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New data on the lophophore anatomy of Early Cambrian linguloids from the Chengjiang Lagerstätte, Southwest China

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Abstract: A succession of developmental types in the lophophores of lingulid brachiopods is reported from the Early Cambrian Chengjiang deposits of South China. These types range from trocholophe, schizolophe to simple coiled spirolophe. Of Atdabanian age, this succession of forms is mirrored in the ontogeny of the lophophore of Recent linguloids, thus demonstrating a close similarity in the development of the lophophores of Cambrian and Recent forms. We illustrate also more than 10 extraordinary specimens with aberrant dispositions of the lophophoral arms that extend to unusual lengths either inside or outside the shell.

Key Words: Linguloidea; Brachiopoda; Lophophore; Lagerstätte; Chengjiang; China; Early Cambrian; Atdabanian

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Résumé : *Nouvelles données sur l'anatomie du lophophore chez des linguloïdes du Cambrien inférieur du Lagerstätte de Chengjiang*, *Sud-Ouest de la Chine*.- Une succession de types de lophophore est décrite chez des brachiopodes linguloïdes dans les dépôts du Chengjiang (Cambrien inférieur) au Sud de la Chine. Ces types vont depuis un lophophore trocholophe, au schizolophe et au spirolophe à enroulement spiral simple. Cette succession d'âge Atdabanien existe encore dans le développement du lophophore chez les linguloïdes actuels, ce qui démontre une similarité entre les lophophores au Cambrien et dans l'Actuel. Des dispositions aberrantes des bras lophophoraux qui tendent à s'étendre de façon inhabituelle dans et hors de la coquille sont illustrées dans une dizaine d'exemplaires.

Mots-Clefs : Linguloidea ; Brachiopoda ; Lophophore ; Lagerstätte ; Chengjiang ; Chine ; Cambrien inférieur ; Atdabanien

Introduction

Brachiopoda and Phoronida, together with Ectoprocta possess a tentacular, ciliated, feeding organ, the lophophore, and thus sometimes have been grouped as Lophophorata (EMIG, 1977, 1997a). Based on traditional morpho-anatomical characters, brachiopods and phoronids are undoubtedly closely related, and usually regarded as sister groups among deuterostomes (NIELSEN, 2001, 2002). However, molecular phylogenetic studies confirm phoronid-brachiopod monophyly and establish their affinities with protostomes (see among others HALANYCH *et alii*, 1995; MACKEY *et alii*, 1996; COHEN *et alii*, 1998). Brachiopods are exclusively marine bivalved lophophorates. As a clade, the most distinctive feature of this group that supposedly differentiates them from the other lophophore-bearing animals is a filtration system in an isolated cavity (POPOV, 1992). However, in view of molecular

