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Architecture and function of the lophophore in the problematic brachiopod *Heliomedusa orienta* (Early Cambrian, South China)☆

Architecture et fonction du lophophore chez Heliomedusa orienta*, un brachiopode problématique du Cambrien inférieur de Chine du Sud*

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Abstract

The detailed structure of the lophophore is a key diagnostic character in the definition of higher brachiopod taxa. The problematic *Heliomedusa orienta* Sun and Hou, from the Lower Cambrian Chengjiang Lagerstätte of Yunnan, southwestern China, has a well-preserved lophophore, which is unlike that of any known extant or extinct brachiopods. Based on a comparative study of lophophore disposition in *H. orienta* and the extant discinid *Pelagodiscus atlanticus*, the in- and excurrent pattern and shell orientation of *H. orienta* are described and discussed. Reconstructions of lophophore shape and function are based on numerous specimens and comparison with *P. atlanticus*. The lophophore is composed of a pair of lophophoral arms that freely arch posteriorly rather than coiling anteriorly as commonly seen in fossil and recent lingulids. The lophophore is attached to the dorsal lobe of the mantle; it has neither calcareous nor chitinous supporting structures, and is disposed symmetrically on either side of the valve midline. The mouth can be inferred to be located at the base of the two brachial tubes, slightly posterior to the anterodorsal projection of the body wall. The lophophoral arms bear laterofrontal tentacles with a double row of cilia along their lateral edge, as in extant lingulid brachiopods. The main brachial axes are also ciliated, which presumably facilitated transport of mucous-bound nutrient particles to the mouth. The unique organization of the lophophore in *Heliomedusa* is not like any known fossil and living brachiopods. This clearly demonstrates that *H. orienta* is not a member of any crown group. It is here considered as a member of the brachiopod stem group, which challenges recent interpretations of a close discinid affinity.

Keywords: Early Cambrian; Stem-group brachiopod; *Heliomedusa*; Lophophore; Lifestyle; Discinid

Résumé

La structure détaillée du lophophore est un caractère diagnostique clé pour la définition des taxons de brachiopodes de rang élevé. Le brachiopode problématique *Heliomedusa orienta* Sun et Hou du Cambrien inférieur du Lagerstätte de Chengjiang (Yunnan, sud-ouest de la Chine) possède un lophophore bien conservé sans équivalent chez aucun brachiopode actuel ou fossile. Les courants inhalants et exhalants, ainsi que l'orientation de la coquille de *H. orienta* sont décrits et discutés sur la base d'une étude comparative de la disposition du lophophore chez *H. orienta* et *Pelagodiscus atlanticus* (brachiopode discinidé actuel). Les reconstitutions de la forme et de la fonction du lophophore sont basées sur de nombreux spécimens et sur des comparaisons avec *P. atlanticus*. Le lophophore est constitué de deux bras qui se courbent postérieurement au lieu de s'enrouler antérieurement comme c'est communément le cas chez les lingulidés fossiles et actuels. Le lophophore est attaché au lobe dorsal du manteau ; il n'a aucune structure de soutien calcaire ou chitineuse et est disposé symétriquement de chaque côté de la ligne médiane de la valve. On déduit que la bouche se situe à la base des deux tubes brachiaux, légèrement derrière la projection antéro-dorsale de la paroi corporelle. Les bras du

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lophophore portent des tentacules latéro-frontaux avant une double rangée de cils le long du bord latéral, comme chez les lingulidés actuels. Les axes brachiaux principaux sont également ciliés, ce qui facilitait vraisemblablement le transport de particules nutritives recouvertes de mucus vers la bouche. L'organisation du lophophore de *Heliomedusa* est unique et ne se retrouve chez aucun autre brachiopode actuel ou fossile. Ceci démontre clairement que *H. orienta* ne fait pas partie d'un groupe couronne. Cette espèce est considérée ici comme appartenant au groupe souche (stem group) des brachiopodes, ce qui remet en cause de récentes interprétations selon lesquelles *H. orienta* aurait d'étroites affinités avec les discinidés.

