

On the origin of hyolith helens

Christian B. Skovsted^{a,b,*}, Mónica Martí Mus^c, Zhiliang Zhang^d, Bing Pan^e, Luoyang Li^{a,b}, Fan Liu^{a,b}, Guoxiang Li^e, Zhifei Zhang^b

^a Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

^b Shaanxi Key Laboratory of Early Life and Environments, State Key Laboratory of Continental Dynamics and Department of Geology, Northwest University, Xi'an 710069, China

^c Área de Paleontología, Universidad de Extremadura, Avenida de Elvas s/n, Badajoz 06006, Spain

^d Department of Biological Sciences, Macquarie University, North Ryde, Sydney 2109, NSW, Australia

^e State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China



ARTICLE INFO

Keywords:

Hyolithida
Orthothecida
Operculum
Clavicles
Evolution
Cambrian

ABSTRACT

Helens, the curved lateral spines inserted between the conch and operculum of some hyoliths, are a unique morphological adaptation characterizing the order Hyolithida. These structures are paired, movable and had a mechanical function, probably related to orienting the hyolith conch and lifting its aperture above the sea floor. We show that helens are intimately associated with the hyolith opercula and are structurally comparable to the rod like units that constitute the clavicles, internal wall-like structures of the hyolithid operculum that probably evolved to secure the operculum from lateral displacement in the conch aperture. In some early Cambrian hyolith taxa that lack helens, such as *Paramicrocornus*, new clavicle rods are added in the gap separating the clavicles from the cardinal processes, the same position where helens are inserted in later hyoliths. We also show that the size of incipient helens at the earliest ontogenetic stage matches the size of the clavicles in associated opercula. We propose that helens are modified clavicle rods that were detached from the operculum and developed into lateral spines through allometric growth during early ontogeny. Further, we suggest a four-step model for the evolution of hyolithid hyoliths from orthothecid ancestors: 1, Externally fitting operculum; 2, Stabilizing, radially arranged structures on the inside of the operculum; 3, Ligula and folded operculum; 4, Detachment of clavicle rods and origin of helens.

1. Introduction

Hyoliths are extinct marine Palaeozoic invertebrates with a history of problematic affinity (Malinky and Yochelson, 2007). Their calcium carbonate (aragonite) shell consists of a cone-shaped conch with a closed apex and an open aperture, a lid-like operculum and, in many taxa, two elongate, spine-shaped lateral elements called helens (Fig. 1; Marek, 1963, 1967; Martí Mus and Bergström, 2005; Martí Mus et al., 2014). Hyoliths evolved in the earliest Cambrian (Terreneuvian) and, although common throughout the Cambrian period, the group was reduced in diversity and abundance later in the Palaeozoic and eventually went extinct at the end of the Permian (Malinky, 2009a). Hence, hyoliths are usually considered to belong to the Cambrian evolutionary fauna (Sepkoski Jr et al., 1981).

Hyoliths have traditionally been divided into two distinct orders, the Hyolithida Sysoev, 1957 and the Orthothecida Marek, 1966. Conchs

of hyoliths usually have an elliptical or subtriangular cross section and a ventral shelf-like projection of the conch aperture, the ligula (Martí Mus and Bergström, 2005; Martí Mus et al., 2014 and references therein). The hyolithid operculum articulates with the conch aperture and is divided into a convex conical shield abutting the ligula and a straight cardinal shield articulating with the dorsal margin of the aperture. Internally, the hyolithid operculum bears projecting cardinal processes and elongate radially arranged clavicles. Hyoliths have laterally projecting helens inserted between the conch and operculum. However, helens appear to be lacking in some early Cambrian taxa that are otherwise very similar to typical hyoliths (Zhang et al., 2018). Orthothecid conchs have circular, triangular, kidney-shaped or quadrate cross sections and a planar aperture (Marek, 1967; Malinky, 2009b). The operculum of orthothecids is usually smaller than the conch aperture and in many taxa could be withdrawn inside the shell although this may not be the case for all Cambrian forms. Internally, the

* Corresponding author at: Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.
E-mail address: Christian.skovsted@nrm.se (C.B. Skovsted).

<https://doi.org/10.1016/j.palaeo.2020.109848>

Received 29 January 2020; Received in revised form 26 May 2020; Accepted 4 June 2020

Available online 10 June 2020

0031-0182/ © 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

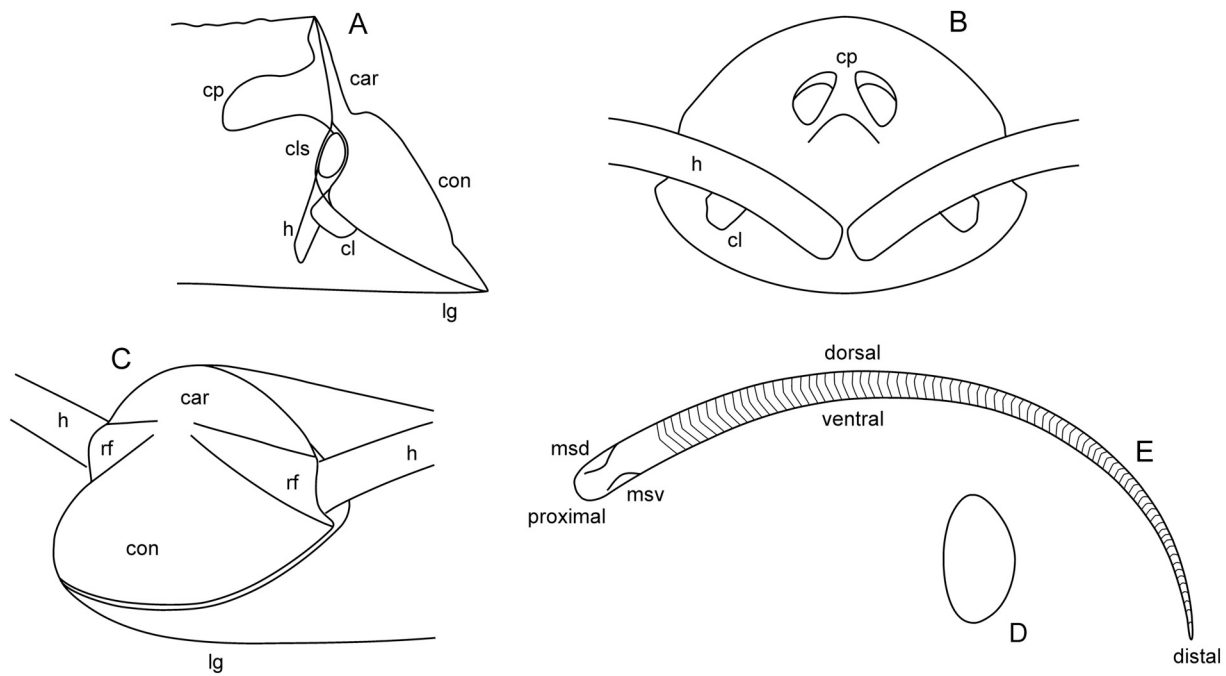


Fig. 1. Schematic drawings illustrating different morphological features of hyolithids. A. anterior portion of a hyolithid in lateral view showing relative position of operculum, conch and helen (sectioned at the conch lateral sinus); conch drawn as if transparent to show position of clavicle, cardinal process and helen inside the conch (redrawn and modified from Martí Mus and Bergström, 2005, text-fig. 20). B. view of operculum and helens from the inside of the conch (redrawn and modified from Martí Mus and Bergström, 2005, text-fig. 19). C. Anterior portion of a hyolithid in frontal lateral view showing relative position of skeletal elements. D. cross-section of a helen (redrawn from Martí Mus and Bergström, 2005, text-fig. 1). E. anterior view of a complete helen; possible three-dimensional curvature not considered (redrawn and modified from Martí Mus and Bergström, 2005, text-fig. 1, and from Martí Mus et al., 2014, Fig. 8). Abbreviations: car: cardinal shield of the operculum; cl: clavicles; cls: conch lateral sinus; con: conical shield of the operculum; cp: cardinal process; h: helens; lg: ligula; msd: dorsal muscle scar; msv: ventral muscle scar; rf: rooflet.