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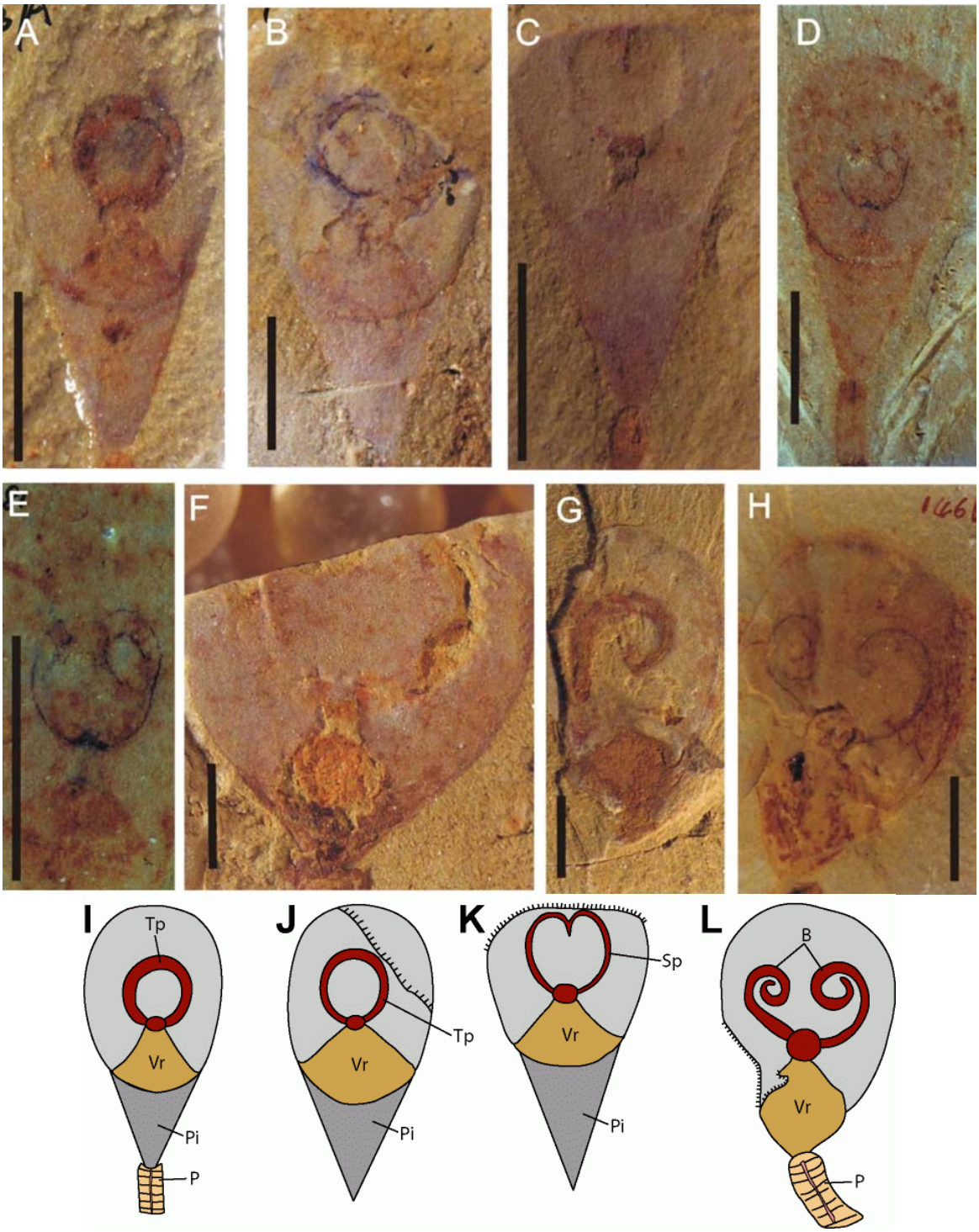

Figure 1: Distinctive disposition of lingulid lophophores from the Lower Cambrian Chengjiang deposits, South China. (*A-E*) lophophores of the lingulellotretid *Lingulellotreta malongensis*. (*F-H*) lophophores of the obolid *Lingulella chengjiangensis.* (*I-L*) interpretative drawings of figures shown here. (*A*) ELI L-0137A, a circular trocholophore imprint; (*B*) ELI L-0157, an impressed trocholophore imprint; (*C*) ELI L-0290, a schizolophe imprint with an anterior-median indentation; (*D-E*) ELI L-0081, a juvenile spirolophe; (*E*) enlargement of the lophophore of (*D*); (*F*) ELI C-0188B, imprint of a recessed round trocholophore; (*G*) ELI C-0030B, a single coiled lophophoral arm; (*H*) ELI C-0146B, showing freely coiled paired brachia; (*I*) Sketch of (*A*); (*J*) Sketch of (*B*); (*K*) Sketch of (*C*); (*L*) Sketch of (*H*).
Abbreviations: B, lophophoral arm; Vr, visceral region; Pi, pseudointerarea; P, pedicle; Tp, trocholophe; Sp, schizolophe. Scale bars 2 mm.

phylogenetic studies this classification seems no longer tenable. COHEN *et alii* (1998) and COHEN (2000) suggest that the phylum Phoronida should be regarded as a subphylum of shell-less brachiopods named Phoroniformea, though this view has been questioned (PETERSON and EERNISSE, 2001; NIELSEN, 2002, 2003).

