Shell structure, ornamentation and affinity of the problematic early Cambrian brachiopod *Heliomedusa orienta*

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Brachiopods, which are firmly nested within the Lophotrochozoa (Halanych et al. 1995; Dunn et al. 2008), represent some of the most important components of marine communities during the Palaeozoic; they dominate the benthos of both the Cambrian Evolutionary Fauna and the Palaeozoic Fauna (Sepkoski 1981, 1984). Although the quality of brachiopod fossils attracts considerable attention of palaeontologists working on Cambrian strata, the origin and early evolution of the phylum remains unclear (Holmer et al. 2002, 2008b; Cohen et al. 2003; Cohen & Weydmann 2005; Skovsted et al. 2009a; Murdock et al. 2014; Harper et al. 2017). The stem and crown group concept (Budd & Jensen 2000) has already been applied successfully for analysing phylogenetic relationship within the Brachiopoda (Holmer et al. 2002; Williams & Holmer 2002; Skovsted & Holmer 2003; Balthasar 2004), revealing a surprisingly rich record of early Cambrian potential stem group brachiopods (Skovsted et al. 2008, 2014; Holmer et al. 2008a; Zhang et al. 2014; Kouchinsky & Bengtson 2017; Sun et al. 2018).

The family Mickwitziidae, as used by Laurie (2000) and others (Skovsted & Holmer, 2003; and Balthasar 2004), includes 6 genera and 12 species (Table 1). It is probably not a monophyletic group but seemingly represent a paraphyletic group in the brachiopod stem lineage, which first appears (questionably) in Cambrian Stage 2 and extends into Stage 4 (Holmer & Popov 2007); the family has a cosmopolitan distribution of west Laurentia, Baltic and Australia (Schmidt 1888; Mount 1976; McMeinnam 1986; Geyer 1994; Rowell 1977; Nemliher 2001; Holmer et al. 2002; Skovsted & Holmer 2003; Balthasar 2004; Skovsted et al. 2009b; Devaere et al. 2014; Butler et al. 2015; Pan et al. 2019; Fig. 1).

The origin of the Brachiopoda has long been a hotly debated topic, and various models have been proposed following the latest finds of exceptionally preserved material. The lower Cambrian (Stage 3) *Heliomedusa orienta* from the Chengjiang Konservat-Lagerstätte, eastern Yunnan of South China, is an important example of exceptional preservation. A wide variety of affinities have been proposed for *Heliomedusa*, but recently it has been suggested to reside within the mickwitziids, which may form a stem group to the Brachiopoda. Detailed studies of exceptionally preserved *Heliomedusa* have increased our knowledge of the soft-part anatomy of this important early brachiopod, but unfortunately, almost nothing is known about its shell structure. Here, we describe new exceptionally preserved specimens from the Chengiang biota to better reveal both shell structure and ornamentation. Its reticulate-pustulose ornament and tubular structure are reminiscent of traits seen in other mickwitziid brachiopods. In addition, two types of setae can be observed. Apart from the pyritized marginal mantle setae, some tubes are filled with iron oxides, potentially representing thinner and shorter penetrative setae. Both valves of *H. orienta* appear to have been less mineralized as compared to *Mickwitzia monilifera*, and the two species differ in diameter and density of tubules and pustules, and in terms of slightly less projected profile of ventral valve with lower umbo posteromedially placed. Although *Heliomedusa* clearly is closely related to *Mickwitzia*, their different preservational modes (compacted poorly mineralized/noncompacted mineralized) make detailed comparison difficult; they are provisionally kept as separate genera pending further studies of better-preserved Chinese material.

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Among previous classifications of the phylum, Schuchert & Levene (1929, p. 11) placed *Mickwitzia* in the paterinids, an assignment adopted with reservation by Rowell (1965, P.H295). Later, it was tentatively excluded from the Brachiopoda by Laurie (2000, p. 156), in view of its enigmatic ‘punctae, three‐layered phosphatic shell’, as well as the lack of any unequivocal brachiopod character apart from the simple bivalved shell. Balthasar (2004) suggested the close relationship between *M. muralensis* (Mural Formation, Canada) and paterinids due to the similarities in their stratiform shell microstructure, parvicostellate ornament with occasional nick points, and posterior margin of juvenile and early‐mature shells. Skovsted & Holmer (2003), Skovsted et al. (2009b, 2010) described two new species (*Mickwitzia* sp. and *Setatella significans*) based on new materials from Australia and Greenland, respectively. The morphology of the dorsal valve apex and the extended cones on the internal surface of the Australian species indicate its close affinity with *M. muralensis* Walcott, 1913, which in turn makes the known range of the stem group brachiopod *Mickwitzia* extend to East Gondwana. *Setatella significans* differs from species of *Mickwitzia* in the presence of shell‐penetrating setae (open tubes) on the pseudointerarea and in the hemiperipheral growth in both valves. Butler et al. (2015) restudied *Mickwitzia occident* and suggested that the inwardly pointing cones are not consistent with the setal bearing structure as previously thought. Furthermore, the presence of acrotretid‐like shell structures and shell‐penetrating setae in *M. occident* strengthen the previously proposed close relationship between stem group brachiopods and tommotiids. Although numerous studies have been completed based on the material

