**A hyolithid without helens preserving the oldest hyolith muscle scars; palaeobiology of
Paramicrocornus from the Shujingtuo Formation (Cambrian Series 2) of South China**

By: Zhi-liang Zhang^{a,b}, Christian B. Skovsted^{a,c} and Zhi-fei Zhang^{a,*}

^a Early Life Institute, State Key Laboratory of Continental Dynamics and Department of Geology,
Northwest University, Xi'an, 710069, China; elizf@nwu.edu.cn or zhangelle@126.com

^b Department of Earth Sciences, Palaeobiology, Uppsala University, Villavägen 16, SE-752 36
Uppsala, Sweden; zhangtensor@hotmail.com

^c Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05
Stockholm, Sweden; christian.skovsted@nrm.se

* Corresponding author. E-mail address: elizf@nwu.edu.cn (ZF Zhang)

Abstract:

The hyolithid *Paramicrocornus zhenbaensis* from the lower Cambrian (Cambrian Series 2) Shujingtuo Formation of southern Shaanxi and western Hubei provinces of the Yangtze Platform is well-preserved in three dimensions. The morphology of the conch and operculum of *P. zhenbaensis* shows that this species lacked helens, which are considered to be characteristic of hyolithids and hence *Paramicrocornus* may belong to a sister group of other hyolithids. The shell structure of *P. zhenbaensis* reveals close similarities to the shell structure of other hyolithids. Furthermore, the smaller size and non-radial orientation of tubules in the shell structure of the operculum also differ from that in orthothecid hyoliths, suggesting that this characteristic may be used to differentiate hyolithids and orthothecids. The phosphatized opercula of *P. zhenbaensis* exhibit a pair of muscle scars located close to the apex of the internal surface. These muscle scars, as well as similar structures

in other hyolithids, probably served as attachment sites of muscles controlling the retraction of the tentaculate feeding organ recently discovered in hyolithids. Without helens, *P. zhenbaensis* may have been sessile with the conch partly buried in the sea floor.

Key words: Operculum, Hyolithida, Tentaculate feeding organ, Functional morphology, Shell structure, Yangtze Platform

1. Introduction

The Yangtze Platform provides a detailed Ediacaran-Cambrian geological record of the Cambrian explosion and the first major diversification event in metazoan history (Zhu et al., 2007; Zhang et al., 2016a). Hyoliths are among the most common skeletal fossils occurring at the beginning of Cambrian, and constitute an important component of the Cambrian Evolutionary Fauna (Sepkoski, 1984; Stanley, 2007). Hyoliths are Paleozoic benthic organisms with a cone-shaped conch and a lid-like operculum (Marek, 1963, 1967). The group is commonly divided into two morphologically distinct groups, Hyolithida (Sysoev, 1957) and Orthothecida (Marek, 1966), which are usually regarded as orders. Hyoliths experienced a rapid evolutionary diversification during the early part of the Cambrian and were a conspicuous element of the benthic fauna throughout the Cambrian and Ordovician (Qian et al., 1999). The group survived until the end of Permian, however they were only a minor component of the benthic fauna in post-Ordovician assemblages (Marti Mus and Bergström, 2007; Marti Mus et al., 2014). Hyoliths represent a unique opportunity to investigate the evolution of Cambrian taxa as they are common constituents of both exceptionally preserved faunas (such as the Burgess Shale and the older Chengjiang Fauna) and the so called Small Shelly Fossil (SSF) faunas. However the biology and phylogeny of hyoliths is still unclear (Marek and Yochelson, 1964; Runnegar, 1980; Valent, 2004; Sun et al., 2016), despite their abundant and global fossil record.

The biology and phylogenetic positions of hyoliths have long been debated. Originally, hyoliths were considered to be planktonic gastropods (pteropods) by Barrande (1847). Later, Yochelson (1961) and Dzik (1978) considered them to represent a new class among mollusks, based on the morphology and the structure of the conch. Well preserved U-shaped gut configurations inside the conch have been used to support an inferred sister-group relationship between sipunculans and hyoliths (Sun et al 2016). However, Runnegar et al. (1975) and Kouchinsky (2000) suggested that the morphology and microstructure of hyoliths excludes all the above assumptions, and supports the placement of hyoliths in a separate phylum (for a detailed summary of the history of hyolith research see Malinky and Yochelson, 2007). Recently, the conclusion that hyoliths belong to the Lophophorata total group (and are closely related to brachiopods), was based on the discovery of an extendable, gullwing-shaped lophophore in hyolithid specimens from the Burgess Shale and Spence Shale Lagerstätten (Moysiuk et al., 2017). However, the presence of a lophophore in hyolithid hyoliths is difficult to reconcile with the relatively common sediment filled guts of orthothecids hyoliths (Thoral, 1935; Devaere et al., 2014 and references therein). Moreover, the distinction between the two main hyolith groups is based mainly on Ordovician taxa (Sysoev, 1957, Marek, 1966). It has been noted that many of the early hyoliths from the Cambrian exhibit combinations of characters typical of both orders and that a considerable number of taxa are difficult to place in the established taxonomical framework (Dzik, 1994, Malinky and Skovsted, 2004, Skovsted et al., 2016). Consequently, more hyolith taxa need to be investigated before we can fully understand their biology or phylogeny.