The brachiopod lophophore functions principally as a ciliary pump and feeding organ by creating currents of water through out the mantle cavity that serve for both the capture of food particles and the uptake of oxygen for respiration (EMIG, 1976). The shape and disposition of the lophophore are apposite with both the inhalant and exhalant "apertures" of brachiopods and with the orientation of the brachiopod shell (EMIG, 1992). As in the phoronids the brachiopod lophophore is composed of a pair of long lophophoral arms or brachia, and is not capable of much extension, even in the inarticulate forms where its musculature is best developed. The brachia are disposed symmetrically about the mouth and variously looped or coiled (EMIG, 1992). They are attached to the anterior body wall, sometimes to the dorsal mantle surface. The spirolophe is characteristic of most inarticulate brachiopods. An adult spirolophe must go through trocholophous and schizolophous stages during its development (EMIG, 1992). However, fossil records hitherto have provided no information regarding this ontogenic process, albeit some well-defined lophophore tissues were reported recently from the Lower Cambrian of China (Z.F. ZHANG *et alii*, 2004; X.G. ZHANG *et alii*, 2003).

In this paper, we provide additional information on the ontogeny of the lophophore in Early Cambrian lingulids, and illustrate some aberrant dispositions of lophophores that differ markedly from those depicted by Z.F. ZHANG *et alii* (2004).

Materials

All the specimens show typical Chengjiang preservation (HOU *et alii*, 1991). As in the phoronids, after weathering the fossils are reddish or dark yellow and are embedded in grayish-green and grayish-yellow mudstone intercalated with grayish-brown silty shale. All of them were recovered from the Ercai village and Hill Jianshan localities at Haikou, Kunming, where the earliest-known agnathan *Haikouichthys* (SHU *et alii*, 2003a) and the enigmatic yunnanozoan *Haikouella jianshanensis* (SHU *et alii*, 2003b) were found. The strata containing the soft-bodied fossils belong to the Yu'anshan Member (*Eoredlichia* Zone), i.e. the upper part of Early Cambrian Heilinpu (formerly Qiongzhusi) Formation, exposed in a wide area around Kunming, Yunnan. Details of the localities and stratigraphy were given in X.L. ZHANG et *alii* (2001). So far, nearly 1,000 specimens of the two lingulid taxa, *Lingulella chengjiangensis* and *Lingulellotreta malongensis*, have been collected from these localities by the work-team of the Early Life Institute (prefixed ELI); all the specimens are deposited in ELI, Northwest University, Xi'an, China. In our lingulid collections, around 80 specimens reveal partial or paired lophophoral imprints, in some cases with well-defined tentacles (Z.F. ZHANG *et alii*, 2004). In this collection there are only 20 specimens where the lophophoral imprints do not display the usual spiral coil (Z.F. ZHANG *et alii*, 2004). Of these apparently aberrant dispositions of lophophores, 6 appear rounded (Fig. 1 A-B and I-J), 2 are crescent-shaped with an introversion of the anterior edge (Fig. 1 C and K), and the remaining lophophores seem to display some extension of the lophophoral arms which are either elongated inside, or protrude from the shell (Fig. 2 A-J).

Description and Discussion

The lophophore of *Lingulellotreta malongensis* has recently been documented by Z.F. ZHANG *et alii* (2004), who considered it to correspond to an early spirolophe stage. However, new material from the same localities shows that some lophophores of *L. malongensis* do not invariably take the shape of simple spiral coils as depicted by Z.F. ZHANG *et alii* (2004). They appear either as rounded or crescent-shaped loops distinctly delimited by two concentric brownish strands (Fig. 1 A-B and I-J). This disposition is closely reminiscent of a taxolophe-trocholophe stage of development (EMIG, 1992). In Fig. 1 C a rounded lophophore has an anterior-median indentation, dividing the lophophore into two lobes: it probably represents a schizolophe stage of development (Fig. 1 C and K). These lingulid shells (Fig. 1 A-C) appear to be smaller (approximately 5mm long) and shorter than those with an early spirolophe (Z.F. ZHANG *et alii*, 2004). Based on a single specimen, the lophophore of the obolid *Lingulella chengjiangensis* has also been described by X.G. ZHANG *et alii* (2003) as a schizolophe stage. However, in the light of evidence from more than 20 specimens of *L. chengjiangensis* numbered ELI C-0030-0146, the lophophores of *L. chengjiangensis*, like those of *Lingulellotreta malongensis*, include trocholophes (Fig. 1 F), schizolophes (X.G. ZHANG *et alii*, 2003) and the less intricately coiled spirolophes (Fig. 1 G-H and L). All these types of lophophores are 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 Ma. Thus, the early stages of lophophoral ontogeny and development appear to be plesiomorphic characters inherited from an ancestral form.