orthotheid operculum typically has prominent cardinal processes but no clavicles, although some Cambrian taxa may exhibit clavicle-like structures (e.g. Dzik, 1994; Malinky and Skovsted, 2004; Pan et al., 2019) and other taxa may lack internal processes altogether (e.g. Skovsted et al., 2014; Liu et al., 2020). No evidence exists to suggest that Orthothecids possessed helens. The distinction between hyolithids and orthothecids is more clear in taxa from the second half of the Cambrian and younger ages, while it has been repeatedly noted that many early Cambrian forms appear to combine hyolithid and orthothecid characters (e.g. Dzik, 1994; Malinky and Skovsted, 2004; Skovsted et al., 2014, 2016; Zhang et al., 2018; Pan et al., 2019), complicating taxonomy of the earliest hyolith faunas. Zhang et al. (2018) relied on the presence of helens to define the Hyolithida and noted that *Paramicrocornus zhenbaensis* from Cambrian Series 2 of South China, which lacked helens, may have been part of the sister group of hyolithids.

Knowledge on the soft anatomy of hyoliths has long been limited to indirect information from muscle scars on both conch and operculum and more directly from the preserved alimentary canal in exceptional specimens (see Devaere et al., 2014 and Berg-Madsen et al., 2018 for a review of preserved guts in orthothecids and Martí Mus, 2016 in hyoliths). More extensive soft parts, including a tentaculate feeding apparatus, were recently discovered in specimens of the hyolithid *Haplophrentis* Babcock and Robison, 1988 from the Cambrian Spence and Burgess Shales of North America (Moysiuk et al., 2017) and the orthothecid *Triplicatella* Bengtson in Bengtson et al., 1990 from the Chengjiang Lagerstätte of South China (Liu et al., 2020).

The biological affinity of hyoliths has long been controversial, although historically most authors have linked them phylogenetically to the Mollusca (see Malinky and Yochelson, 2007 for a full historical review; also Moore and Porter, 2018). After the discovery of a lophophore-like feeding apparatus in *Haplophrentis* (Moysiuk et al., 2017),

hyoliths have been referred to the lophophorate stem group (Moysiuk et al., 2017), the brachiopod stem group (Sun et al., 2018a) or even the brachiopod crown group (Zhao et al., 2017). However, the direct comparison of the tentaculate feeding apparatus of *Haplophrentis* to the lophophores of brachiopods and phoronids has been questioned by Liu et al. (2020) who concluded that hyoliths are likely to occupy a more basal position in the lophotrochozoan tree. A lophophorate affinity of hyoliths is also questioned by new data on the shell structure of Cambrian hyoliths, which is closely comparable, even on a very detailed level, to that of early Cambrian molluscs (Moore and Porter, 2018; Li et al., 2019), implying they shared a common biomineralization toolkit. These structures are very different from those of the earliest convincing lophophorate fossils (i.e. the phosphatic tommotiids; Balthasar et al., 2009).

The functional morphology and ecology of hyoliths have been almost as controversial as their biological affinity with different authors interpreting these animals as filter or suspension feeders, deposit feeders, coprovores or scavengers (Runnegar et al., 1975; Missarzhevsky, 1989; Moysiuk et al., 2017; Sun et al., 2018b; Kimmig and Pratt, 2018), and as active swimmers, sedentary mud stickers, sediment recliners, active epibenthic crawlers or infaunal burrowers (Fisher, 1962; Babcock and Robison, 1988; Martí Mus and Bergström, 2005, 2007; Landing and Kröger, 2012; Kimmig and Pratt, 2018; Sun et al., 2018b). To a large extent, the function of helens is at the core of most of these hypotheses. Therefore, it seems that the origin and function of helens is key to understanding the trophic ecology of hyoliths and hence the evolutionary pressures that shaped their evolution. In this paper we explore the origin and early evolution of helens through a detailed study of selected early Cambrian hyolith taxa (primarily their helens and opercula) from China, Australia and Greenland.

2. Materials and methods

The following review is based on data compiled from the literature on hyoliths, although we have complemented this with original observations on material from a number of localities worldwide. New material included herein comes from the Shuijingtuo Formation of Hubei and Shaanxi Provinces, South China (see Zhang et al., 2018 for detailed locality information), the Xinji Formation of Shaanxi, Henan and Anhui provinces, North China Platform (see Li et al., 2019; Pan et al., 2019 for locality information), the Chengjiang and Guanshan biotas of Yunnan Province, South China (see Chen et al., 2019 for locality information), the Bastion Formation of North-East Greenland (see Malinky and Skovsted, 2004; Skovsted, 2006) and the Ajax Limestone of South Australia (see Bengtson et al., 1990; Betts et al., 2016).

Institutional abbreviations: NRM (Naturhistoriska Riksmuseet, Swedish Museum of Natural History, Stockholm, Sweden), ELI (Early Life Institute, Northwest University, Xian, China), NIGPAS (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China).

3. Hyolithid helens

Helens, the laterally projecting spines of hyolithids are unique skeletal elements, which lack obvious analogues in other modern or fossil lophotrochozoans. They are elongate, curved skeletal structures that project downwards and backwards between the conch and operculum (Fig. 1; Marek, 1963; Martí Mus and Bergström, 2005, 2007). In cross section they are often oval and flattened, although the exact morphology varies from one species to another. Growth took place at the proximal end of the helens, which was internal and embedded in a secreting epithelium. Muscle scars, located at the dorsal and ventral edges of the proximal end, indicate that helens could move by the action of specific muscles (Fig. 1E; Martí Mus et al., 2014). Helens have sometimes been interpreted as completely withdrawable inside the conch (Babcock and Robison, 1988; Butterfield and Nicholas, 1996; Sun et al., 2016), but their large size and curvature seem to preclude this. Indeed, the apparent accommodation structures of the conch (lateral sinus) and operculum (rooflets) also suggest that the helens extended outside the conch when the aperture was completely closed. In addition, minute brachiopods are found as epibionts on hyolith helens in specimens with exceptionally preserved soft parts from the Burgess and Spence Shales (Moysiuk et al., 2017), confirming that these structures were permanently exposed during the life of the animal.

The function of hyolith helens has been widely debated in the past. The structures have been variously interpreted as supports for external soft parts, for feeding, respiration (Dzik, 1980; Babcock and Robison, 1988; Missarzhevsky, 1989), or swimming (Fisher, 1962); and as having a mechanical function, providing stability on the sea floor and limited benthic mobility (Marek, 1963; Marek et al., 1997) and raising the aperture of the conch above the sea floor to facilitate filter or suspension feeding (Marek et al., 1997; Galle and Parsley, 2005; Martí Mus et al., 2014; Martí Mus, 2016; Moysiuk et al., 2017).