Herein, we describe abundant and well preserved hyolith fossils from the Shuijingtuo Formation of the Zhenba region of southern Shaanxi and Aijiahe in the Three Gorges area of western Hubei province in South China. Hyoliths were previously reported from these regions by Qian (1978), Wang et al. (1987), Qian et al. (1999, 2001), Xie (1988), Wang et al. (2010), Yang et al. (2015) and Zhang et al. (2016a). The new material is dominated by the species *Paramicrocornus zhenbaensis* Qian, Xie and He, 2001. Although most aspects of its morphology clearly indicates that *P. zhenbaensis* is a hyolithid, we demonstrate that it could not have had any helens, previously thought to be characteristic of the Order Hyolithida (Marek, 1963, 1967; Marti Mus and Bergström, 2005, 2007; Marti Mus et al.,

2014). This observation indicate that *P. zhenbaensis* may occupy a sister group position relative to other hyolithids. The opercula of this hyolithid species also preserve the oldest known hyolith muscle scars, and we show that their likely function was to control the position of the lophophore-like organ recently demonstrated in hyolithids (Moysiuk et al. 2017).

2. Geological setting

Neoproterozoic to Palaeozoic strata are well developed and distributed in the southern Shaanxi and western Hubei regions. The hyolith conchs and opercula described here were collected from the lower part of the Shuijingtuo Formation at the Xiaoyangba section, in Xiaoyang village, approximately 10 km southeast of Zhenba County, southern Shaanxi (Fig. 1B) and from the Aijiahe section, close to the village of Aijiahe, 10 km southwest of Sandouping town of Yichang, western Hubei Province (Zhang et al., 2016a, Fig. 1C). Both localities are located on the northern part of the Yangtze Platform (Fig. 1A). At the Xiaoyangba section, the Precambrian-Cambrian stratigraphic succession is especially well exposed along the river, comprising the Dengying Formation, Shuijingtuo Formation, Shipai Formation and Shilongdong Formation in ascending order (Fig. 1C). At the top of Dengying Formation, there exists ca. 8.4-m-thick Xihaoping Member, composed of dark grey fossiliferous limestones interbedded with silty dolostones. Disconformably overlying the Xihaoping Member of the Dengying Formation, the 81-m-thick Shuijingtuo Formation can be subdivided into two parts. The lower Shuijingtuo Formation consists of dark, thin silty limestones, while the upper part is composed of siltstones interbedded with thin limestones. Abundant phosphatized fossils have been reported from the Xihaoping Member and Shuijingtuo Formation at the Xiaoyangba section, including hyoliths (Xie, 1988, Qian et al., 2001), brachiopods (Li and Holmer, 2004) and other small shelly fossils (Li and Ding, 1995, Steiner et al., 2004, Yang et al., 2015). The Redlichiid trilobite *Eoredlichia* was reported from the Xiaohaoping Member, although a detailed description has not been published (Xie, 1988). Many specimens of the eodiscoid trilobite *Tsunyiidiscus niutitangensis* (Chang, 1964) have been documented in the Shuijingtuo Formation frequently associated with the brachiopods *Palaeobolus*,

Eohadrotreta and *Lingulellotreta* (Li and Holmer, 2004, Yang et al., 2015, Zhang et al., 2016a). In light of trilobite-based biostratigraphy, the Xihaoping Member has been correlated with Cambrian Stage 3 (Qian et al., 1999, Li and Holmer, 2004), and thus the lower Shuijingtuo Formation may correspond chronostratigraphically to Stage 4 (Shu, 1990, Zhang et al., 2016a). However, the exact boundary level between Cambrian Stage 3 and Stage 4 at the Xiaoyangba section is difficult to determine and is potentially missing, as there is a significant hiatus in the basal part of the Shuijingtuo Formation.

At the Aijiahe section, the Shuijingtuo Formation can be subdivided into three parts, with the basal-most part (10 m thick), characterized by condensed black shale intercalated with black limestone concretions up to ca. 1 m across. The oldest trilobite *Tsunyiidiscus actus* in this region first appears ca. 3-5 m above the limestone concretions (Wang et al., 1987; Lin et al., 2004; Dai and Zhang, 2011). Above the black shale and concretions, the depositional succession in the middle of the formation (40 m thick) is represented by alternating black shales and thin-bedded limestones yielding abundant skeletal fossils including trilobites, lingulate brachiopods, archaeocyaths, hyoliths, and sponge spicules, (Zhang, 1953; Wang et al., 1987; Li and Holmer, 2004; Wang et al., 2010; Yang et al., 2015; Zhang et al., 2016a, b). The uppermost part of the formation consists of greyish-black medium-thin laminated argillaceous limestone (about 20 m thick) with sparse fossil fragments.

3. Material and methods

Thousands of hyolith conchs and opercula were recovered through acetic acid (~10%) preparation of samples from thin-bedded bioclastic limestones collected from the lower Shuijingtuo Formation at the Xiaoyangba section in Xiaoyang village, Southern Shaanxi. Specimens were manually picked from the acid-resistant residues and selected specimens were studied further using SEM facilities at Northwest University and Uppsala University. Additional material was collected from the Shuijingtuo Formation at the Aijiahe section in the Three Gorges Area (Zhang et al., 2016a, b) and studied using the same methods. The terminology and orientation of the hyolith conchs and opercula follows that

established by Marek (1963, 1967) and Marti Mus and Bergström (2005). Measurements of the length and width of the opercula as well as the length of the cardinal processes and height of clavicles and their angle of divergence were made on the best preserved specimens of the most abundant species (Table 1). Scatter plots showing the length/width ratio and the length of the cardinal process in relation to length and the length and height of the clavicles in relation to length were constructed (Fig. 2).