| Family      | Genera       | Species                             | Occurrence                                                                 |
|-------------|--------------|-------------------------------------|-----------------------------------------------------------------------------|
| Mickwitziidae | *Mickwitzia* | *Mickwitzia monilifera* (Linnarsson, 1869) | File Haidar Fm., Mickwitzia Sandstone Member, Västergötland, Sweden          |
|             |              | *M. occident* Walcott, 1908          | Bastion Fm., Hudson Land, Northeast Greenland, Poleta Fm., Esmeralda County, Nevada, USA |
|             |              | *M. muralensis* Walcott, 1913        | Flinders Ranges (Arrowie Basin), Australia                                  |
|             |              | *M. lochmanae* n. sp. McNamara 1992 | Mural Fm., Rocky Mountains, Canada                                          |
|             |              | *M. multipunctata* n. sp. McNamara 1992 | Puerto Blanco Fm., White‐Inyo Mountains, California, USA                    |
| Kerberellus  | *Kerberellus* | *K. marcouensis* Devaere, Holmer, & Clausen, 2015 | Kallavere Fm., Kunda River, Estonia                                         |
| Microschedia | *Microschedia* | *M. amphitrite* Geyer (1994)         | Amouslek Fm., western Anti‐Atlas, Morocco                                   |
| Setatella    | *Setatella*   | *S. significans* Skovsted, Streng, Knight, & Holmer, 2010 | Bastion and Ella Island Fm., Greenland; Forteau Fm., Labrador               |
| Helomedusa   | *Helomedusa*  | *H. orienta* Sun & Hou, 1987         | Yuanshan Fm., Kunming, Yunnan Province, China                               |
| Paramickwitzia | *Paramickwitzia* | *boreussinaensis* Pan et al. 2019 | Xinji Fm., Ruicheng county, Shanxi Province, China                         |

Fig. 1. Palaeogeographical distribution of mickwitziids from early Cambrian (palaeogeographical map modified from Yang et al. 2015).
from different localities, the detailed research about shell structure and ornamentation of the type species, *M. monilifera*, still remains unclear apart from some brief studies (Schmidt 1888; Tynni 1982; Nemliher 2001; Holmer & Popov, 2007; Butler *et al.* 2015).

The enigmatic *Heliomedusa orienta* Sun & Hou, 1987, first identified as a jellyfish, is one of the most common species from the early Cambrian Chengjiang Konserat-Lagerstätte (Yuanshan Formation), eastern Yunnan of South China. Jin & Wang (1992) studied the specimens and reassigned it to the Craniida. Chen *et al.* (2007) restudied the morphology and organization of the enigmatic lophophore, which is composed of a pair of lophophoral arms that arch posteriorly rather than coiling anteriorly as commonly seen in fossil and recent lingulids, and the arms bear tentacles with a double row of cilia along their lateral edge, as in extant lingulid brachiopods. This unique organization of the lophophore in *Heliomedusa* demonstrates that this species is possibly a brachiopod stem group member (Zhang *et al.* 2009). In contrast, details of shell structural texture and ornament have never been reported, aside from the brief review in the latest version of Treatise (Holmer & Popov, 2007). New material described herein demonstrates that *Heliomedusa* is closely related to *Mickwitzia* based on their overall similarities in shell structure and ornamentation.

**Materials and methods**

Around 3000 specimens of *Heliomedusa orienta* were collected from eight localities in the SW of the Yangtze Platform by the team of the Early Life Institute (prefix: ELI) (see Zhang *et al.* 2009, fig. 1); all specimens are deposited in the collections of the institute. Most of the specimens examined here were derived from Jianshan section at Haikou area and Sanjiezi section at Jinning area.

The comparative materials of the type species of *Mickwitzia, Mickwitzia monilifera* (Linnarsson, 1869) come from lower Cambrian (Series 2, Stage 4) Mickwitzia Sandstone Member of the File Haidar Formation, near Lugnäs, Västergötland, Sweden (deposited in the collections of the Swedish Museum of Natural History, prefix: NRM).

Fossils were examined under a Zeiss Stemi 305 microscope and photographed with the Zeiss Smart Zoom 5 Stereomicrographic system and Cannon camera mounted on a photographic system. Some uncoated specimens were analysed with secondary electron microscope (SEM) and Backscatter Scanning Electron Microscope (BSEM) Quanta FEG 450, with attached energy-dispersive X-ray spectrometry (EDS) system, with 20.0 KV, 60Pa and WD 11.4 mm at the State Key Laboratory of Continental Dynamics, Northwest University, Xi’an. Thin sections were made in Shaanxi Key Laboratory of Early Life and Environments before they were photographed. Some specimens were tested by Bruker M4 Tornado tabletop energy-dispersive micro-X-ray fluorescence (μ-XRF) to get the characterization of the elemental abundances in samples from the fluorescence spectrum.