Another noteworthy fact, identified in more than 10 specimens (see: Fig. 2 A-J) is lophophoral arms that are either elongated inside or extend outside the shell. In specimen ELI C-0078 (Fig. 2 A and G) paired lophophoral imprints arise from the anterior-medial visceral

region. One extends forward and curves outward inside the shell, and the other projects laterally outward, and then curves backward outside the shell. On the outer portion of this lophophoral arm are some reddish-brown grains that may represent organic particles interpreted as nutrient, or at least particles filtered by the tentacles. In specimen ELI C-0040 (Fig. 2 B and H), a pair of lophophoral tubes protrude from both sides of the shell. They are disposed symmetrically about the midline. In the center of the paired lophophoral axes (Fig. 2 A-B and G-H) runs a dark strand. It is taken to mark the hollow lophophoral canal (or lophophoral coelomic cavity) (Fig. 2 A-B and G-H). In Fig. 2 C-D, one lophophoral arm outside the shell appears as a coiled counterclockwise inwards imprint (Fig. 2 C-D and I); the aspect of the other arm is unknown because it is absent in the broken specimen. Nonetheless, it is in the aberrant single lophophoral axis that the tentacles are clearly visible, and closely arranged in a single palisade (Fig. 2 C-D and I). As seen in Fig. 2 E and J, one lophophoral arm appears freely coiled, whereas the other one apparently spreads antero-laterally inside the shell (Fig. 2 E and J). In addition, in the specimen ELI L-0127 the paired lophophoral arms appear to cross each other (Fig. 2 F). However, none of the brachiopod shells were crushed and deformed laterally, and their marginal edge is also well preserved. The state of preservation suggests that the animal is most probably in an undisturbed life position, possibly as a result of storm-induced rapid burial. This is likely because the organic component of the shell is so quickly hydrolysed or digested by microbes and the exposed apatitic framework so easily abraded hydro-dynamically (EMIG, 1990), that fossilization of lingulid shells could only have taken place after catastrophic changes provoking rapid burial were developed in the post-mortem environment (EMIG, 1997b).

The aberrant disposition of lophophores is not easily explained. Several hypotheses may be proposed. The atypical forms may have been caused by oxygen deprivation during a living burial produced by turbidity currents (BABCOCK and W.T. ZHANG, 2001). The symmetrical protrusion of both brachia from the shell (Fig. 2 B and H) suggests this conjecture. However, this proposal is considered less likely because of the fact, as seen in Fig. 2 E and J, that one of lophophoral arms is coiled as usual while the other appears to form an elongated extension. Furthermore, in one specimen (Fig. 2 A and G), both the lophophoral arms are broadly spread. They extend asymmetrically toward one side and then protrude out of the shell, rather than diverge rapidly toward two sides (Fig. 2 A and G). Such a disposition appears truly aberrant compared with the normal (Fig. 1 H and L). In addition, this interpretation of the imprints may be less tenable if the paired lophophoral arms cross each other (Fig. 2 F). The distinctive layout of lophophoral arms may be the result of *post-mortem* relaxation and re-distribution, possibly consequent on the weight of a layer of covering silt for instance. This seems a simple explanation, but may be inconsistent with the coiled shape of most lophophores (Fig. 1 A-L). In addition, *post-mortem* change cannot account for the different degrees of spread in the brachia of the several discrete animals because their integuments were not crushed or strongly distorted laterally, although flattened dorso-ventrally. The most probable hypothesis is that the lophophores of Cambrian lingulids were capable of some extensional movement. Both lophophoral arms could stretch inside and freely extend out of the mantle cavity under certain specific conditions. The known series of aberrant lophophore patterns (Fig. 2) accords well with this supposition, so it may be a valid explanation of the phenomena observed. The presence of nutrient particles on the outer lophophoral arm (Fig. 2 A and G) and the normal (counterclockwise) coil of the lophophoral arm outside the shell (Fig. 2 C-D and I) are congruent with a probable extensional motion of the lophophore for nutrient capture.