For comparative reasons, we have also studied internal moulds of hyolith opercula from the Bastion Formation of northeastern Greenland (Cambrian Stage 4; see Malinky and Skovsted, 2004 and Skovsted, 2006 for age and locality details) preserved in a similar manner to the specimens from the Shujingtuo Formation. The hyolith fauna of the Bastion Formation contains a number of hyolithid taxa (Malinky and Skovsted, 2004) and it is not possible to securely determine which species the specimens illustrated here belong to. However, the elongated sub-apical projection (representing a mould of the furrow between the cardinal processes) resembles the construction of the opercula described by Malinky and Skovsted as *Parkula?* sp. (Malinky and Skovsted, 2004, Fig. 4C, D) and we tentatively refer the specimens to this species.

4. Hyoliths from the Shujingtuo Formation

The hyolith material from the Shujingtuo Formation in our collection contains both opercula and often fragmentary conchs. The specimens are preserved by secondary phosphatization through epitaxial coating of the shell surface, sometimes with the outermost shell layers partly replaced by phosphate. However, the internal shell surface is typically much more strongly phosphatized and the external surface is often broken or completely removed, resulting in specimens representing a negative (mould) of the internal surface of the operculum (Figs. 3-5). The apical part of conchs are often preserved as internal moulds as well (Fig. 6A-C).

All complete conchs in our collections from Xiaoyangba section are identified as belonging to *Paramicrocornus zhenbaensis* Qian, Xie and He, 2001 (Fig. 6) while the opercula of two different species are present. The majority of specimens in this collection are interpreted to represent the

opercula of *P. zhenbaensis* (Figs. 3-7). Opercula of *P. zhenbaensis* were not described by Qian et al. (2001) in the original description of the species. However, these authors referred to specimens identical to the opercula discussed herein as *Conothea*? sp. As described below, these opercula match the conch morphology of *P. zhenbaensis* in size, outline and shape of the aperture. Conchs of a similar morphology were illustrated as *Diperygovitus lentiformis* (Qian, 1978) by Yang et al. (2015, Fig. 8N) together with conchs of a similar shape but with a more pronounced protoconch that were referred to *Microcornus parvulus* Mambetov, 1972 (Yang et al. 2015, Fig. 8K-M). From the same deposit, Yang et al. (2015, Fig. 8R) also illustrated opercula identical to those of *P. zhenbaensis* as unidentified “disarticulated hyolithid operculum”. Despite minor differences in preservation the material from Aijiahe section is closely similar to the new collections from Xiaoyangba section and represents the same hyolith taxa (Fig. 8).

A second hyolith operculum is represented by a few specimens in our collections from Xiaoyangba section. This operculum is sub-circular in outline and has an almost flat dorsal surface without clear differentiation of conical and cardinal shields (Fig. 9). This operculum lacks differentiated cardinal processes but exhibits strongly developed blade-like clavicles. Opercula of a similar morphology were illustrated by Qian and Zhang (1983) as Aimitidae indet. (Qian and Zhang. 1983, pl. 1, Fig. 1) and moulds of comparable morphology were illustrated by Yang et al. (2015, Fig. 8L, M, O) inside the aperture of conchs referable to both *Microcornus parvulus* (Mambetov, 1972) and *Cupithea mira* (He in Qian, 1977). Due to the small number of specimens, imperfect preservation and uncertain affinity, we refer these specimens to Hyolith operculum A (Fig. 9), although we note that the sub-circular outline and lack of differentiated cardinal processes and clavicles indicate this is an orthothecid hyolith.

5. The morphology of *Paramicrocornus zhenbaensis*

5.1. Conch

The conchs of *Paramicrocornus zhenbaensis* are slender and slowly expanding, with an asymmetrical lenticular or sub-triangular cross section with flattened ventral and gently domed dorsal sides (Fig. 6A, B). The dorsum lacks a median ridge and other types of longitudinal ornaments (Fig. 6B3). The dorsal apertural edge is straight and the semi-circular ventral ligula is very short (Fig. 6A1, B1). There are no slit-like openings or lateral sinuses at the dorso-ventral transition of the conch. The initial part of the conch appears to be a simple apex without clearly delineated protoconch. The only external ornaments are fine transverse growth lines; straight across the dorsum and gently arched towards the aperture on the ventral surface to mirror the shape of the ligula. Internal moulds of conchs exhibit a spoon-shaped depression close to the apex, presumably representing an internal shell thickening on the ventral side of the conch (Fig. 6A3, C).

5.2. Operculum

The opercula of *Paramicrocornus zhenbaensis* are oval in dorsal outline, 0.5- to 1.7-mm-long and 0.7- to 2.1-mm-wide (length/width ratio 0.70 to 0.83; average 0.78; N = 33; see Table 1, Fig. 2A) with a domed conical shield and a narrow, poorly developed cardinal shield (Fig. 3A-C). No rooflets are developed, and the border between cardinal and conical shields is a gentle bend, not a sharp furrow (Fig. 3C1, E1). The external surface is ornamented by fine growth lines (Fig. 6D). On the internal surface the opercula exhibit a pair of narrow cardinal processes clearly separated from the high, blade-like clavicles by a deep but narrow gap (Fig. 3C3, D).

The cardinal processes have a triangular base and a laterally flattened blade-like termination ornamented by a row of 3-7 short, rounded pustules (Fig. 4B, J, L). The length of the processes increase proportionally with specimen size up to a maximum length of 450 μm (Fig. 2C) (average process length/total length 0.27; N = 15; Table 1). The cardinal processes attach close to the apex of the conical shield and diverge by 49° to 66° (average 57°; N = 27; Table 1).