**Terminology**

**Dorsal/ventral valves**

Dorsal and ventral valves are difficult to identify with certainty in *Heliomedusa* This is largely both due to the complex compacted preservation of the available material and due to the lack of a pedicle, pedicle groove or cleft to accommodate a pedicle. The only inferred cast of a pedicle illustrated by Chen *et al.* (2007, figs 5, 6, 7) is without doubt a thickened visceral cavity (Zhang *et al.* 2008, fig. 4d; Zhang *et al.* 2009), and this type of preservation of the body cavity has been found in contemporaneous lingulid brachiopods (see: Zhang *et al.* 2005, fig. 1C). The most notable difference between the valves is the shape of the visceral cavity. In the dorsal valve, the visceral cavity is composed of two parts, a posterior subcircular area and an anterodorsal projection of the body wall (Zhang *et al.* 2009), which extends longer from the dorsal posterior margin than that in the ventral valve. In addition, the ventral valve could be distinguished from the dorsal valve in the former possessing a posteromedially pointing umbo, extending slightly beyond the posterior ventral margin, which ordinarily compressed and flattened into a triangular structure of ‘pseudointerarea’ as depicted in Zhang *et al.* (2008, 2009). It is in the ‘pseudointerarea’ that the reticulate–pustulose ornaments of the ventral umbo are remarkably revealed.

**Metamorphic shell**

The terminology used for describing the early ontogenetic stages of brachiopods have varied through time, and some common terms – including the protogulum, embryonic shell, first-formed shell and larval shell – have been used widely in different ways (Balinski 1997; Williams 2003; Popov *et al.* 2012, etc.). Here, we follow the terminology introduced by Zhang *et al.* (2018). The metamorphic shell is formed...
during metamorphosis and includes simultaneously secreted protegulum and the incrementally growing birethral shell. The length of the metamorphic shell of *H. orienta* is about 200 μm, which is similar to that of *Eohadrotreta zhenbaensis* and *Eohadrotreta? zhuji–ahensis* (Cambrian Series 2, Shuijingtuo Formation, Three Gorges area, South China) described by Zhang et al. (2018). However, we cannot clearly distinguish the boundary between the protegulum and birethral shell clearly due to the poor preservation in shale facies.

**Tubules and pustules**

Different terms have been used to describe various internal tubular shell structures in mickwitziids – inwardly pointing cones, punctae, tubules, tubular openings, etc. Balthasar (2004) pointed out that the term ‘punctae’ is deeply misleading, as the tubes of *Mickwitzia* are entirely distinct from brachiopod punctae. Real brachiopod punctae have an irregular lateral wall and are never associated with significantly inward bending shell layers (Owen & Williams 1969). In addition, among the mickwitziid material reported previously, only *Setatella significans* (Skovsted & Holmer 2003; Skovsted et al. 2010) exhibits acrotretoid-type columns, while *Mickwitzia muralensis* (Balthasar 2004), *Mickwitzia occidens* (Butler et al. 2015), *Paramickwitzia boreussinaensis* (Pan et al. 2019) and *Mickwitzia* sp. (Skovsted et al. 2009b) exhibit only shell-penetrating tubules, which are also found in *H. orienta* and *M. monilifera*. Therefore, ‘tubules’ are used to describe this structure herein.

A pustulose ornament is another distinctive feature of all described species of *Mickwitzia* (referred to as ‘papillose ornamentation’ by Walcott 1912 and McMenamin 1992), which is found on the outermost shell surfaces. The pustules form dome-like or cone-like structure in acid-etched shell fragments from limestone. However, as for *H. orienta* preserved in shale facies, pustules endured highly compression and preserved as a moulded reticulate ornament, as described by Zhang et al. (2008).

**Description of Heliomedusa orienta**

**General morphology and ontogeny**

The overall shape of shells of *Heliomedusa orienta* is ovate to subcircular with a ratio of shell length to width about 1.01 (*N* = 286) (Table 2). The length and width of the adult shells could reach 21.59 and 21.27 mm, respectively (Fig. 2). The ventral valve is more convex and has the apex located close to the shell margin (Fig. 3). The ventral valves exhibit both holoperipheral and mixoperipheral growth in different specimens (Fig. 3A–F). It is likely that dorsal valve, with a submarginal apex, is slightly convex to planar. The dorsal valve with subcircular posterior margin could be preserved to be allied well with the organization of the lophophore with palisades of tentacles (Fig. 4A–C). Specimens that are smaller than 4 mm are regarded as juveniles, some of which had developed marginal mantle (larval) setae in the plane of the shell (Fig. 3G–I). The metamorphic shell has diameter of about 200 μm, lacking any ornament (Fig. 3B, C, E, F). The boundary of the metamorphic shell and the post-metamorphic shell is indicated by the onset of costellate ornament (Fig. 3A–F).