That helens had mechanical functions is now clear. They were massive, mineralized spines, not associated with external soft tissues and attached to muscles proximally. They must have evolved to facilitate hyolithids to move, orient and lift themselves above the substrate. However, helens are quite peculiar structures that don't look particularly well designed for these functions, and their evolutionary origin has remained uncertain. No comparable structures are known from the stratigraphically older orthothecids, and some early Cambrian taxa lack helens although they are otherwise indistinguishable from hyolithids (Zhang et al., 2018; Pan et al., 2019). This indicates that helens are an innovation of hyolithid hyoliths; a new anatomical feature that was added to an existing body plan. Herein we attempt to show that helens developed from pre-existing structures of the hyolith skeleton: the rod-like units that constitute the basic element of the clavicles on the inside

of the operculum. The evolution of helens involved detachment from the opercular surface and differential growth of these rod-like units.

4. The early fossil record of hyoliths and fossil evidence for helens

The first hyoliths appear in SSF assemblages in the early Terreneuvian (middle Fortunian Stage) of Siberia, Mongolia and South China (Maloof et al., 2010; Kouchinsky et al., 2012). In the clastic succession of Avalonia, the first occurrence of hyoliths is reported from member 2B of the Chapel Island Formation in eastern Newfoundland (described as annelid tubes in Landing, 1993). In all cases, the oldest hyoliths are represented by elongate tubes with a circular or sub-circular cross section, sometimes associated with simple sub-circular opercula, and can be readily identified as orthothecid hyoliths. No evidence exists to suggest that these fossils had helens, or even internally projecting clavicles or cardinal processes on the opercula. Later, during the early Cambrian (Stages 2–4), orthothecids with diverse types of internally projecting opercular processes appeared.

The earliest hyolithids are more difficult to identify. Only a few early Cambrian hyolith specimens where helens are found in association with conchs and opercula have been reported to date. Almost without exceptions these specimens are found in trilobite bearing strata and are hence referable to Cambrian Stage 3 or younger (see review in Peel, 2010). A possible exception is from the Czarna Formation of Poland where Orłowski and Waksmundzki (1986) reported hyolithid specimens with preserved helens in supposedly pre-trilobitic strata. However, the age of the Czarna Formation is contested and at least the upper parts of the formation, where the hyolith specimens came from, may be attributable to Cambrian Stage 3 (Stachacz, 2012).

In the absence of fully articulated material or preserved isolated helens, it is possible to deduce the presence of helens in hyolith specimens from shelly assemblages through the presence of the accommodation structures, lateral sinuses, on the lateral margins of the conch aperture and the corresponding rooflets on the operculum, which allow the helens to project when the aperture is closed (Marek, 1963; Martí Mus and Bergström, 2005). The oldest well dated taxa where lateral sinuses and rooflets are documented are *Parkula bounites* Bengtson in Bengtson et al., 1990 and *Parakorilithes mammillatus* He and Pei in He et al., 1984 from the Ajax Limestone of Mt. Scott (Bengtson et al., 1990) and the Wirrapowie Limestone south of Moro Gorge (Jacquet et al., 2019). *Parkula bounites* and *Parakorilithes mammillatus* occur here in the pre-trilobitic upper part of Cambrian Stage 2 (*Micrina etheridgei* Zone; Betts et al., 2016, 2017, 2018; Jacquet et al., 2019). In addition, higher levels of the Ajax Limestone at Mt. Scott (*Dailyatia odyseji* Zone, lower Stage 3; Betts et al., 2016, 2017, 2018) has yielded numerous 3-dimensionally preserved isolated helens (Fig. 2I–K). A number of possibly older hyolith conchs with subtriangular cross section and well developed ligula has been described from Cambrian Stage 2 equivalent strata around the world (such as *Burites*; Rozanov et al., 1969; Kouchinsky et al., 2015) but few of these taxa are well known and it is not clear that they had accommodation structures for helens. Like *Paramicrocornus* from South China, some of these taxa may belong to a group of hyoliths lacking helens, from which the hyolithids sensu stricto must have evolved. In any case, it remains clear that hyoliths with helens appeared substantially after the initial radiation of hyoliths in the Terreneuvian.

The later stratigraphic appearance of hyolithids with helens, compared to orthothecids, is mirrored in the appearance of hyoliths in the famous Lagerstätten of South China. In the Cambrian of South China, articulated hyoliths are found in several exceptionally preserved biotas including the Chengjiang (Hou et al., 1999, 2004, 2017; Chen, 2004) and Guanshan faunas (Luo et al., 2008; Hu et al., 2013) of Yunnan Province and in the Balang Formation of Guizhou Province (Sun et al., 2016, 2017). In the older Chengjiang fauna (Cambrian Stage 3; Hou et al., 2017), at least three hyolith taxa are found with conch and operculum in association (Fig. 3). Of these species, two are orthothecids; *Triplicatella opimus* Yu, 1974 (Fig. 3C; Liu et al., 2020) and



Fig. 2. Phosphatized hyolithid helens from North China and South Australia. A-H; helens from the Xinji Formation (Cambrian Stage 3–4) of North China Platform; A, ELI LC06-02-18, almost complete specimen; B, ELI LC06-02-09, proximal part of helens; C-E, ELI LC06-02-05; C, lateral view of helens; D, detail of proximal part of helens; E, detail of D showing fibrous structure; F, ELI LC06-17-04, proximal part of helens; G, ELI LC06-18-08, proximal part of helens; H, ELI LC06-18-03, broken helens with preserved surface ornament. I-K; NRM Mo191118; complete helens from the Ajax Limestone (*D. odyseii* Zone, Cambrian Stage 3), Mt. Scott, South Australia; I, overview; J, oblique view; K, detail of proximal part with fibrous shell structure. Scale bars equal 500 μm in A, 200 μm in B, C, F-J, 50 μm in D, K and 5 μm in E.

Pedunculotheca diania Sun, Zhao and Zhu in Sun et al., 2018 (Fig. 3D–E; Sun et al., 2018a) while the third (most recently referred to ‘*Ambrolinevitus*’ *ventricosus* Qian, 1978; Sun et al., 2018b) is hyolithid-like with triangular conch cross section, a ligula and an operculum divided into cardinal and conical shields (Fig. 3A–B; Sun et al., 2018b). However, no specimen of either of these species shows evidence of helens, despite the common articulation of conchs and opercula and the otherwise excellent preservation of the shell and sometimes soft parts (Fig. 3C; Liu et al., 2020). In contrast, hyolithid specimens from the slightly younger Guanshan biota (Cambrian Stage 4; Luo et al., 2008) are found with helens directly associated with conch and operculum, although the shells are generally less well preserved than those in the Chengjiang biota (Fig. 4).

5. The construction of helens

Helens are elongate, curved structures, often with a mild helical twist or a gentle backward bend (Fig. 2). The cross section is often lenticular and asymmetrical, with a curved anterior face and a flatter posterior face. Helens with a blade-shaped, more symmetrical flattened cross section are also known. In terms of surface structure, helens are divided into two zones, a distal zone with dense transverse growth lines and a much shorter, smooth proximal zone with rounded termination (Martí Mus and Bergström, 2007; Martí Mus et al., 2014). The proximal zone was the location of active shell formation and the site of muscle attachments, and was permanently inserted in the soft parts. The distal zone projected outside the aperture and was permanently exposed. Internally, helens are constructed of thin concentric layers surrounding a central lamella likely of organic composition. New phosphate-



Fig. 3. Hyoliths from the Chengjiang Lagerstätte (Cambrian Stage 3), Yunnan, South China. A–B, ELI H-186A, *Ambrolinevitus ventricosus*; A, overview; B, detail of apertural part of conch and operculum with left part of cardinal shield broken off, showing *Paramicrocornus*-like clavicles composed of rods (indicated by arrows). C, ELI H-188A, two specimens of *Triplicatella opimus* (Yu, 1974) showing association of conchs and opercula and preservation of soft parts associated with operculum (see Liu et al., 2020). D–E, *Pedunculotheca diania* Sun, Zhao and Zhu in Sun et al., 2018; D, ELI H-182B, specimen showing broken conch and associated circular operculum; E, ELI SJZ-H-1348, conch showing cone-shaped apical end with flattened lateral margins. Scale bars equal 3 mm in C, E, 2 mm in D, 1 mm in A and 500 μ m in B.

replicated helens from Small Shelly Fossil (SSF) assemblages from the Xinji Formation of North China and the Ajax Limestone of South Australia (Fig. 2) show that the outer layers of the helens had a fibrous shell structure (Fig. 2E). Individual fibres appear to be longitudinally arranged with a slight offset relative the long axis of the helen (Fig. 2K). This structure is similar to the fibrous structure documented in organically preserved helens from the middle Cambrian Little Bear biota of northwest Canada (Butterfield and Nicholas, 1996, Fig. 4.1).