Brachiopods and phoronids were commonly grouped together with bryozoans (HYMAN, 1959; EMIG, 1977, 1997a; HALANYCH, 1995, 1996; HALANYCH *et alii*, 1995), and sometimes with pterobranch hemichordates (NIELSEN, 1987, 2001, 2002; RIISGÅRD, 2002) because they possess a ciliated tentacular structure that invades the mesocoelomic cavity and surrounds the mouth but not the anus. This grouping is based primarily on the inferred homology of their ciliated tentacular feeding structures (HYMAN, 1959; HALANYCH, 1996; NIELSEN, 1987, 2002). 18s rDNA sequence data suggest, however, that pterobranchs and lophophorates (consisting of the brachiopods, phoronids, and bryozoans) are in different metazoan subkingdoms and are not closely related (HALANYCH, 1995, 1996; MACKEY *et alii*, 1996). If so, the shared possession of a lophophore-like apparatus may be the result of evolutionary convergence (HALANYCH, 1996). Within the Bilateria the placement of the lophophorate bryozoans is perhaps the most puzzling (NIELSEN, 2002; HALANYCH *et alii*, 1995; GIRIBET *et alii*, 2000, PETERSON and EERNISSE, 2001; PASSAMANECK and HALANYCH, 2004). Based on morphological analyses (NIELSEN, 1987, 2001, 2002), bryozoans were repeatedly separated from the phoronid-brachiopod clade, and are not monophyletic with brachiopods and phoronids. Nevertheless, the filter-feeding process in phoronids and bryozoans is remarkably similar (RIISGÅRD, 2002; LARSEN and RIISGÅRD, 2002). Morphological analyses indicate indisputably that brachiopods and phoronids are closely related (NIELSEN, 2001, 2002). They share numerous developmental and anatomical traits that are largely in accordance with the molecular phylogenetic data (HALANYCH *et alii*, 1995; ERBER et *alii*, 1998; COHEN *et alii*, 1998; COHEN, 2000).