**Ornamentation**

The reticulate–pustulose ornamentation could be observed in the posterior part of the shell (Fig. 3), extending one third of the shell length from the posterior margin. However, this ornamentation could not be discerned in the anterior part of the valve, possibly due to exfoliation or diagenetic loss of features. The distance between the crests of costellae is on average about 30 μm, and new costellae originate between neighbouring costellae. The domes in this ornament form pustules, separated by pits, with a diameter of 5–10 μm, forming the gaps between the pustules (Fig. 3A–F). The ornament in juvenile shells is composed of separated pustules arranged in straight, radiating rows (Fig. 3G–I), and the diameter of these pustules is around 20 μm, with the longitudinal distance between each pustule about 20 μm and each radiating row about 40 μm apart (Fig. 3H), which seems to be more dispersely arranged than that in adult shell. This ornament is closely comparable to the reticulate–pustulose ornament in

**Table 2. Average dimensions and ratios of valves of Heliomedusa orienta and Mickwitzia monilifera.**

|                | *H. orienta* |          |          |          |          |          |          |          |
|----------------|--------------|----------|----------|----------|----------|----------|----------|----------|
|                | Count        | L        | W        | L/4      | W/4      | L/W      | L4/L    | W4/W    |
| Min            | 238          | 3.08     | 2.66     | 0.97     | 0.81     | 0.69     | 0        | 0        |
| Max            | 29.9         | 21.27    | 11.65    | 11.02    | 1.38     | 0.62     | 0.72     |          |
| Mean           | 12.05        | 12.00    | 5.28     | 3.67     | 1.01     | 0.37     | 0.26     |          |
| SD             | 3.80         | 3.70     | 1.86     | 1.49     | 0.10     | 0.17     | 0.13     |          |

|                | *M. monilifera* |          |          |          |          |          |          |          |
|----------------|-----------------|----------|----------|----------|----------|----------|----------|----------|
|                | Count          | L        | W        | L/W      |          |          |          |          |
| Min            | 20             | 4.99     | 8.09     | 0.93     |          |          |          |          |
| Max            | 25.9           | 27.82    | 1.59     |          |          |          |          |          |
| Mean           | 19.66          | 18.09    | 1.10     |          |          |          |          |          |
| SD             | 4.57           | 4.26     | 0.13     |          |          |          |          |          |
**Mickwitzia occidens** (Butler et al. 2015, figs 5–8); however, they are more closely spaced in *Mickwitzia occidens*.

**Setae and tubules**

The marginal mantle setae are observed in some well-preserved specimens (Fig. 4A–E). These setae are 50 μm in diameter and up to 4 mm in length, and most of them are preserved as reddish-brown linear imprints, while some were biominalized and preserved in pyrite, with a distinct pseudomorphed frambooidal texture (Fig. 4E). The marginal setae are oriented in a radial fashion originating from the centrod, but with a posterior-facing tendency along the posterolateral margins (Fig. 4A–E). In addition, another type of pyritized setae – interpreted as representing penetrative setae herein – is broadly distributed across the whole valve (Fig. 4F–J). The diameter (about 20–40 μm) of the penetrative setae is thinner as compared with the marginal ones. These penetrative setae are supposed to be associated with (and possibly emerging from) tubules (Fig. 5), which sometimes only preserved on a small part of the shell (Fig. 5A–G), possibly due to exfoliation or the loss during diagenesis. The diameter of the tubules is about 20–40 μm, similar to the size of the penetrative setae. Some granular texture, preserved as iron oxides, could be observed inside the tubules, which possibly represent the proximal penetrative setae (Figs 5E–G, 6).

**Tubule distribution**

The density and mean distance of tubules vary between *H. orienta* and *M. monilifera* (Table 3). In *H. orienta*, the tubules have a higher density, about 65–77 in 1 mm², and the distances to the mean nearest neighbour range from 79 to 103 μm. However, the distribution of tubules in *M. monilifera* is comparatively more disperse, and the distance between neighbouring tubules is longer (about 267–277 μm).

**Comparisons**

To better understand the morphology and ultrastructure of *Heliomedusa orienta*, we studied specimens of the potentially related *Mickwitzia monilifera* from the lower Cambrian Mickwitzia sandstone of Västergötland, Sweden, for comparison (Fig. 7). The external reticulate–pustulose ornament in *M. monilifera* is similar to that of *H. orienta*, but one of the differences is that the ornament could be observed from the whole valve surface of *M. monilifera* (Fig. 7A, B, K–M). The average distance between the crests of costellae is about 50 μm, which is slightly wider than that in *H. orienta* (30 μm). At the posterior margin of the shell, where this ornament begins to radiate, there is an irregular zone potentially lacking any ornament, but unfortunately was exfoliated or covered by matrix in available specimens (Fig. 7B). Some pustules are likely arranged orderly in a row (Fig. 7L), while others seem to be randomly distributed, probably due to the early diagenesis. The diameter of the pustules (around 50 μm) is almost twice that of *H. orienta* (Fig. 7M). This ornament, typical of mickwitziids, is found on the outermost shell surface, and it becomes weaker with increasing degree of exfoliation. Most valves of the Swedish *M. monilifera* are much larger than *H. orienta* (Fig. 2). Some specimens are preserved three dimensionally, and the maximum height could reach 8mm (Fig. 7 N–P), but unfortunately these specimens preserve almost no information about setae, lophophore and other soft tissues which hinder the comparison between two species at the soft anatomy level. Moreover, due to the compacted and complex moulded preservation of all available material of *H. orienta*, the morphometric data are not comparable.