The clavicles extend laterally from the base of the cardinal processes, terminating close to the widest part of the operculum (Fig. 4A, D). The angle between the clavicles is 67° to 83° (average 74°;

N = 16; Table 1) and this angle appears to increase slightly with specimen size. The length of the clavicles varies from 0.1 to 1 mm but their relative length clearly increases with specimen length (length of clavicles/total length varies from 0.24 to 0.52 in specimens under 1 mm long and 0.43 to 0.6 in larger specimens; Table 1, Fig. 2B). The height of the clavicles is greatest close to the cardinal processes and decreases gradually toward the lateral termination (Fig. 3A1, C3). The clavicles are composed of a number of parallel tubular or rod-shaped elements that expand in width towards the lateral termination (Fig. 4G, H). The number of rod-shaped elements increases with specimen length, varying from 5 with a maximum length of 0.7 mm to 15 with maximum length of 1.1 mm (Fig. 4C, H-J). The borders between rods are reflected by narrow walls on the internal moulds showing that the diameter of the rods increase from about 10 or 20 μm close the apex to about 50 μm at the lateral termination (Fig. 4F-H). Close to the crest of the clavicles the rods appear to be separated, forming a row of short spines or cone-shaped pustules (Fig. 4I-K, M).

Close to the summit, many internal moulds exhibit a pair of pustules. The pustules are located on the inner slope of the combined base of the cardinal processes, and close to the ridge representing the gap between the cardinal processes and the clavicles (Fig. 5A-E). The pustules are 20-50 μm wide and may be up to 50 μm high (Figs. 5I, 8F), the size increasing with specimen width. The shape of the pustules is variable, from low, rounded structures to flattened triangular projections. The apical pustules on the internal moulds represent shallow depressions on the internal surface of the original operculum. We interpret these structures as muscle scars located close to the internal summit of the operculum. Associated with the pustules are in some cases shallow depressions close to the base of the clavicles or reticulate micro ornaments (diameter of individual cells approximately 5 μm) (Figs. 5J, K, 7B).

5.3. Shell structure

The shell structure of *Paramicrocornus zhenbaensis* is exposed in well preserved phosphatized conchs and opercula. The shells of both skeletal components show very similar structures and are

composed of two layers. The outer layer preserves fine external growth lines (Fig. 6D, G) and is about 10 to 25 μm thick. The outer shell itself is poorly preserved but narrow tubules are often found perforating the shell. The tubules, represented by elongate columns of phosphate, are vertically oriented in relation to the shell surface of the conch (Figs. 6C, 7E). However, in some specimens longitudinally oriented fibers can be observed on the external surface of the conch (Fig. 6F). In the operculum, as illustrated by specimens from the Three Gorges area (Fig. 8H), these columnar structures are often slightly curved. Columns, about 1 μm in diameter, 10-20 μm long, penetrate both the outer and inner shell layers (Fig. 7C). They tend to be inclined and easily broken, leaving small tubercles on moulds of the inner surface of the operculum (Fig. 7D, G). The internal surface of the conch and operculum sometimes preserve imprints of fine transverse fibers, about 1 μm in width (Figs. 6E, 7F). No pore channels are observed between the fibers. Concentric ornamentation of growth lines can sometimes be observed on the internal surface of the inner layer of the conch (Fig. 6H).

6. Discussion

6.1. *A hyolithid without helens*

The commonly accepted defining characteristics of hyolithids are the sub-triangular cross section of the conch with a ventral ligula, the division of the operculum into conical and cardinal shields, the presence of both cardinal processes and clavicles on the interior of the operculum as well as the presence of a pair of helens (Valent, 2004; Marti Mus et al., 2014 and references therein). Helens are a third kind of spine- or oar-like lateral skeletal element that projects between the conch and operculum (Marti Mus and Bergström, 2005, 2007; Marti Mus et al., 2014) which are not known to occur in orthothecid hyoliths.

Although hyolithid helens are uncommon as fossils due to their delicate nature, their insertion between the conch and operculum leaves traces in the form of lateral sinuses close to the border between dorsal and ventral sides of the conch and close to the junction of cardinal and conical shields in the operculum, the latter is often reflected as rooflets on the exterior surface of the operculum

(Valent, 2004; Marti Mus and Bergström, 2005, 2007, Marti Mus et al., 2014). On the internal side of the operculum, the helens extend between the cardinal processes and clavicles where softly curved gaps accommodate the base of the helens (Marti Mus and Bergström, 2005; Marti Mus et al., 2014). In *Paramicrocornus zhenbaensis*, no sinus is present anywhere along the aperture of the conch (Fig. 6A, B) and no rooflets or lateral sinuses are found in the operculum (Figs. 3C, 8C). In addition, the high, blade-like clavicles reach their highest point close to the cardinal processes, leaving almost no gap to accommodate the internal part of helens (Figs. 3A-D, 4A, I), at least in larger specimens (Figs. 3E2, 4D). Our conclusion, based on these observations, is that *P. zhenbaensis* likely lacked helens or any comparable laterally projecting skeletal elements. However, in all other respects, *P. zhenbaensis* conforms closely with the morphology of hyolithids (sub-triangular cross-section, ligula, distinct cardinal and conical shields in operculum, separate cardinal processes and clavicles). This conclusion has great impact on interpretations of the functional morphology and the evolution of hyoliths.