6. The construction of clavicles

Clavicles are internal, ridge-like projections of the hyolith operculum. These structures are traditionally considered to be characteristic of hyolithids and typically diverge laterally from close to the cardinal processes along the internal line formed by the transition from cardinal to conical shield. The morphology of hyolithid clavicles varies greatly and a single or multiple pairs of sub-parallel clavicles may be present (Marek, 1967; Martí Mus and Bergström, 2005). A complex terminology based on the number of clavicles was proposed by Marek (1967). The clavicles may be directly fused to the internal surface of the operculum or lifted above it, being supported by vertical walls (Valent et al., 2017). The highest point of the clavicles in most taxa is at their lateral termination, and the cardinal processes and clavicle ends are typically separated by a wide gap (Martí Mus and Bergström, 2005; Martí Mus et al., 2014).

The function of clavicles is not entirely clear. Hyolith opercula exhibit a range of internal muscle scars testifying to a complex muscular system, but no muscle scars have been reported from the clavicles themselves. These internal projections may have functioned in stabilizing the operculum within the aperture when the shell was closed (Martí Mus and Bergström, 2005). This function also explains the absence of clavicles in many orthothecids, as their opercula were often withdrawable inside the conch and thus more protected than in hyolithids where the opercula abutted directly to the conch aperture. Orthothecids are usually considered to lack clavicles (Marek, 1967), but at least in some early Cambrian taxa such as *Allathea*, *Conothecha* or *Paratriplicatella*, clavicle-like structures are present in the form of radial ridges on the dorsal and lateral margins of the operculum, often forming an inner circular structure on the internal surface of the operculum (Fig. 5D–F; Dzik, 1994; Malinky and Skovsted, 2004; Skovsted and Peel, 2007; Pan et al., 2019). In well preserved specimens, these circular structures appear to be constructed of radially arranged rod-like units (Bengtson et al., 1990; Kouchinsky et al., 2015, fig. 30) and these were referred to as “incipient clavicles” by Dzik (1994). Other taxa such as *Neogloborilus* or Operculum B of Malinky and Skovsted (2004) seem to have well defined, wall-like clavicles more similar to those of typical hyolithids (Fig. 5A–C; Pan et al., 2019). It is likely that these internal structures are homologous to and served a similar function as the clavicles of hyolithids and that the opercula of these taxa may have abutted the conch aperture and were not withdrawable as in other orthothecids.

The structure of clavicles has rarely been studied in detail. In common for most clavicles and clavicle-like structures across both hyolith orders is that they are composed of rod-like units attached in various configurations directly to the internal surface of the operculum. These rod-like units may occur as a single pair (monoclavicate sensu Marek, 1967). In other taxa (including many Cambrian species), clavicles form aggregates of parallel rod-like units attached in groups side by side along the internal surface (*Slapylites*, *Parakorilithes*; Valent et al., 2017; Pan et al., 2019). In other taxa the rods may be directly attached to each other, forming a palisade-like structure along the margin of the operculum (*Protomicrocornus* and *Paramicrocornus*; Figs. 5G–I, 7; Zhang et al., 2018; Pan et al., 2019).

The composition of the clavicle rods is uncertain. In some hyolithid opercula, preservational features indicate that the clavicles may have been partly empty, or alternatively weakly mineralized and partly filled with organic material (Martí Mus and Bergström, 2005, text-figs. 2D, 10C–D). In internal moulds of hyolithid opercula from the early Cambrian of North-East Greenland (referred to *Parkula* sp. by Malinky and Skovsted (2004) but potentially representing a new genus according to Pan et al. (2019)), partly phosphatized clavicles are found attached to the surface of the mould (Fig. 6). The clavicles are composed of a multitude of phosphatized fibres arranged in parallel bundles (Fig. 6E, G). Individual fibres have an average diameter of about 5 μ m and are longitudinally arranged in relation to the long axis of the bundles. The



Fig. 4. Unidentified hyolithids with associated conchs, opercula and helens from the Guanshan Lagerstätte (Cambrian Stage 4), Yunnan, South China. A, ELI WD-SJJ-987B; B, ELI WD-SJJ-987A; C, ELI WD-SJJ-986A. Scale bars equal 1 mm in A, B and 2 mm in C.

preservation of the fibres indicates that they represent diagenetic phosphate infill in narrow canals, originally occupied by organic material, within a larger skeletal structure. This preservational process is comparable to the phosphatization of the stroma of echinoderm ossicles in the same sediment samples (Skovsted, 2006). We interpret the fibrous bundles as clavicle rods composed of fine organic canals in a weakly mineralized matrix.

7. *Paramicrocornus* and *Protomicrocornus* and the origin of helens

Paramicrocornus zhenbaensis Qian et al., 2001 was recently re-described by Zhang et al. (2018) based on partly phosphatized specimens. The conch of *Paramicrocornus* has a small ligula but no lateral sinuses, and the operculum is divided into conical and cardinal shields but has no rooflets. Internally, the operculum is hyolithid-like in having long, narrow cardinal processes and well-developed clavicles. However, the narrow gap between clavicles and cardinal processes leaves no space for the insertion helens. All these features indicate the absence of helens in *Paramicrocornus* (Fig. 7). As suggested by Zhang et al. (2018), *Paramicrocornus* may belong to the lineage of hyoliths leading to hyolithids. *Protomicrocornus* (Pan et al., 2019) is very similar in terms of opercular morphology, but lacks the narrow gap between cardinal processes and clavicles, which instead seem to form a continuous wall along the dorsal side of the interior of the operculum (Fig. 5G–I; Pan et al., 2019). *Protomicrocornus* may thus belong to the same hyolithid lineage as *Paramicrocornus*, perhaps representing an even less derived condition (Pan et al., 2019).

The clavicles in *Paramicrocornus* are composed of straight, sub-parallel rod-like elements in a fan-like arrangement, extending as a palisade from the inner surface of the operculum toward the cardinal processes (Fig. 7; Zhang et al., 2018). Individual rods seem to be fused together lengthwise, but at least their terminal tips appear to be free (Fig. 7; Zhang et al., 2018). The initial rod was arranged flush with, and apparently fused to, the internal surface of the operculum (Fig. 7) but during ontogeny, new rods were successively added at a slight angle to pre-existing ones, along the free edge of the palisade, facing the narrow gap that separates clavicles from cardinal process (Fig. 7). In the smallest specimens reported by Zhang et al. (2018, p. 6), the clavicles

are composed of five rods but larger specimens may have up to 15 rods. However, the length and width of individual rods also increase during ontogeny. The clavicles of *Paramicrocornus* differ mainly from more conventional clavicles in younger taxa by the arrangement of the rods as a palisade (individual rods fused to each other) rather than in a side by side arrangement (several rods individually fused to the base of the operculum). The clavicles of *Protomicrocornus* also appear to be constructed of individual rod-like units, the main difference with *Paramicrocornus* being the lack of a gap separating them from the cardinal processes (Fig. 5G–I).