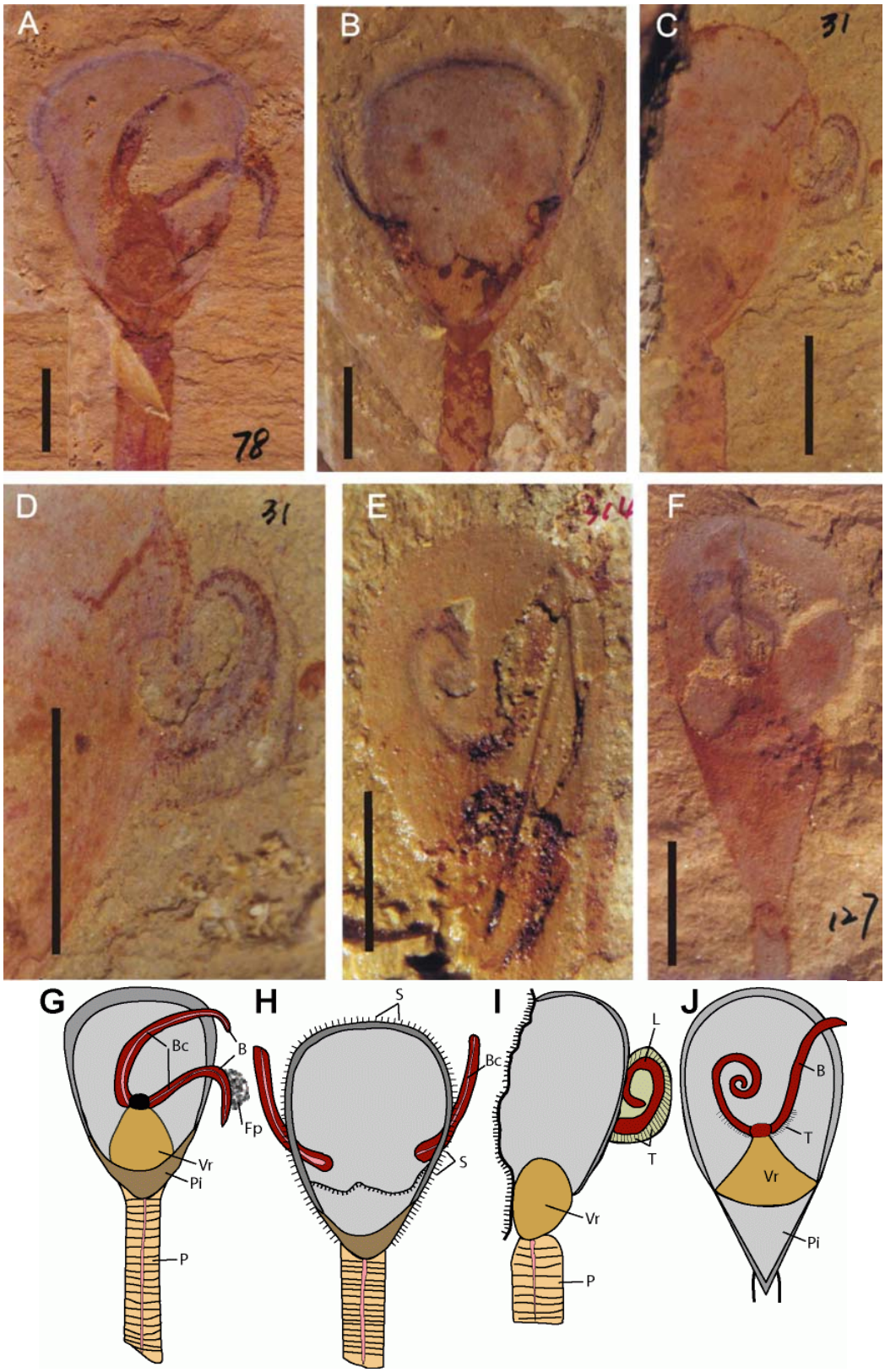

Figure 2: Aberrant disposition of lingulid lophophores from the Lower Cambrian, China. (*A-D*) of *Lingulella chengjiangensis*. (*E-F*) of *Lingulellotreta malongensis*. (*G-J*) interpretative drawings. (*A*) ELI C-0078, note the extended paired lophophoral arms, with the right one apparently outside the shell; (*B*) ELI C-0040, showing the symmetrically protruded lophophoral tubes and finely impressed setal fringe; (*C*) ELI C-0031, imperfectly preserved spcimen, showing a coiled lophophore protruding from the shell; (*D*) details of the lophophore in (*C*), showing the well-defined tentacles; (*E*) ELI L-0314 a flattened specimen, showing the left arm freely coiled and the right one extended anterolaterally; (*F*) ELI L-0127, showing the paired crossed lophophoral arms preserved in the sediment infilling between valves; (*G*) Sketch of (*A*); (*H*) Sketch of (*B*); (*I*) Sketch of (*C*); (*J*) Sketch of (*E*).
Abbreviations: B, lophophoral arm; Fp, food particle?; Vr, visceral region; Pi, pseudointerarea; P, pedicle; S, mantle setae; Bc, lophophoral canal; T, tentacle; L, lophophore. Scale bars 2 mm.

The series of forms in the development of lophophores during Atdabanian times (see Fig. 1) indicate that Early Cambrian lingulids are represented in the larval-juvenile developmental stage of their Recent relatives. Hence, their inhalant and exhalant currents could resemble those of the schizolophous and early spirolophous stages (CHUANG, 1974; EMIG, 1992), and most probably differ from the three apertures (the central for exhalant current water, and the outer two for inhalant current) of Recent *Lingula* because of the absence of a pointed medially lophophore filter cone and three pseudosiphons of setae. In addition, the fossils illustrated herein (Fig. 1-2) indicate that like Recent linguliforms, Early Cambrian lingulids lack median tentacles. Lophophore palisades and the brachial lip in the trocholophe stage are of critical importance to an understanding of brachiopod phylogeny (HOLMER *et alii*, 1995). Unfortunately, data regarding these aspects cannot be confidently demonstrated in the collected specimens. Continuing investigation of the unique Chengjiang deposits may yield information bearing on these issues.

The aberrant lophophore layouts discussed herein suggest extensibility in the Cambrian lingulid lophophore under certain stringent conditions. The extended paired feeding apparatuses (Fig. 2 A and G) are surprisingly reminiscent of lophophore-like tentacular feeding arms of rhabdopleurid pterobranchs. This high degree of ostensible similarity presumably reflects a certain selective pressure on these brachiopod taxa from the surroundings at that time, which resulted in morphological convergence (HALANYCH, 1996). Brachiopods have two coelomic cavities in the lophophore, a large brachial canal which is restricted to the base of the lophophore and a small brachial canal with extension into each tentacle (NIELSEN, 2002). In the fossil brachiopods (Fig. 2 A-B and G-H) the large brachial canal appear to be visible as a dark lineation in the centre of either lophophoral axis, and the presence of the small brachial canal is suggested by the well-defined tentacles (Fig. 2 C-D and I). However, Phoronids have a single coelomic cavity in the lophophore, that lacks a brachial lip as well as cartilage-like connective tissue (HOLMER *et alii*, 1995; NIELSEN, 2002). Thus it is unlikely that the phoronid lophophore represents a derivation of the brachiopod lophophore and if the molecular data are correct (HALANYCH et *alii*, 1995; COHEN *et alii*, 1998, 2003; COHEN, 2000; PASSAMANECK and HALANYCH, 2004), it is reasonable to assume that the respiratory function of the lophophore of the Brachiopoda now known only in an isolated cavity (the shell) could be an apomorphy derived from a stem lophophore ancestor.

