunal mode of life, or its large size may have served only to increase water currents within the shell cavity because the trocholophous-schizolophous type is more primitive and simple than the spirolophous one. This variety of the lophophores also argues for an early diversification among the inarticulated brachiopods with only minor changes at least after Cambrian times.

Based on the lophophore, a key structure shared by the Lophophorata, many phylogenetic hypotheses have been proposed. With the new evidence from molecular clocks (Halanych *et al.* 1995), the phylogenetic relationships among brachiopods and their near relatives become more complex. However, a relatively late acquisition of the lophophore (Conway Morris 1995; Conway Morris & Peel 1995) by brachiopods is not in concordance with our discovery. Instead, the presence of lophophores of brachiopods from the Lower Cambrian may argue for an even earlier appearance of this key soft organ. The brachiopods and halkieriids may have derived from separate Precambrian ancestors which, as with many other invertebrate lineages, independently and abruptly acquired shells during the Cambrian explosion. Furthermore, the presence of a true lophophore in Early Cambrian inarticulated brachiopods lends support to the conclusion that the earliest crown-group brachiopods appeared around the Atdabanian (Holmer & Popov 1996; Budd & Jensen 2000). This discovery gives us a new puzzle to solve. How can such an essential apparatus have achieved an advanced level by the Early Cambrian and change so little during its subsequent evolutionary history? It also reveals that among the synapomorphies shared by the brachiopods the lophophore should be considered such a character.

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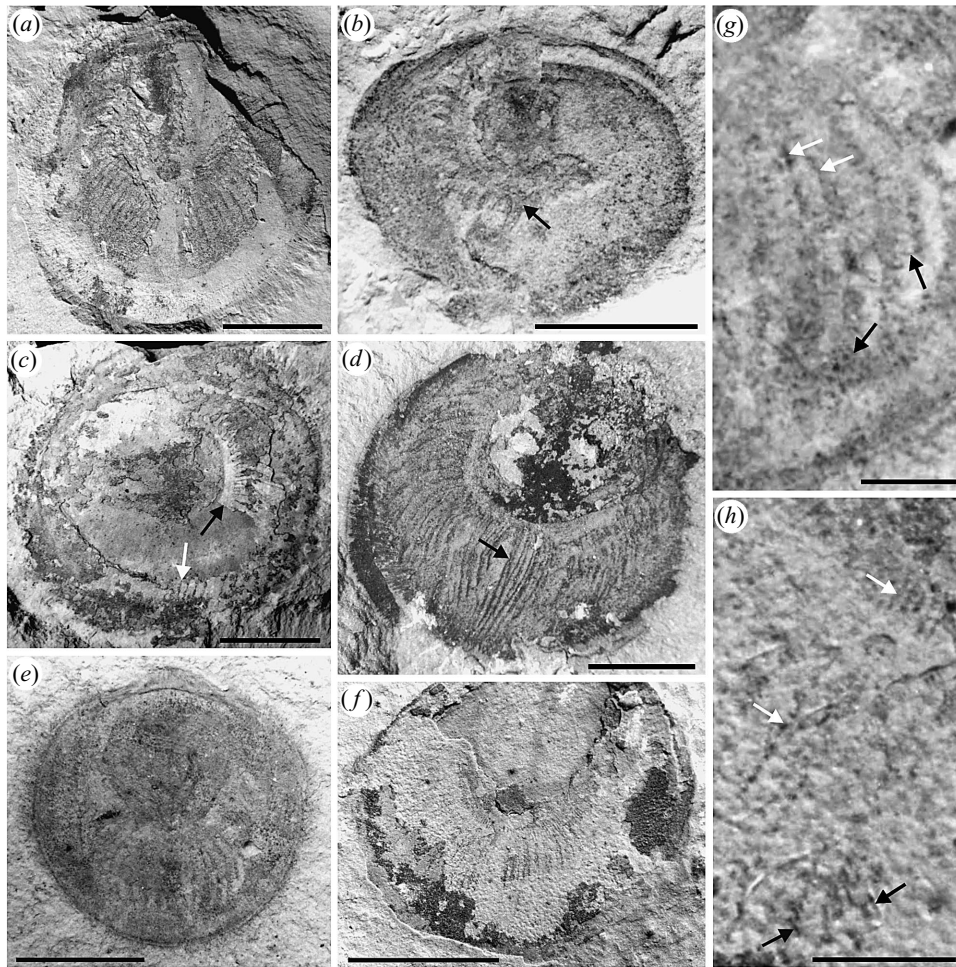


Figure 2. *Heliomedusa oriente* from the Lower Cambrian Qiongzhusi Formation at Haikou, Kunming, Yunnan Province. (a) Dorsal view of ventral valve (RCCBYU10203a) with 3D-preserved lophophores in the original position. (b) Dorsal view of a medium-sized individual with dorsal valve partially preserved (RCCBYU10205), its lophophore (arrowed) has shifted to some extent from its original position. (c) Interior view of a dorsal valve (RCCBYU10208) with the left branch of the lophophore preserved showing brachidium axis (black arrow), the tentacles of the right branch of the lophophore were partially preserved (white arrow). (d) Interior view of a dorsal valve (RCCBYU10204) showing two crossed tentacles (arrowed). (e) Interior view of a juvenile dorsal valve (RCCBYU10210). (f) Interior view of a dorsal valve (RCCBYU10209) with partially preserved tentacles. (g) Details of (e) showing tentacles (black arrows) and delicate cilia (white arrows). (h) Details of (f) showing tentacles (black arrows) and delicate cilia (white arrows). Scale bars (a–f), 5 mm; (g,h), 1 mm.

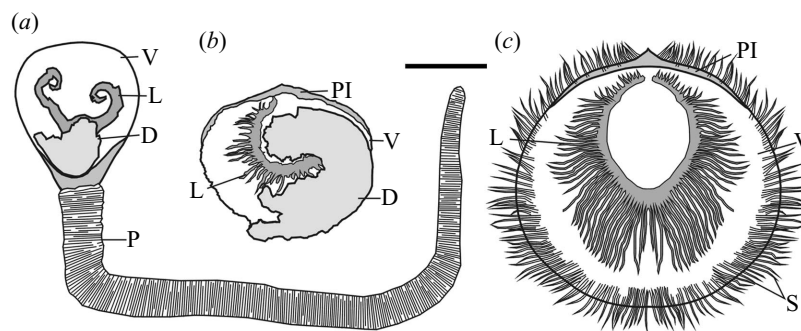


Figure 3. Sketches of inarticulated brachiopods. (a) Reconstruction of *L. chengjiangensis*. (b) Camera lucida drawings of *H. oriente* (based on specimen RCCBYU10205). (c) Reconstruction of a full-size *H. oriente*. Abbreviations: D, dorsal valve; L, lophophore; P, pedicle; PI, pseudointerarea; S, setae; V, ventral valve. Scale bar, 5 mm.

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