The hyolith ‘*Ambrolinevitus*’ *ventricosus* commonly occurs in large clusters in the Chengjiang biota of South China (Fig. 3A–B; Sun et al., 2018b). No helens are found in association with these hyoliths despite the common occurrence of articulation of conch and operculum similar to hyolithids. The excellent preservation of these shells in three dimensions allows observation of fine details of the opercula, including the structure of the clavicles. The clavicles are high, wall-like and like in *Paramicrocornus*, constructed of parallel rods (Fig. 3B), suggesting that this species also belongs to the hyolithid lineage.

As mentioned in the section on the early fossil record of hyoliths above (chapter 4), the Cambrian fossil record has also yielded a range of taxa where an orthothecid-like conch is associated with an operculum that is somewhat hyolithid-like on its internal surface. These opercula have clavicles, or clavicle-like raised walls, composed of rod-like units. Examples include *Paratriplicatella* and *Neogloborilus* from North China (Fig. 5A–F; Pan et al., 2019). These orthothecids may also belong to the hyolithid lineage, suggesting that a clavicate, non-withdrawable operculum may have been one of the earliest hyolithid characters to be acquired in the hyolithid lineage.

In terms of their general morphology and position, helens are comparable to clavicles. Like the individual clavicle rods of *Paramicrocornus*, helens are unbranched, radially arranged and have a somewhat elliptical cross section. Also, the insertion of new clavicle rods occurs at the margin of the gap separating the clavicles from the cardinal processes, which is the position of helens, between conch and operculum in hyolithids (Fig. 1; Martí Mus and Bergström, 2005, 2007). Although the clavicle rods themselves are not preserved in *Paramicrocornus*, imprints of fine fibrous structures on the phosphatized wall of the clavicle rods (Fig. 7H, I), indicate that they, like the clavicles of *Parkula* sp. (sensu Malinky and Skovsted, 2004) from Greenland (Fig. 6F, H, K), may have had a fibrous ultrastructure, which may also be compared to that of helens (Fig. 2). These similarities suggest that helens may be directly derived from the rods forming the clavicles. If the clavicle-forming part of the mantle that secreted the operculum invaginated and detached slightly from the operculum, the basis for the formation of a separate skeletal unit (a proto-helen) would have been established. Continued growth of the rod, extending the structure beyond the aperture would complete the formation of helens.

Further evidence in favour of the above hypothesis is that helens tend to be displaced together with the operculum in slightly disarticulated specimens (e.g. Harvey and Butterfield, 2011; Martí Mus, 2016) and may even be preserved attached to completely disarticulated opercula in acid macerated samples (Butterfield and Nicholas, 1996, Fig. 4.2), suggesting that the soft parts that housed and secreted the helens were closely associated to those of the operculum.

8. Incipient helens and allometric growth of helens

Butterfield and Nicholas (1996) described exceptionally preserved hyolithid specimens from the Little Bear Small Carbonaceous Fossil biota. The illustrated specimens include one representing a very early developmental stage (protoconch and the first 3–4 growth increments; Butterfield and Nicholas, 1996, Fig. 4.4; Martí Mus and Bergström, 2007, text-Fig. 1E). Other specimens, including larger conchs and opercula with well-preserved clavicles and associated, larger helens, presumably belonging to the same species, are also illustrated

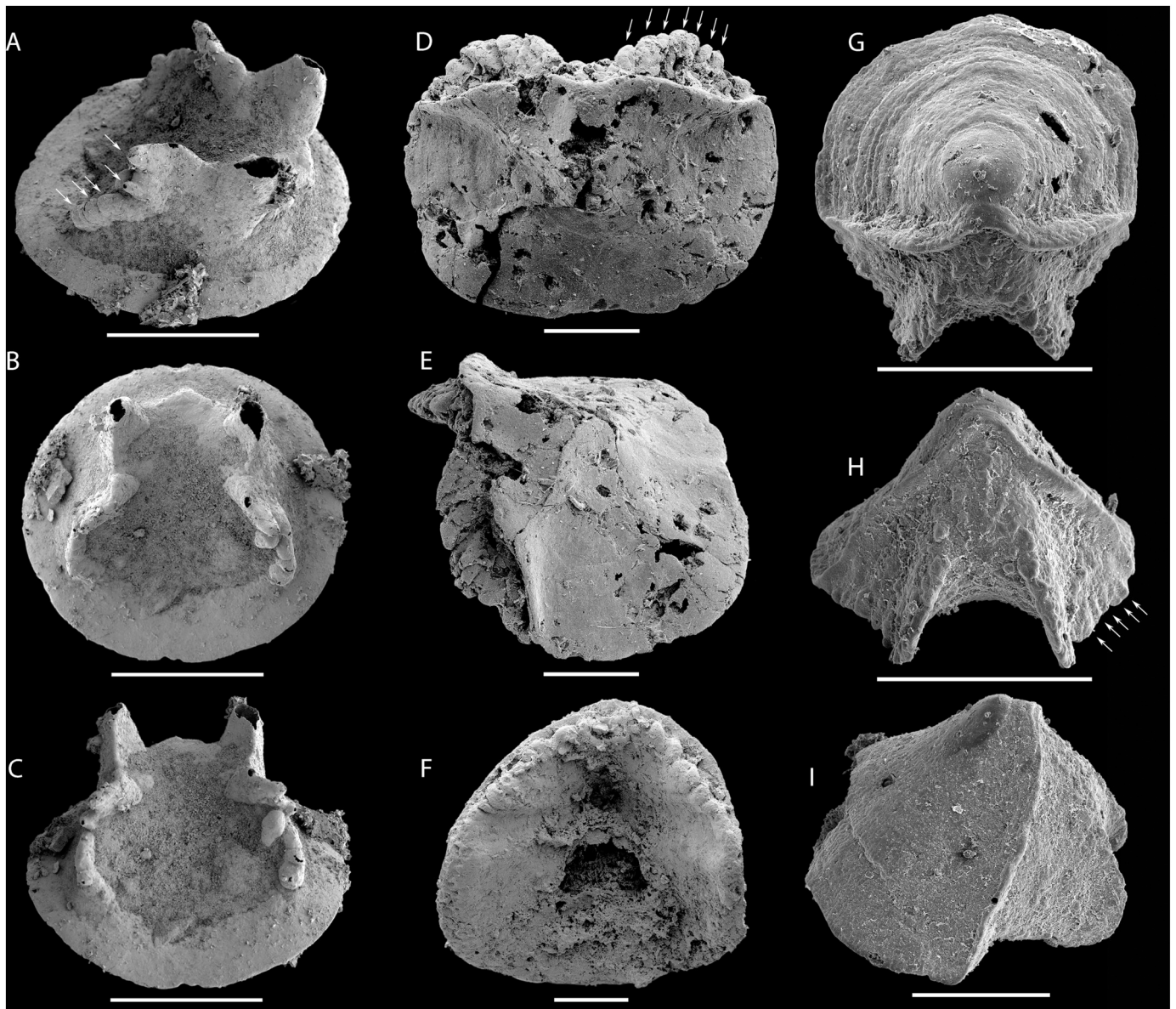


Fig. 5. Phosphatized hyolith opercula from the Xinji Formation (Cambrian Stage 3–4), North China. A–C, ELI LC06-22-01, *Neogloborilus applanatus* Qian and Zhang, 1983; A, oblique lateral view of operculum showing high cardinal processes and conjoined “clavicles” composed of rod-like units (indicated by arrows); B, internal view of operculum; C, Oblique posterior (ventral) view of operculum. D–F, *Paratriplicatella shangwanensis* Pan, Skovsted, Sun and Li, 2019; D–E, NIGPAS 172170 in (D) external view and (E) oblique lateral view, showing palisade-like row of rods (indicated by arrows in D) along anterior (dorsal) margin; F, NIGPAS 172171, internal view. G–I, *Protomicocornus triplicensis* Pan, Skovsted, Sun and Li, 2019; G–H, NIGPAS 167873 in oblique external (G) and anterior (H) views showing prominent, wall-like clavicles composed of rod-like units (indicated by arrows); I, NIGPAS 167872 in lateral view. All scale bars equal 200 μm .