Mots clés : Cambrien inférieur ; Groupe souche des brachiopodes ; *Heliomedusa* ; Lophophore ; Mode de vie ; Discinidé

1. Introduction

Brachiopods are exclusively marine bivalved lophophore-bearing invertebrates. As a clade, the most distinctive feature, supposedly differentiating them from other lophophore-bearing animals, is the unique filtration system in an isolated cavity (i.e. the mantle or lophophoral cavity), which is enclosed between the dorsal and ventral valves. The architecture of the lophophore is a key diagnostic character for the definition of higher brachiopod taxa, and has had a pivotal role in previous phylogenetic analyses (Blochmann, 1900; see also Holmer et al., 1995; Williams et al., 1996). However, the lophophore is very rarely fossilized and thus its organizational evolution can often only be inferred. Interestingly, exceptionally-preserved fossil lophophores are known from most of the Early Cambrian brachiopods of the Chengjiang Lagerstätten biota of Yunnan, SW China, including the lingulid *Lingulellotreta malongensis* (Rong, 1974; Holmer et al., 1997), '*Lingulella' chengjiangensis* (Jin et al., 1993), *Longtancunella chengjiangensis* (Hou et al., 1999), *Xianshanella haikouensis* (Zhang and Han, 2004; Zhang et al., 2006), the problematic *Heliomedusa orienta* (Sun and Hou, 1987), as well as the recently described calcareous-shelled *Kutorgina chengjiangensis* (Zhang et al., 2007b). *Heliomedusa orienta* exhibits a completely different type of lophophore with backwards-pointing arms (Zhang X.G. et al., 2003), whilst the other five Chengjiang species preserve trocholophous, schizolophous to simple spirolophous lophophores that are well known also from extant brachiopods (Rudwick, 1970; Emig, 1992).

The lophophore creates a continuous, laminar water flow, induced by the lateral cilia on the tentacles. The water flow is divided generally into distinct inhalant and exhalant currents. As shown by Emig (1992), the lophophoral architecture is closely related to the in- and excurrent water patterns of brachiopods. The distinct water currents through the mantle cavity are also closely associated with the orientation of the brachiopod shell relative to the substrate because they tend to minimize the energy needed for the creation of feeding and respiratory currents and avoid recirculation of previously filtered water (Williams et al., 1997). The ecology and detailed life habits of extinct brachiopod has been the subject of a long debate (Rudwick, 1970; Holmer, 1989; Jin et al., 1991; Emig, 2000; Ushatinskaya, 2001; Zhang et al., 2005), and Cambrian brachiopods were assumed to exhibit several types of substrate relationships (Ushatinskaya, 2001), including pedicle-anchoring, free-lying, cemented epifaunal, infaunal, quasi-infaunal, and interstitial. Recent reports of soft-tissue preservation of brachiopods have substantially increased our understanding of the Cambrian palaeoecology of the phylum (Zhang Z.F. et al., 2003, 2004a, 2004b, 2005, 2006, 2007a, 2007b, 2007c, 2008; Holmer and Caron, 2006; Pettersson Stolk et al., in press). Studies of the brachiopods with preserved pedicles from Burgess shale-type Lagerstätten (e.g., Chengjiang and Burgess Shale) suggest that attachment by a pedicle to the substrate was probably the most common life habit of Cambrian brachiopods (Holmer and Caron, 2006; Zhang et al., 2008; Pettersson Stolk et al., in press), although a somewhat larger ecological diversity has also been reported (Jin, 2005). The enigmatic brachiopod *Heliomedusa orienta* is one of the most common species in the Early Cambrian Chengjiang fauna (Sun and Hou, 1987; Chen and Erdtmann, 1991; Jin and Wang, 1992; Popov and Holmer, 2000; Holmer et al., 2003; Chen et al., 2007; Holmer and Popov, 2007). The palaeoecology of *H. orienta* was initially investigated in 1991, when it was considered to be cemented as a juvenile, but free-lying in adults. Subsequently, a detailed morphological description of the brachiopod shell further supported that it was free-lying (Jin and Wang, 1992). Nonetheless, the free-lying view was challenged recently by the re-interpretation of *Heliomedusa* as a discinid with an inferred pedicle emerging ventrally from the posteromedian position of the ventral valve (Chen et al., 2007).

In the present study, we give an account of the detailed architecture and function of the lophophore of *H. orienta*, as well as an analysis of the life habit and ecology of this enigmatic brachiopod. In order to better understand the functional disposition of the lophophore and in- and ex-current patterns in *H. orienta*, the structurally similar lophophore of the extant discinid brachiopod *Pelagodiscus atlanticus* is used for comparison. The unique lophophoral architecture supports that *Heliomedusa* is not closely related to any living member of the phylum, but can be regarded as a stem group brachiopod (Holmer and Popov, 2007; Holmer et al., 2008). This also shows that there was a rapid diversification of the lophophore organization of brachiopods at the onset of Cambrian, and it clearly underlines the danger of assuming that the anatomy of stem group brachiopods can be directly extrapolated from the extant group (Zhang et al., 2003).

2. Material and methods

About 1500 specimens of *Heliomedusa orienta* have been collected in 8 localities in the SW of the Yangtze Platform