The division of hyoliths into hyolithids and orthothecids is widely accepted in the literature (Marek, 1967; Valent, 2004; Malinky and Yochelson, 2007 and references therein), although difficulties in correctly placing Cambrian hyoliths into these categories have been noted (Malinky and Skovsted, 2004; Skovsted et al., 2004, 2014, 2016). The discovery of hyolithids lacking the characteristic helens add further proof that early Cambrian hyoliths do not conform well with the established concepts of hyolith morphology. One possible conclusion is that *Paramicrocornus zhenbaensis* belongs to a group of Cambrian hyoliths that represent a sister group of hyolithids as conventionally defined. Rooflets and lateral sinuses that indicate the presence of helens are known from many early Cambrian hyolithids, including *Microcornus* Mambetov, 1972, *Parkula* Bengtson et al., 1990 and *Hyptiotheca* Bengtson et al. 1990 (All known from Cambrian Series 2 of Australia; Bengtson et al., 1990; Betts et al., 2016, 2017). But the distribution of these characteristics in many other early Cambrian hyoliths has yet to be analyzed and it is possible that other taxa lacking helens could be identified among hyolithids where no operculum has yet been identified.

The functional morphology of hyolithids as discussed by most authors is mainly based on the presumed function of the helens to stabilize the animal on soft sediment (Marek 1963), to support soft

parts extending outside the conch (Dzik 1980; Babcock and Robison 1988) or allow it to manipulate its position in relation to the sea floor or prevailing currents (Marti Mus and Bergström 2005, 2007; Marti Mus et al., 2014; Moysuik et al., 2017). Regardless of the actual function of hyolithid helens, the absence of helens in *Paramicrocornus zhenbaensis* indicate that this hyolithid, like all orthothecid hyoliths, would have had a more passive life mode. The life mode of orthothecids is not well understood (and has been largely ignored in hyolith research) but at least one possible earliest Cambrian orthothecid; “*Ladatheca*” *cylindrica* from southeastern Newfoundland has been found in presumed life position (Landing 1993). The conchs of this taxon were found vertically or steeply embedded with the apex down in both siliciclastic and carbonate rocks indicating a possible mud-sticking life style. It remains uncertain if the proposed life mode of “*Ladatheca*” *cylindrica* can be applied also to other orthothecids, but this mode of life would not be dependent of the presence of helens and could possibly be extended also to *P. zhenbaensis*.

6.2 Shell structures of hyolithid opercula

The shell structure of hyoliths has been intensely studied in the past and two shell layers are commonly described from both orthothecid and hyolithid hyoliths from the early Cambrian to the Permian although different authors have described several kinds of structures in different hyolith taxa (see review in Kouchinsky, 2000). However, most studies have concentrated on hyolith conchs, and only Kouchinsky (2000) described the shell structure of orthothecid opercula while the shell structure of hyolithid opercula has remained unstudied. The preservation of the hyoliths from the Shuijingtuo Formation described herein does not allow a detailed discussion of hyolith microstructures but some observations, particularly of the structure of the operculum reveal clear differences from the structure of the orthothecid opercula described by Kouchinsky (2000).

The diameter of the vertically oriented columnar structures in the conch and opercula of *Paramicrocornus zhenbaensis* is much smaller (ca. 1 μm) than the tubules of orthothecid shells, (10 μm in diameter, about 100 μm long; Kouchinsky, 2000). In addition, the tubules of the orthothecid

opercula described by Kouchinsky (2000) are radially oriented, in sharp contrast to the slightly curved but almost vertical columns in opercula of *P. zhenbaensis* (compare Figs. 7D, 8H to Kouchinsky 2000, Fig. 7). Kouchinsky (2000) interpreted the radially oriented columnar structures as channels filled with phosphate and interpreted the pitted depression at the end of the columns as the opening of the tubules (diameter ca. 5 μ m; Kouchinsky, 2000). The size of the orthothecid tubules can be compared to the prisms of Cambrian orthothecid conchs (Kouchinsky, 2000) and molluscs (Vendrasco et al., 2010), while the columns in *P. zhenbaensis* are much smaller. Based on the similarly sized tubercles on the surface of internal moulds of hyolithid opercula from northeastern Greenland (Fig. 10H), it is possible that the observed non-radial orientation and small diameter of the columns in *P. zhenbaensis* is characteristic of hyolithids. If this pattern can be demonstrated to be widely distributed among hyolithids, the orientation and diameter of the columns may be a way to distinguish problematic groups of hyoliths.

Following the recent reinterpretation of hyoliths as fossil lophophorates, it is interesting to note that the size of the tubules in *Paramicrocornus zhenbaensis* can be compared to the secondary columnar structures of acrotretid brachiopods such as the co-occurring *Eohadreotreta zhenbaensis* (Zhang et al., 2016b). Incidentally, comparison between hyoliths and acrotretid brachiopods had been already made by Matthew (1901). However, the significant differences in shell composition (calcareous in hyoliths, organophosphatic in acrotretids) make the value of this comparison uncertain, despite the recent suggestion that hyoliths represent an extinct lophophorate group (Moysiuk et al., 2017).