(Butterfield and Nicholas, 1996, Fig. 4). The smallest specimen preserves what appear to be two short, spine-like miniature helens inside the conch. These two structures presumably represent incipient helens or very early stages in helen development (Martí Mus and Bergström, 2007). The length of the incipient helens in this specimen is approximately 50 μm , which is slightly less than half of the opercular width, and therefore comparable to what would have been the length of the clavicles (the operculum is also preserved inside the conch, but not well enough to allow identification of clavicles). Larger specimens in the same sample illustrate that with a doubling of width of the operculum, the length of the conch increased about 2.5 times while the increase in helen length is close to 12 times, which means a much faster growth rate of helens compared to conchs and opercula, at least in early growth stages (Butterfield and Nicholas, 1996). A growth series of the helens of a Silurian species is illustrated in Martí Mus et al. (2014; Fig. 4), showing how the smallest helens are short and spine-like and develop a

long, relatively open logarithmic spiral as they grow.

These observations show that helens were formed at an early growth stage, but later than the other elements of the hyolithid skeleton, that they were formed fully inside the conch and physically separated from other parts of the skeleton from the beginning. The length of the incipient helens roughly matches the calculated length of the clavicles at the same growth stage, as would be expected if helens were derived from clavicle rods during early ontogeny. The hyolithid did thus not possess functional helens in its earliest growth stages, but through rapid allometric growth, the incipient helens soon extended outside the operculum and probably attained sufficient length to allow the full range of helen functions before the hyolithid grew to a significant length.

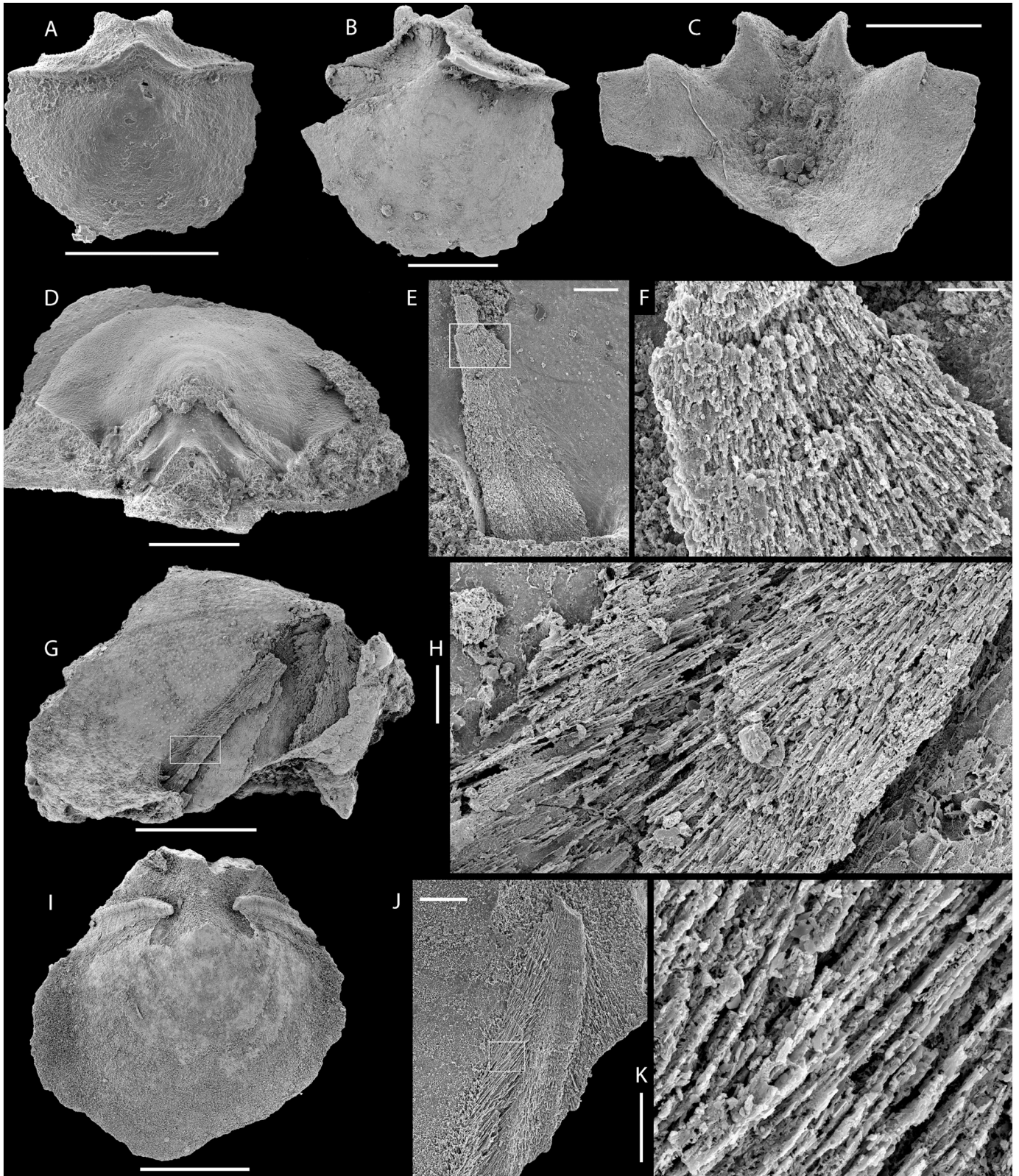


Fig. 6. Phosphatized hyolith opercula (*Parkula* sp. sensu Malinky and Skovsted, 2004) from the Bastion Formation, North-East Greenland (Cambrian Stage 4). A, NRM Mo191119, phosphatized operculum in dorsal view showing external morphology; B, NRM Mo191120, phosphatized operculum with left part of cardinal shield missing showing part of underlying internal mould with phosphatized clavicles; C, NRM Mo191121, internal posterior view of phosphatized operculum showing relative position of clavicles and cardinal processes separated by a wide trough; D-F, NRM Mo191122, internal mould with phosphatized clavicles; D, in oblique anterior view; E, lateral view of left phosphatized clavicle; F, detail of rectangular area in E, showing fibrous structure of clavicle; G-H, NRM Mo191123, internal mould with phosphatized clavicles; G, oblique lateral view; H, detail of rectangular area in G, showing fibrous structure in phosphatized clavicle; I-K, NRM Mo191124, internal mould with phosphatized clavicles; I, dorsal view; J, oblique lateral view of left clavicle; K, detail of rectangular area in J, showing fibrous structure of clavicle. Scale bars equal 500 μ m in A, B, D, G, I, 300 μ m in C, 100 μ m in E, J, 20 μ m in F, H and 10 μ m in K.