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References

BABCOCK L.E., ZHANG W.T. (2001).- Stratigraphy, paleontology, and depositional setting of the Chengjiang Lagerstätte (Lower Cambrian), Yunnan, China.- *Palaeoworld*, Nanjing, vol. 13, pp. 66-86.

CHUANG S.H. (1974).- Observations on the ciliary feeding mechanism of the brachiopod *Crania anomala.- Journal of Zoology*, London, vol. 173, pp. 441-449.

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*, *London*, *Series B*, vol. 267, pp. 225-231.

COHEN B.L., GAWTHROP A., CAVALIER-SMITH T. (1998).- Molecular phylogeny of brachiopod and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences.- *Proceedings of the Royal Society*, *London*, *Series B*, vol. 353, pp. 2039-2061.

COHEN B.L., HOLMER L.E., LÜTER C. (2003).- The brachiopod fold: A neglected body plan hypothesis.- *Palaeontology*, Oxford, vol. 46, n° 1, pp. 59-65.

EMIG C.C., (1976).- Le lophophore structure significative des Lophophorates - Brachiopoda, Bryozoa, Phoronida.- *Zoologica Scripta*, Göteborg, vol. 5, pp. 133-137.

EMIG C.C. (1977).- Un nouvel embranchement: les Lophophorates.- *Bulletin de la Société zoologique de France*, Paris, vol. 102, pp. 341-344.

EMIG C.C. (1990).- Examples of post-mortality alteration in Recent brachiopod shells and (paleo) ecological consequences.- *Marine Biology*, New York, vol. 104, pp. 233-238.

EMIG C.C. (1992).- Functional disposition of the lophophore in living Brachiopods.- *Lethaia*, Oslo, vol. 25, pp. 291-302.

EMIG C.C. (1997a).- Les Lophophorates constituent-ils un embranchement ?- *Bulletin de la Société zoologique de France*, Paris, vol. 122, pp. 279-288.

EMIG C.C. (1997b).- Ecology of inarticulated

brachiopods. *In*: KAESLER R.L. (eds.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda.- Geol. Soc. Amer. & Univ. Kansas Press, Boulder, Kansas, vol. 1, pp. 473-495.

ERBER A., RIEMER D., BOVENSCHULTE M., WEBER K. (1998).- Molecular phylogeny of metazoan intermediate filament proteins.- *Journal of Molecular Evolution*, New York, vol. 47, pp. 751-762.

GIRIBET G., DISTEL D.L., POLZ M., STERRER W., WHEELER W.C. (2000).- Triploblastic relationships with emphasis on the acoelomates and the position of Gnathostomulida, Cycliophora, Plathelminthes and Chaetognatha: A combined approach of 18s rDNA sequences and morphology.- *Systematic Biology*, Levittown, vol. 49, pp. 539-562.

HALANYCH K.M. (1995).- The phylogenetic position of the pterobranch Hemichordates based on 18s rDNA sequence data.- *Molecular phylogenetics and Evolution*, Detroit, vol. 4, n° I, pp. 72-76.

HALANYCH K.M. (1996).- Convergence in the feeding apparatuses of Lophophorates and pterobranch hemichordates revealed by 18s rDNA: An interpretation.- *Biological Bulletin*, Woods Hole, vol. 190, pp. 1-5.

HALANYCH K.M., BACHELLER J.D., AGUINALDO A.M.A., LIVA S.M., HILLIS D.M., LAKE J.A. (1995).- Evidence from 18s ribosomal DNA that the lophophorates are protostome animals.– *Science*, Washington D.C., vol. 267, pp. 1641-1643.