6.3 Function of muscle scars in *Paramicrocornus zhenbaensis*

The paired apical muscle scars of the opercula in *Paramicrocornus zhenbaensis* are located on the apical slope of the base of the cardinal processes, close to the furrows separating the clavicles from the cardinal processes (Figs. 5F-K, 8D, E). The muscular system of hyolithids is best known from *Maxilites* from the middle Cambrian and *Gompholites* of the late Ordovician from the Czech Republic (Marti Mus and Bergström 2005). Both *Maxilites* and *Gompholites* are clearly hyolithids, preserving

in situ helens between the conch and operculum. The internal surface of the operculum of *Gompholites* exhibits a central muscle scar at the apex and in *Maxilites*, and an elongate muscle scar in a position high on the conical shield was considered to be homologous with the apical scar in *Gompholites* by Marti Mus and Bergström (2005). The apical position suggests that the muscle scars identified in *Paramicrocornus* may be homologous with the central muscle scars of *Gompholites* and *Maxilites*. Both the opercula of *Maxilites* and *Gompholites* preserve muscle scars on other parts of the interior of the operculum, but the exact pattern of muscle scars is highly variable between these and other hyolithids where muscle scars have been reported (see discussion in Marti Mus and Bergström 2005). The function of the muscle scars on hyolithid opercula have been interpreted as either attachment sites for muscles moving the operculum in relation to the conch to close the aperture or to control movements of the helens to attain a suitable orientation of the hyolith in the physical environment and perhaps to give the hyolith a limited movement capability as well (Marti Mus and Bergström 2005). No specific function for the apical scars of *Gompholites* and *Maxilites* has been suggested.

The apical portion of a well preserved internal mould of the second operculum (orthotheid Hyolith operculum A) from the Shujingtou Formation in our collection preserves a single, knob-like structure with a reticulate ornament (Fig. 9D-F) (contrasting to the pitted ornament (Fig. 9G) of other areas in the same specimen), which could be interpreted as muscle attachment structures. Similarly, apical structures are found on internal moulds of hyolithid opercula from northeastern Greenland (Fig. 10C-G). Although more specimens should ideally be investigated before any firm conclusions can be made, these observations may suggest that apical muscle attachment sites were present in all hyoliths. The presence of apical muscle scars in orthothecids (Hyolith operculum A herein) and in hyolithids without helens (*Paramicrocornus zhenbaensis*) would suggest that the muscles inserted here could not be related to the movements of helens. The apical placement of these scars, internally of the cardinal processes and consequently directed away from the hinge between operculum and conch also seem difficult to reconcile with muscles used to move the operculum in relation to the conch.

In a recent description of exceptionally preserved specimens, Moysiuk et al. (2017) illustrated a tentacular feeding organ surrounding a central mouth in the hyolithid *Haplophrentis* Babcock and

Robison, 1988 from the middle Cambrian Burgess Shale of Canada and Spence Shale of Utah. The lophophore-like morphology of this feeding organ led Moysiuk et al. (2017) to conclude that hyoliths are lophophorates and are closely related to brachiopods. Moysiuk et al. (2017) also noted that the tentaculate feeding organ was intimately associated with the operculum in *Haplophrentis*, even in specimens where the operculum had been shifted in relation to the conch. Further, poorly preserved “connective tissue” was found close to the apex of the operculum, and Moysiuk et al. (2017) also noted that the feeding organ appeared to be retractable in relation to the operculum. Although less well preserved, a similar association of presumed feeding organs with the operculum was noted for an Ordovician hyolithid from the Fezouata biota of Morocco (Marti Mus 2016). The central position, close to the apex of the operculum of the muscle scars in *Paramicrocornus*, as well as *Gompholites*, *Maxilites* and possibly in Hyolith operculum A and *Parkula?* sp., suggest that the muscles attaching here may have been predominantly used to retract the tentaculate feeding organ of the hyolith when the animal needed to close its shell. The lack of other muscle scars in *Paramicrocornus* (compared to the more complex pattern of muscle scars in other hyolithids) could be a natural consequence of the lack of helens in this taxon as it would not need the complex muscular apparatus of *Gompholites* and *Maxilites* and other hyolithids with helens.

7. Conclusions

New collections of the hyolith *Paramicrocornus zhenbaensis* from the Shuijingtuo Formation of South China (southern Shaanxi and western Hubei provinces) with well preserved conchs and opercula reveal a number of new morphological and ultrastructural features. *Paramicrocornus zhenbaensis* shares a number of morphological features with hyolithid hyoliths (conch with sub-triangular cross section and ligula, operculum divided into cardinal and conical shields and with separate cardinal processes and clavicles). However, all available evidence suggests that this species lacked helens, the lateral spines inserted between the conch and operculum, previously thought to be characteristic of all hyolithids. Consequently, *P. zhenbaensis* is interpreted as a hyolithid without

helens, perhaps belonging to a sister group of hyolithids. The shell structure of *P. zhenbaensis* is characterized by gently curved perforating columns that are interpreted to represent phosphatized tubules through the shell as found in other hyoliths. However, the smaller size of these tubules clearly differentiates them from the wider tubules in orthothecid hyoliths, the non-radial arrangement of these tubules in the operculum is also different from that in orthothecids. This evidence strengthens the interpretation that *P. zhenbaensis* belongs to the hyolithid hyoliths. Internal moulds of the operculum of *P. zhenbaensis* preserve a pair of pronounced tubercles close to the apex. These structures are interpreted as representing muscle scars on the internal surface of the operculum. The function of the muscle scars is inferred to be related to the withdrawal of the tentaculate feeding organ recently documented in hyolithids, and this function may apply to the apical muscle scars on other hyolithid opercula as well. The life mode of *P. zhenbaensis* remain uncertain but without helens to manipulate the orientation of the conch, the animal may have lived a semi-sessile life with the conch partly buried in the sediment of the sea floor.