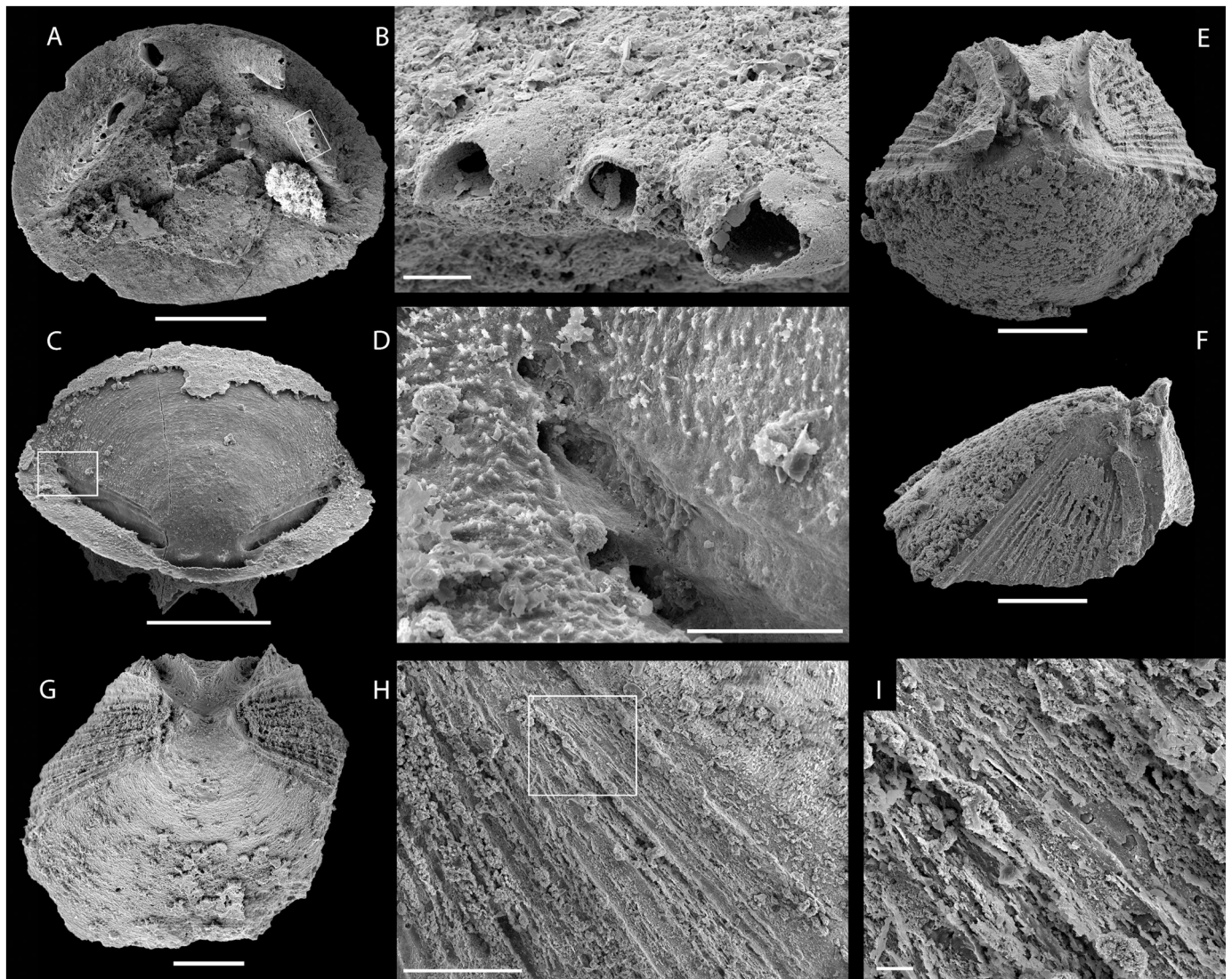


Fig. 7. Opercula of *Paramicrocornus zhenbaensis* Qian et al., 2001 from the Shuijingtuo Formation (Cambrian Series 2) of Shaanxi and Hubei provinces, South China. A, ELI XYB 13 AD-05, internal view. B, enlargement of rectangular area in A showing hollow tips of clavicle rods. C, ELI XYB 13 U-02, external view of exfoliated specimen showing slit-like hollows representing clavicles. D, enlargement of rectangular area in C showing hollow impressions of clavicle rods. E-F, ELI AJH S05 AJ-05, E, oblique view from the dorsal side of internal mould; F, lateral view, showing fan-like arrangement of clavicle rods. G-I, ELI AJH SJT 8-2-1 DF; G, dorsal view of internal mould; H, detail of left clavicle showing impressions of clavicle rods; I, detail of rectangular area in H, showing fibrous structure of individual clavicle rods. Scar bars equal 200 μm in A, C, E, F, G, 100 μm in H, 50 μm in D and 10 μm in B, I.

9. Helens and the evolution of hyolithids

As discussed above, hyolithids are characterized by having helens, a unique skeletal element, and an apomorphy of hyolithids that indicates that they form a monophyletic group. The late appearance of hyolithids compared to orthothecids, which lack helens, further indicates that hyolithids evolved from orthothecid ancestors and that the order Orthothecida is paraphyletic.

9.1. Evolution of helens

The evolution of hyolithids from orthothecid ancestors can be reconstructed through a distinct sequence of events.

1. *Externally fitting operculum.* Contrary to the majority of orthothecids, which had a retractable operculum, some early Cambrian taxa appear to have evolved externally fitting opercula. The inside of the opercula in some orthothecids such as *Cupitheca holocyclata* (Skovsted et al., 2016) expresses a raised rim, situated slightly inside

the margins of the opercula. This rim appears ideally constructed to secure the operculum from being displaced from the aperture of the conch when closing the aperture but makes little sense in a hyolith with a retractable operculum.

2. *Stabilizing, radially arranged structures on the inside of the operculum.* In some Cambrian orthothecids, such as *Conotheca* and *Majatheca* (Bengtson et al., 1990; Malinky and Skovsted, 2004; Kouchinsky et al., 2015; Pan et al., 2019), the internal raised rim is reinforced by a series of radially arranged rods attached to the internal surface of the operculum. These structures are reminiscent of clavicles in later hyolithids and were interpreted as protoclavicles by Dzik (1994). The most obvious function of these structures would be to protect the operculum from slipping sideways during for example a predatory attack. It seems likely that the well-defined clavicles of later hyolithids evolved from this kind of raised, radially arranged structures.
3. *Ligula and folded operculum.* Taxa such as *Protomicrocornus* (Pan et al., 2019) and *Paramicrocornus* (Zhang et al., 2018) illustrate that the ligula, and the folded operculum that accommodates to it, were