The tubules, one of the characteristic features among mickwitziids, are more pronounced and more widely distributed in *M. monilifera* (Table 3), the diameter of which is larger (about 50–70 μm) compared with that of *H. orienta* (about 40–50 μm). In addition, some tubules are encapsulated by secondary concentric phosphatic walls (Fig. 7G–J). These individual walls are 2–12 μm thick and typically become thicker outwards, and the separated walls are thought to be formed at different stages during shell secretion. The walls are separated by

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*Fig. 2. XY graph of the length and width of the shells of *Heliomedusa orienta* (N = 286) and *Mickwitzia monilifera* (N = 19).*
individual gaps that successively thicken outwards, which most likely represent originally organic membranes. These structures are closely comparable to those in *M. muralensis* and *M. occidens* described by Balthasar (2004, figs 7–9) and Butler *et al.* (2015, fig. 10.7), respectively.

Another significant difference is that the shells of *M. monilifera* are preserved in calcium phosphate as shown by the μ-XRF results of high abundance of calcium and phosphorus (Fig. 7D–F). From the cross sections of specimens of *M. monilifera*, it could be observed that the shell is about 600 μm thick (Fig. 8). In addition, tubules extend downwards about 800 μm, and some of these are likely to change in diameter along the length as they pass through the laminated shell layers (Fig. 8). At the interface of the tubules with the parallel lamellae, a pronounced inward bending of the phosphatic lamellae around the tubules was observed. Some exquisite pyrite framboids have been present along the laminated layers (Fig. 8D, E). These pyrite framboids can act as an indicator of redox conditions (Wilkin *et al.* 1996), and the size-frequency distribution of framboids found in *M. monilifera* may help us understand oxygen states of palaeo-waters, though this is outside the scope of this paper. Inside some tubules, a black cylinder could be observed; however, this structure only displays the loss of iron without any other elemental contrast (Fig. 8C, D, H).

**Discussion**

**Preservation and taphonomy**

The material of *H. orienta* exhibits Burgess Shale-type preservation of non-mineralized tissues (Butterfield 1995) in the fashion typical of the Chengjiang
deposits (Hou et al. 2017). Some chitinous setae and lophophore are preserved as iron oxides indicated by a high elemental abundance of iron compared with the matrix in μ-XRF and EDS observations (Fig. 4B). It is significant that Ca was not detected in any of the fossils, and a likely interpretation is that the alteration of pyrite to iron oxides released small quantities of sulphuric acid, which would have leached the calcium from phosphates (Gabbott et al. 2004). *H. orienta* is thought to have originally organophosphatic, but the original composition of the shell is invariably no longer present and in part is replaced by iron oxides during preservation as thin films (Figs 3–5), most of which cannot easily distinguished in cross, which possibly result from the relatively lower degree of mineralization of the shells.

Many specimens tend to split roughly between the two valves to reveal casts or moulds of the unmineralized lophophore and setae. In contrast, the shells of *M. monilifera* seem to exhibit higher biomineralization, and the thickness of the shell could reach 600 μm despite the loss of decay-prone periostracum and first-formed shell layers.

**Development and ontogeny**

The metamorphic shell, which has a diameter of about 200 μm and lacks any ornament, is the only early ontogenetic stage, which could be observed in *H. orienta*. It shows great similarity to *M. occidens* as interpreted by Butler et al. (2015, p. 951) as the ‘first-formed shell’ (200 μm in diameter; Butler et al. 2015,
Outside the metamorphic shell, the post-metamorphic shell exhibits the characteristics of the adult organism, the reticulate–pustulose ornament. Other early ontogenetic stages could not be observed in the material at hand due to the poor preservation in shale facies. Balthasar (2009) described two pairs of lobes on the metamorphic shell of *Mickwitzia muralensis* and interpreted them...
as the impression of setal sacs, but unfortunately these lobes could not be found in Chengjiang material. The transition from juvenile shell to mature shell in *H. orienta* is indicated by the gradual appearance of the reticulate–pustulose ornament, which is similar in *Setatella significans* as suggested by Skovsted & Holmer (2003). This metamorphosis suggests that the ontogenetic pattern was characterized by indirect development, and this may be plesiomorphic for all major brachiopod lineages, and probably evolved within the stem group brachiopods with subsequent heterochronic changes (Zhang *et al.* 2018).
Unlike most of other Chengjiang brachiopods, there is no trace of a pedicle found in any of the H. orienta specimens (Jin et al. 1993; Zhang et al. 2008). It is likely that juvenile H. orienta had a functional pedicle in early life, probably analogous to those of some ambitopic strophomenide taxa which lost their attachment and became relative thick-shelled which help avoid the danger of being swept away by currents or buried by sediment (Bassett 1984; Hoel 2014).