Acknowledgments:

The authors would like to thank J.S. Peel (Uppsala University) for access to comparative material from Greenland. Thanks are also given to T. Topper (Durham University) for improving the English, PhD student F.Y. Chen (Northwest University) for fossil collection, and to Mrs Q.C. Feng for sample preparation in Xi'an. The first author would like express heartfelt thanks to G.X. Li (Nanjing Institute of Geology and Palaeontology) and L.E. Holmer (Uppsala University) for kind help and suggestions. Financial supports from the National Natural Science Foundation of China (to Z.F. Zhang) for Z.L. Zhang for a one-year visiting study at Uppsala University are gratefully acknowledged. This work was supported by the National Natural Science Foundation of China (grants 41621003, 41425008), National 973 program (grant 2013CB835002), 111 projects of China (grant P201102007) and the Swedish Research Council to CBS (grant VR2016-04610). Constructive reviews by J.M. Malinky and one anonymous reviewer greatly improved the manuscript.

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<Figure captions>

Fig. 1. Fossil locality and stratigraphic column of the Early Cambrian Shuijingtuo Formation at Xiaoyangba section, Zhenba County, southern Shaanxi Province. A. Map showing the location of the Zhenba area (box) on the northern Yangtze Platform. B. Geographic map, showing the location of studied areas in Shaanxi Province, South China. C. Stratigraphic column of the Lower Cambrian at the Xiaoyangba section, showing the stratigraphic horizon of *Paramicrocornus zhenbaensis*.

Fig. 2. Bivariate plots of the operculum of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at the Xiaoyangba section, Zhenba County, southern Shaanxi Province. A, plots of the maximum length-maximum width ratio. B, plots of the length of clavicle-maximum length ratio. C, plots of the length of apical process-maximum length ratio. D, plots of the height of clavicle- maximum length ratio.

Fig. 3. Opercula of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at Xiaoyangba section, Zhenba County, southern Shaanxi Province. A, ELI-XYB 13 AD-004, internal surface; A1, oblique lateral view; A2, dorsal view; A3, internal view, noting the short clavicle crest with six cone-shaped pustules in a small operculum (735 µm in width). B, ELI-XYB 13 AI-005, oblique view from the dorsal side, note the cardinal process and clavicle. C, ELI-XYB 13 AD-015; C1, dorsal view; C2, oblique dorsal view; C3, lateral view showing prominent internal features. D, ELI-XYB 13 T-057, internal view, noting the developed clavicle with ten cone-shaped pustules at the crest of a large operculum (1189 µm in width). E, ELI-XYB 13 AI-003; E1, external view, noting a pair of muscle scars by double-headed arrows; E2, oblique dorsal view, show very developed cardinal process and clavicles in a very large specimen (1863 µm in width). Abbreviations: CP = cardinal process; CL = clavicle; CS = cardinal shield; MS = muscle scars;

Fig. 4. Opercula of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at the Xiaoyangba section, Zhenba County, southern Shaanxi Province. A-C, ELI-XYB 13 U-024; A, internal surface of a small specimen (737 μm in width); B, enlargement of the flattened cardinal process of A; C, enlarged view of the clavicle crest with five cone-shaped pustules of A. D, ELI-XYB 13 AD-007, internal view, note the triangular form of the base of the cardinal process. E-F, ELI-XYB 13 U-018; E, external surface, note the obvious rod-shaped elements of clavicles on both sides, F, enlargement of the rods of the clavicle. G, ELI-XYB 13 AD-009, details of the rod-shaped elements of the clavicle. H, ELI-XYB 13 AT-060, exposed clavicle with thirteen ridges in an exfoliated specimen, showing apical muscle scar by double-headed arrow. I-K, ELI-XYB 13 AD-005; I, internal view of a small specimen (864 μm in width), box indicates area enlarged in J; J, showing the apical process, and clavicle with eight cone-shaped pustules, box indicates area enlarged in K; K, enlargement of the cone-shaped pustules of clavicle. L, ELI-XYB 13 U-024, little curving cardinal process in a larger specimen (904 μm in width). M, ELI-XYB 13 AD-002, enlarged view of the clavicle, noting variation of clavicle with two rows of pustules in the middle part.

Fig. 5. Opercula of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at the Xiaoyangba section, Zhenba County, southern Shaanxi Province. A-B, ELI-XYB 13 T 062; A, oblique dorsal view, showing muscle scar by double-headed arrows, box indicates area enlarged in Figure 6D; B, enlargement of the pair of muscle scars in A. C-D, ELI-XYB 13 AI-003; C, oblique dorsal view, showing muscle scar by double-headed arrows; D, detail of the pair of muscle scars in C. E, ELI-XYB 13 T-066, enlarged view of muscle scar in a larger specimen (about 1800 μm in width). F-G, ELI-XYB 13 T-060; F, lateral dorsal view of an exfoliated operculum; G, enlargement of the summit, showing muscle scar at the apical slope of the base of the cardinal processes by double-headed arrows. H, ELI-XYB 13 U-017, enlargement of the summit, showing muscle scars at the apical slope of the base of the cardinal processes by double-headed arrows. I, ELI-XYB 13 U-007, enlargement of spine-like moulds of muscle scars. J, ELI-XYB 13 U-002, showing muscle scar by double-headed arrow and a lateral depression by the arrow. K, ELI-XYB 13 U-004, enlarged view of the summit, note the shallow depressions at the base of clavicles, box indicates area are shown in Figure 7B.