HOU X.G., RAMSKÖLD L., BERGSTRÖM J. (1991).- Composition and preservation of the Chengjaing fauna – a Lower Cambrian soft-bodied biota.- *Zoologica Scripta*, Göteborg, vol. 20, pp. 395-411.

HOLMER L.E., POPOV L.E., BASSETT M.G., LAURIE J. (1995).- Phylogenetic analysis and ordinal classification of the brachiopoda.- *Palaeontology*, Oxford, vol. 38, n° 4, 713-741.

HYMAN L.H. (1959).- The invertebrates: Smaller coelomate groups, Chaetognatha, Hemichordata, Pogonophora, Phoronida, Ectoprocta, Brachiopoda, Sipunculida, the Coelomate Bilateria.- McGraw-Hill, New York, 783 p.

LARSEN P.S., RIISGÅRD H.U. (2002).- On ciliary sieving and pumping in bryozoans.- *Journal of Sea Research*, Texel, vol. 48, pp. 181-195.

MACKEY L.Y., WINNEPENNINCKX B., WACHTER R.D., BACKELJAU U., EMSCHERMANN P., GAREY J.R. (1996).- 18s rDNA suggests that Entoprocta are protostomes, unrelated to Ectoprocta.- *Journal of molecular Evolution*, New York, vol. 42, pp. 552-559.

NIELSEN C. (1987).- Structure and function of metazoan ciliary bands and their phylogenetic significance.- *Acta zoologica*, Stockholm, vol. 68, pp. 205-262.

NIELSEN C. (2001).- Animal evolution: Interrelationships of the living phyla, 2nd edition.- Oxford Univ. Press, Oxford, pp. 385-406.

NIELSEN C. (2002).- The phylogenetic position of Entoprocta, Ectoprocta, Phoronida, and Brachiopoda.- *Integrative and Comparative Biology*, Seattle, vol. 42, n° 3, pp. 685-691.

NIELSEN C. (2003).- Defining phyla: morphological and molecular clues to metazoan evolution.- *Evolution and Development*, Seattle, vol. 4, pp. 386-393.

PASSAMANECK Y.L., HALANYCH K.M. (2004).- Evidence from Hox genes that bryozoans are lophotrochozoans.- *Evolution and Development*, Seattle, vol. 6, n° 4, pp. 275-281.

PETERSON K., EERNISSE D.J. (2001).- Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18s rDNA sequences.- *Evolution and Development*, Seattle, vol. 3, pp. 170-205.

POPOV L. E. (1992).- The Cambrian radiation of brachiopods. *In*: J.H. LIPPS and P.W. SIGNOR (eds.), Origin and early evolution of the Metazoa.- Plenum Press, New York, pp. 399-423.

RIISGÅRD H.U. (2002).- Methods of ciliary filter feeding in adult *Phoronis muelleri* (phylum Phoronida) and in its free-swimming actinotroch larva.- *Marine Biology*, New York, vol. 141, pp. 75-87.

SHU D.G., CONWAY MORRIS S., HAN J., ZHANG Z.F., YASUI K., JANVIER P., CHEN L., ZHANG X.L., LIU J.N., LI Y., LIU H.Q. (2003a).- Head and backbone of the Early Cambrian vertebrate Haikouichthys. – *Nature*, London, vol. 421, pp. 526-529.

SHU D.G., CONWAY MORRIS S., ZHANG Z.F., LIU J.N., HAN J., CHEN L., ZHANG X.L., YASUI K., LI Y. (2003b).- A new species of yunnanozoan with implications for deuterostome evolution.– *Science*, Washington D.C., vol. 299, pp. 1380-1384.

ZHANG X.G., HOU X.G., EMIG C.C. (2003).- Evidence of lophophore diversity in Early Cambrian Brachiopoda.- *Proceedings of the Royal Society*, *London*, *Series B*, (Suppl.), vol. 270, pp. S65-S68.

ZHANG X.L., SHU D.G., LI Y., HAN J. (2001).- New sites of Chengjiang fossils: crucial windows on the Cambrian explosion.- *Journal of the Geological Society*, London, vol. 158, pp. 211-218.

ZHANG Z.F., HAN J., ZHANG X.L., LIU J.N., SHU D.G. (2004).- Soft tissue preservation in the Lower Cambrian linguloid brachiopod from South China.- *Acta Palaeontologica Polonica*, Warsaw, vol. 49, n° 2, pp. 259-266.