**Tubules and setae**

Interpreting the structure and function of tubules in mickwitziids remains difficult. Three models have been proposed. One is that the tubules are homologous to acrotretid-type columns, but this can be discounted due to apparent differences, such as the variable width of tubules in both H. orienta and M. monilifera compared to the near-constant diameter of acrotretid-type columns; in addition, the tubules have surrounding inwardly bending shell layers (Fig. 8) rather than orthogonal pillars interspersed between phosphatic layers in acrotretoid type. Another possibility is that they represent traditional brachiopod punctae (Walcott 1912, 1913; Rowell 1977; McMenamin 1992). However, the tubules of Mickwitzia are clearly distinct from brachiopod punctae as pointed out by Balthasar (2004), and he suggested that the tubular structures more likely to represent punctae-like outfolding of mantle tissue.
The third interpretation is that the tubules (‘inwardly pointing cones’) originally housed setae (Balthasar 2004). In Setatella significans (=Mickwitzia cf. occidentis sensu Skovsted & Holmer 2003), the longitudinal tubes located on the pseudointerareas are striated, which indicate the presence of setae (Skovsted et al. 2010). Such striated perforations also present in tannuolinid tommotiids Micrina, Tannuolina and Oymurania; (Holmer et al. 2008a; Skovsted et al. 2014; Kouchinsky, & Bengtson 2017), which have been interpreted as setigerous tubes, with corresponding casts of microvilli (Holmer et al. 2002; Williams & Holmer 2002). All perforations in M. muralensis are non-striated, orthogonally shell-penetrating tubes; however, Balthasar (2004) pointed out that the only known epithelial pockets in the mantle of brachiopods that could be associated with the smooth orthogonally shell-penetrating pores present in M. muralensis are setal follicles. Besides, the tubes are straight and similar in diameter to brachiopod setae. Under this interpretation, M. muralensis had both shell-penetrating tubules which hosted setae secreted by outer-epithelial follicles, and follicular setae occurring at the mantle margin, where they were oriented in the plane of the shell as in modern brachiopods (Balthasar 2004). According to the observations of new Mickwitzizidae species, Paramickwitzia boreusinaensis from North China, Pan et al. (2019) suggest that previously formed shell laminae exhibit cylindrical indentations in front of each tubule opening, which strongly indicate that these tubules were originally occupied by needle-like objects, the shell penetrative setae, extending from the shell.

As for Heliomedusa orienta, we also lack evidence of tubes with casts of microvilli or cylindrical indentations. However, the short linear pseudomorphed frambooidal pyrite observed on the shell and iron oxides inside the tubes (both are in the same diameter and are remarkably thinner compared to the marginal setae) indicate the existence of shell penetrative setae (Figs 4F–G, 5, 9). These setae are similarly thought to have been secreted by the inwardly bending outer-epithelial follicles (Fig. 9D; Balthasar 2004). As for Mickwitzia monilifera, penetrative setae or other soft tissues were not preserved in material at hand. However, there is a cylinder found inside the tubules (Fig. 8C), which indicate the possible
existence of the penetrative setae. The marginal mantle setae, one of the most prominent characters of *H. orienta*, are more common distinguished than penetrative setae. They are embedded in and secreted by follicles oriented within the plane of the shell at the shell margin which clearly do not penetrate the shell (Fig. 9C). Each new seta makes its appearance either within the follicle of an older seta and then branches off laterally forming its own follicle; or else it appears with its own follicle mid-way between two older setae (Rudwick 1970). In addition, the radiating costellae suggest repeated radiating folds of the mantle. Judging from their size and disposition, these folds are likely to represent initial setal follicles oriented within the plane of the shell.

**Affinity of Heliomedusa**

All Chengjiang materials of *Heliomedusa* are invariably preserved as shale-hosted complex compressed moulds, while most specimens of *Mickwitzia* were preserved three dimensionally in limestone and sandstone, which make the detailed comparison including comparative biometric data difficult to obtain. Based on overall similarities in shell morphology, ornamentation and structure, it is reasonable to presume that *Heliomedusa* is closely related to *Mickwitzia*, while some detailed differences still remain obvious. Firstly, the diameter and distance of pustules in *H. orienta* (20 μm; 20 μm) are smaller than that of *M. monilifera* (40 μm; 100 μm), and tubules are significantly more closely distributed in *H. orienta* (Table 3). Furthermore, the lower mineralization of the shells of *H. orienta* is supported by preservation of displaced valves with soft sediment intruded, accompanied by the organization of the exquisite lophophore, while almost no information about lophophore or other internal soft tissues demonstrated in all *Mickwitzia* species. Although it has been suggested that *Heliomedusa* is a junior synonym of *Mickwitzia* (Butler et al. 2015), this can only be solved by thorough comparison of better-preserved material, especially three dimensionally preserved *Heliomedusa*. Accordingly, the authors would like to take a conservative view and provisionally keep them as separate genera, pending further studies of better-preserved Chinese material. Furthermore, the usage of more advanced techniques, synchrotron X-ray tomographic microscopy, for example, in both *Heliomedusa* and *Mickwitzia* should be employed to further examine the affinities of these intriguing and important taxa.