Fig. 6. Conchs and Opercula of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at the Xiaoyangba section, Zhenba County, southern Shaanxi Province. A, ELI-XYB 13 AD-012, conch; A1, lateral view, showing the absence of the lateral sinus; A2, lateral dorsal view; A3, enlarged view of the distal

part, showing a spoon-shaped depression close to the apex of internal mould. B, ELI-XYB 13 AI-006, conch; B1, oblique lateral view showing the dorsal curvature and shape of short ligula ; B2, oblique dorsal view showing the aperture; B3,dorsal view showing shape of ligula. C, ELI-XYB 13 S-088, ventral view showing the distal part of internal mould of conch, box indicates area enlarged in Figure 7C. D, ELI-XYB 13 T 062, external concentric ornamentation of conch with fine growth lines. E, ELI-XYB 13 AD-013, fine transverse fibers on the internal surface of conch. F, ELI-XYB 13 AD-014, longitudinally oriented fibers on the external surface of conch. G, ELI-XYB 13 U-006, ornamentation on the outer and inner layers of operculum, noting the columnar structure. H, ELI-XYB 13 AD-013, concentric ornamentation of the inner layer of conch.

Fig. 7. Microstructure of the opercula and conchs of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at the Xiaoyangba section, Zhenba County, southern Shaanxi Province. A, ELI-XYB 13 U-010, enlarged apical part of internal mould of operculum, showing mould of muscle scar by double-headed arrow and adjacent reticulate ornament by the arrows respectively. B, ELI-XYB 13 U-004, reticulate micro ornament at the base of clavicle. C, ELI-XYB 13 S-008, showing columnar structure of the outer layer (double-head arrow) and inner layer (arrow) of the conch. D, ELI-XYB 13 U-003, the columnar structure and the tuberculate structure of internal mould of the operculum, note the outer layer (double-head arrow) and inner layer (arrow). E, ELI-XYB 13 AD-010, detail of columnar structure of the conch. F, ELI-XYB 13 U-002, moulds of transverse fibers on the internal surface of the operculum. G, ELI-XYB 13 U-001, enlarged view of tuberculate structures on the inner surface of the operculum.

Fig. 8. Microstructure of the opercula of *Paramicrocornus zhenbaensis*, from the early Cambrian Shuijingtuo Formation at the at the Aijiahe section, Three Gorges Area, western Hubei Province. A, ELI-AJH SJT S05 AJ-005, dorsal external; A1, dorsal view, box indicates the area in D; A2, external view; A3, lateral view. B, ELI-AJH SJT S05 AJ-003; B1, internal view, note the broken apical process and clavicle; B2, dorsal view, showing the paired muscle scars indicated by double-head arrow; B3, oblique lateral view. C, oblique dorsal view. D, enlarged view of the summit area in A1, note the paired muscle scars indicated by double-head arrows. E, detail of muscle scar and the summit region in B3. F, enlarged muscle scars of A1 from an oblique lateral view. G, ELI-AJH SJT S05 AJ-002, enlargement of the clavicle, showing the rod-shape elements. H, ELI-AJH SJT S05 AJ-004, slightly curved columnar shell structure of the outer layer.

Fig. 9. Opercula of *Hyolith operculum* A, from the early Cambrian Shuijingtuo Formation at Xiaoyangba section, Zhenba County, southern Shaanxi Province. A, ELI-XYB 13 AI-001, internal surface; A1, oblique lateral view, note strongly developed blade-like clavicles; A2, internal view. B-C, ELI-XYB 13 AI-002; B1, external view, showing the apical structure indicated by arrow; B2, dorsal view showing prominent clavicles; B3, lateral view; C, detailed apical structure of B1. D-G, ELI-XYB 13 U-016, D, oblique dorsal view of an exfoliated operculum, box indicates the position of E; E, the enlargement of the summit with a single, knob-like structure, box indicates the area shown in F; F, detailed reticulate ornament; G, the pitted ornament on the external surface of the operculum. H-I, ELI-XYB 13 T-055, H, oblique dorsal view, showing the apical structure in I; I, detailed apical structure.

Fig. 10. Opercula of *Parkula?* sp, from sample GGU 314919 from the early Cambrian Bastion Formation of C.H. Ostenfeld Nunatak, northeastern Greenland. A, NRM XXXX-1; A1, oblique dorsal view; A2, dorsal view; A3, oblique external view. B, NRM XXXX-2; B1, lateral view; B2, oblique dorsal view. C, NRM XXXX-3; C1, external view; C2, lateral view; C3, dorsal view. D, enlarged view of summit area of C2. E, enlarged area of C3, showing apical muscle attachment sites by double-headed arrows. F, enlarged summit of C2 in dorsal view, showing apical muscle attachment sites by double-headed arrows. G, enlarged apical muscle attachment sites of F. H, detailed tuberculate structures on the external surface of A.

<Table caption>

Table 1. Average dimensions and ratios of opercula of *Paramicrocornus zhenbaensis*.

Abbreviations: L = length; W = width; L_p = length of cardinal process; W_p = width of cardinal process; A_p = angle of cardinal process; L_c = length of clavicle; H_c = Height of clavicle; A_c = angle of clavicle; SD = Standard Deviation.

	L	W	L _p	W _p	A _p	L _c	H _c	A _c	L/W	L _p /L
N	33	37	18	22	27	16	10	16	33	15
Mean	980	1231	250	127	57°	457	147	74°	77,6%	26,8%
Min	515	735	133	80	49°	125	86	67°	69,9%	20,6%
Max	1730	2103	450	220	66°	1010	291	83°	83,8%	34,0%
Median	905	1168	245	121	59°	442	154	72°	77,2%	26,8%
SD	323	365	88	39	5°	237	58	5°	3,2%	3,6%

L_c/L	H_c/L
16	8
46,4%	18,02%
24,3%	14,67%
59,7%	24,38%
48,3%	18,45%
10,5%	3,37%