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**References**

Balinski, A. 1997: Evolution of the embryonic development in lingulid brachiopods. *Acta Palaeontologica Polonica* 42, 45–56.

Balthasar, U. 2004: Shell structure, ontogeny and affinities of the Lower Cambrian bivalved problematic fossil *Mickwitzia muralensis* Walcott, 1913. *Lethaia* 37, 381–400.

Balthasar, U. 2009: The brachiopod *Eoobola* from the early Cambrian Mural Formation (Canadian Rocky Mountains). *Palaeontologische Zeitschrift* 83, 407–418.

Bassett, M.G. 1984: Life strategies of Silurian brachiopods. *Special Papers in Palaeontology* 32, 237–263.

Budd, G.E. & Jensen, S.A. 2000: A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Reviews* 75, 253–295.

Butler, A.D., Streng, M., Holmer, L.E. & Babcock, L.E. 2015: Exceptionally preserved *Mickwitzia* from the Indian Springs Lagerstätte (Cambrian Stage 3), Nevada. *Journal of Paleontology* 89, 933–955.

Butterfield, N.J. 1995: Secular distribution of Burgess-Shale-type preservation. *Lethaia* 28, 1–13.

Chen, J.Y., Huang, D.Y. & Chuang, S.H. 2007: Reinterpretation of the Lower Cambrian brachiopod Heliomedusa orienta Sun and Hou, 1987 as a discinid. *Journal of Paleontology* 81, 38–47.

Clark, P.J. & Evans, F.C. 1954: Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35, 445–453.

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 & Evolution* 5, 253–273.

Cohen, B.L., Holmer, L.E. & Lüter, C. 2003: The brachiopod fold: a neglected body plan hypothesis. *Palaeontology* 46, 59–65.

Devaere, L., Holmer, L.E., Claussen, S. & Yachard, D. 2014: Oldest mickwitziid brachiopod from the Terreneuvian of southern France. *Acta Palaeontologica Polonica* 60, 755–768.

Dunn, C.W., Heijno, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., Sørensen, M.V., Haddock, S.H.D., Schmidt-Rhaesa, A., Okusu, A., Kristensen, R.M., Wheeler, W.C., Martindale, M.Q. & Gribet, G. 2008: Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452, U745.

Gabbott, S.E., Hou, X.G., Norry, M.J. & Siveter, D.J. 2004: Preservation of Early Cambrian animals of the Chengjiang biota. *Geology* 32, 901–904.

Geyer, G. 1994: An enigmatic bilateral fossil from the Lower Cambrian of Morocco. *Journal of Paleontology* 68, 710–716.

Halanych, K.M., Bacherell, J.D., Aguinaldo, A.M., Liva, S.M., Hillis, D.M. & Lake, J.A. 1995: Evidence from 18s ribosomal DNA that the lophophorates are protostome animals. *Science* 267, 1641–1643.

Harper, D.A.T., Popov, L.E. & Holmer, L.E. 2017: Brachiopods: origin and early history. *Palaeontology* 60, 609–631.

Hoel, O.A.: 2014: Palaeobiology of Silurian Leptaeninae (Brachiopoda) from Gotland, Sweden. *Palaeontology Journal* 2014, 1–14. https://doi.org/10.1155/2014/716053

Holmer, L.E. & Popov, L.E. 2007: Organophosphatic bivalve stem-group brachiopods. *In Williams, A., Brunton, C.H.C. & Carlson, S.J.* (eds): Treatise on Invertibrate paleontology, *Part...*
Early Cambrian brachiopod Heliomedusa orienta

H. Brachiopoda (Revised), volume 6, 2581–2590. Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.

Holmer, L.E., Skovsted, C.B. & Williams, A. 2002: A stem group brachiopod from the Lower Cambrian: support for a Micrina ( halkieriid) ancestry. Palaeontology 45, 875–882.

Holmer, L.E., Skovsted, C.B., Brock, G.A., Valentine, J.L. & Pater- son, J.R. 2008a: The Early Cambrian tommotoid Micrina, a ses- sile bivalved stem group brachiopod. Biology Letters 4, 724–728.

Holmer, L.E., Popov, L.E. & Streng, M. 2008b: Organophosphatic stem group brachiopods: implications for the phylogeny of the subphylum Linguliformea. Fossils and Strata 34, 3–11.

Hou, X.G., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Cong, P.Y., Gabbott, S.E., Ma, X.Y., Purnell, M.A. & Williams, M. 2017: The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, 2nd edn, 316 pp. Wiley-Blackwell, New York.

Jin, Y.G. & Wang, H.Y. 1992: Revision of the Lower Cambrian brachiopod Heliomedusa Sun & Hou, 1987. Lethaia 25, 35–49.

Jin, Y.G., Hou, X.G. & Wang, H.Y. 1993: Lower Cambrian pedicu- late lingulids from Yunnan, China. Journal of Paleontology 67, 788–798.

Kouchinsky, A. & Bengtson, S. 2017: X-ray tomographic micro- scope tightens affinity of the early Cambrian Oymurania to the brachiopod stem group. Acta Palaeontologica Polonica 62, 39–43.

Laurie, J.R.2000: Class Paterinata. Invertebrate Paleontology. Part H. Brachiopoda

Mémoires (Series 7) 36, 1–27.

Schuchert, C. & LeVene, C.M. 1929: Brachiopoda (generum et genotyporum index et bibliographia). In Pompejki, J.F. (ed): Fossilium Catalogus, volume I, Animalia, Pars 42, 144 pp. W. Junk, Berlin.

Sepkoski, J.J. 1981: A factor analytic description of the Phanero- zoic marine fossil record. Paleobiology 7, 36–53.

Sepkoski, J.J. 1984: A kinetic model of Phanerozoic taxonomic diversity; III. Post-Palaeozoic families and mass extinctions. Paleobiology 10, 246–267.

Skovsted, C.B. & Holmer, L.E. 2003: The Early Cambrian (Boto- mian) stem group brachiopod Mickwitzia from Northeast Greenland. Acta Palaeontologica Polonica 48, 1–20.

Skovsted, C.B., Brock, G.A., Paterson, J.R., Holmer, L.E. & Budd, G.E. 2008: The scleritome of Excentrotheca from the Lower Cambrian of South Australia: Lophophorate affinities and implications for tommotiid phylogeny. Geology 36, 171–174.

Skovsted, C.B., Holmer, L.E., Larsson, C.M., Högström, A.E.S., Brock, G.A., Topper, T.P., Balthasar, U., Stolk, S.P. & Paterson, J.R. 2009a: The scleritome of paterimitra: an early Cambrian stem group brachiopod from south Australia. Proceedings of the Royal Society B: Biological Sciences 276, 1651–1656.

Skovsted, C.B., Brock, G.A., Holmer, L.E. & Paterson, J.R. 2009b: First report of the early Cambrian stem group brachiopod Mickwitzia from East Gondwana. Gondwana Research 16, 145–150.

Skovsted, C.B., Streng, M., Knight, I. & Holmer, L.E. 2010: Setatella signiflans, a new name for mickwitziid stem group bra- chiopods from the lower Cambrian of Greenland and Labrador. GFF 132, 117–122.

Skovsted, C.B., Clausen, S., Álvaro, J.J. & Ponleve, D. 2014: Tommotids from the early Cambrian (Series 2, Stage 3) of Morocco and the evolution of the tannuolinid scleritome and setigerous shell structures in stem group brachiopods. Palaeontology 57, 171–192.

Sun, W.G. & Hou, X.G. 1987: Early Cambrian medusae from Chengjiang, Yunnan, China. Acta Palaeontologica Sinica 26, 257–270.

Sun, H.J., Smith, M.R., Zeng, H., Zhao, F.C., Li, G.X. & Zhu, M.Y. 2018: Hyoliths with pedicles illuminate the origin of the bra- chiopod body plan. Proceedings of the Royal Society B: Biological Sciences 285, 20181780.

Tynni, R. 1982: New results of studies on the fossils in the Lower Cambrian sediments of the Söderfjärden Basin. Bulletin of the Geological Society of Finland 54, 57–68.

Walcott, C.D. 1913: New Lower Cambrian subfauna. Proceedings of the Geological Society of America 23, 845.

Yang, B., Steiner, M. & Keupp, H. 2015: Early Cambrian palaeo- biography of the Zhenba-Fangxian Block (South China): independent terrane or part of the Yangtze Platform? Gond- wana Research 28, 1543–1565.

Zhang, Z.F., Shu, D.G., Han, J. & Liu, J.N. 2005: Morpho-anatom- ical differences of the Early Cambrian Chengjiang and Recent lingulids and their implications. Acta Zoologica 86, 277–288.

Zhang, Z.F., Robson, S.P., Emig, C.C. & Shu, D.G. 2008: Early Cambrian radiation of brachiopods: A perspective from South China. Gondwana Research 14, 241–254.
Zhang, Z.F., Li, G.X., Emig, C.C., Han, J., Holmer, L.E. & Shu, D.G. 2009: Architecture and function of the lophophore in the problematic brachiopod *Heliomedusa orienta* (Early Cambrian, South China). *Geobios* 42, 649–661.

Zhang, Z.F., Li, G.X., Holmer, L.E., Brock, G.A., Balthasar, U., Skovsted, C.B., Fu, D.J., Zhang, X.L., Wang, H.Z., Butler, A., Zhang, Z.L., Cao, C.Q., Liu, J.N. & Shu, D.G. 2014: An early Cambrian agglutinated tubular lophophorate with brachiopod characters. *Scientific Reports* 4, 4682.

Zhang, Z.L., Popov, L.E., Holmer, L.E. & Zhang, Z.F. 2018: Earliest ontogeny of early Cambrian acrotretoid brachiopods — first evidence for metamorphosis and its implications. *BMC Evolutionary Biology* 18, 42.