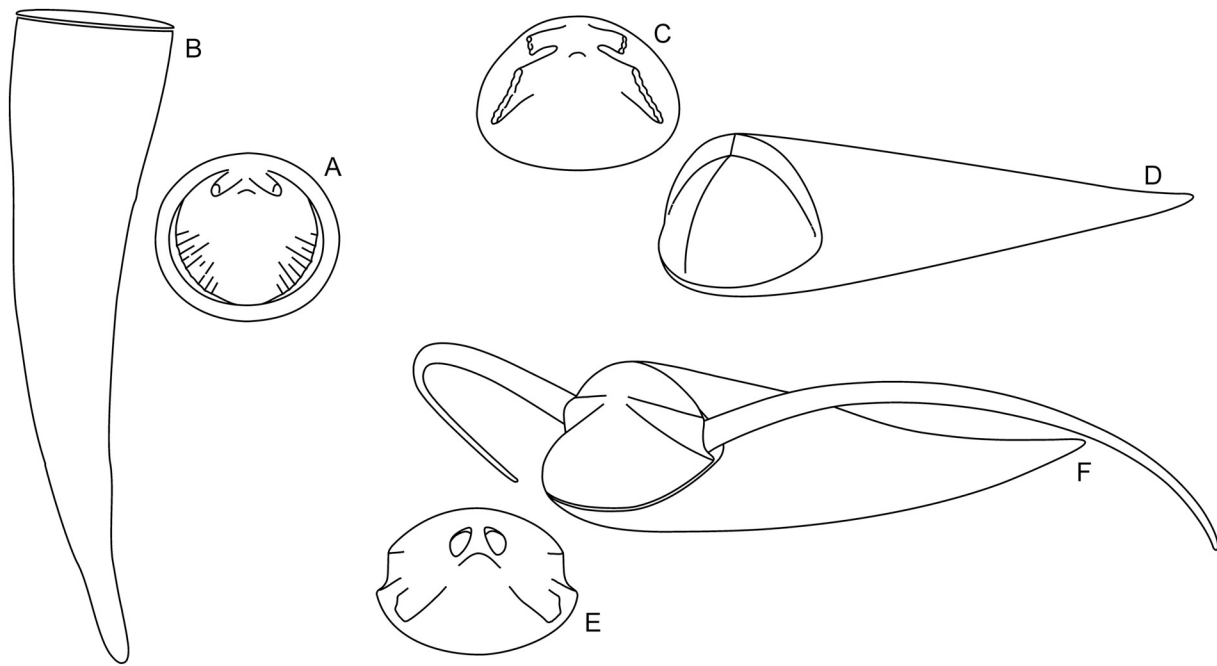


Fig. 8. Schematic drawings of hyoliths in their presumed life position, illustrating stages in the evolution of hyoliths discussed in the text. A-B, internal surface of the operculum and complete skeleton of a *Conotheca*-like hyolith illustrating stage 2; C-D, internal surface of the operculum and complete skeleton of a *Paramicrocornus*-like hyolith illustrating stage 3; internal surface of the operculum and complete skeleton of a typical (post early Cambrian) hyolithid illustrating stage 4.

acquired before helens. The presence of a ligula, an extended ventral shelf hindering the access of the soft parts to the substrate, points to filter- or suspension feeding adaptations in the hyolithid lineage. In the above taxa, clavicles are well defined and consist of a series of laterally oriented, radially arranged rods that are progressively added along the opercular fold.

4. *Detachment of clavicle rods and origin of helens.* A later step in the evolution of the Hyolithida would be the detachment of a pair of clavicle rods from the opercular surface, and the subsequent allometric growth of the rods into helens. Taxa such as the early Cambrian *Parkula* and *Parakorilithes* (Bengtson et al., 1990) already represent this stage, having acquired all the features that characterize hyolithids.

10. Conclusions

Hyolith helens were morphological innovations defining a hyolith subgroup, the Order Hyolithida, and first appear in the fossil record around the start of Cambrian Series 2. Helens were massive, mineralized spines, not associated with external soft tissues and attached to muscles proximally, and must have had mechanical functions. There is evidence suggesting that helens were used as stilts to elevate the aperture and feeding organs above the sea floor to facilitate filter/suspension feeding. The helens could also have been used to orient the animal in relation to prevailing currents, further improving filter/suspension feeding efficiency.

In early Cambrian hyolithid-like hyoliths such as *Protomicrocornus* and *Paramicrocornus*, clavicles are constructed of rod-like units forming palisade-like walls. We propose that hyolithid helens evolved from clavicles through detachment and continued growth of individual clavicle rods. These structures share a basic morphology as unbranched rods with lenticular cross section. Both clavicle rods and helens have a fibrous microstructure, and may have had an important component of organic matter. Also both structures start to form at the same location, internally, paralleling the fold of the operculum.

The monophyletic Hyolithida evolved from ancestors within a paraphyletic Orthothecida. The evolution of hyolithids can be

reconstructed through a sequence of evolutionary events including: 1, *Externally fitting operculum*; 2, *Stabilizing, radially arranged structures on the inside of the operculum*; 3, *Ligula and folded operculum*; 4, *Detachment of clavicle rods and origin of helens*.

Helens evolved relatively late in the hyolithid lineage, and their late ontogenetic development probably mirrors their late appearance in the phylogeny of hyoliths. During the ontogeny of hyolithids, they start to form inside the conch, as small spines coinciding in length with the clavicles. As the hyolithid develops, helens experience allometric increase in length and extend outside the conch. This growth pattern is to be expected if the main functions of helens was to re-orient the shell on the seafloor and to lift the conch aperture above the sea floor to increase efficiency of filter/suspension feeding.

Declaration of Competing Interest

The authors report no conflicts of interest.

Acknowledgements

The authors wish to extend a warm thank you to John S. Peel, Glenn A. Brock, Xingliang Zhang and Timothy P. Topper for valuable discussions and access to specimens. The continuous fossil collections of various members of the Early Life Institute, Northwest University, Xi'an are sincerely acknowledged. We thank Martin Valent and an anonymous reviewer for constructive reviews that substantially improved the manuscript.

Funding

This work was financed by grants from the Swedish Research Council [VR2016-04610 to CBS]; the Spanish Ministerio de Economía y Empresa (MINECO) [CGL2017-87631-P to MMM]; the National Natural Science Foundation of China [41890844, 41425008, 41621003 and 41720104002 to ZZ; 41772002 to CBS]; the Independent Innovation Project of graduate students of Northwest University [YZZ17196 to LF]; and the Overseas Expertise Introduction Centre for Discipline Innovation [111 Center: D17013].

References

- Babcock, L.E., Robison, R.A., 1988. Taxonomy and paleobiology of some Middle Cambrian *Scenella* (Cnidaria) and hyolithids (Mollusca) from western North America. In: University of Kansas Paleontological Contributions. 121. pp. 1–22.
- Balthasar, U., Skovsted, C.B., Holmer, L.E., et al., 2009. Homologous skeletal secretion in tommotiids and brachiopods. *Geology* 37 (12), 1143–1146.
- Bengtson, S., Conway Morris, S., Cooper, B.J., et al., 1990. Early Cambrian fossils from South Australia. In: Memoir of the Association of Australasian Paleontologists. 9. pp. 1–364.
- Berg-Madsen, V., Valent, M., Ebbestad, J.O.R., 2018. An orthothecid hyolith with a digestive tract from the early Cambrian of Bornholm, Denmark. *GFF* 140 (1), 25–37.
- Betts, M.J., Paterson, J.R., Jago, J.B., et al., 2016. A new lower Cambrian shelly fossil biostratigraphy for South Australia. *Gondwana Res.* 36, 163–195.
- Betts, M.J., Paterson, J.R., Jago, J.B., et al., 2017. Global correlation of the early Cambrian of South Australia: Shelly fauna of the *Dalrympia odyseae* Zone. *Gondwana Res.* 46, 240–279.
- Betts, M.J., Paterson, J.R., Jacquet, S.M., et al., 2018. Early Cambrian chronostratigraphy and geochronology of South Australia. *Earth Sci. Rev.* 185, 498–543.
- Butterfield, N.J., Nicholas, C.J., 1996. Burgess Shale-type preservation of both non-mineralizing and 'shelly' Cambrian organisms from the Mackenzie Mountains, north-western Canada. *J. Paleontol.* 70 (6), 893–899.
- Chen, J.Y., 2004. The Dawn of Animal World. Jiangsu Science and Technology Press, Nanjing, China, pp. 1–366 (in Chinese with English summary).
- Chen, F., Zhang, Z., Betts, M.J., Zhang, Z., Liu, F., 2019. First report on Guanshan Biota (Cambrian Stage 4) at the stratotype area of Wulongqing Formation in Malong County, Eastern Yunnan, China. *Geosci. Front.* 10 (4), 1459–1476.
- Devaere, L., Clausen, S., Álvaro, J.J., et al., 2014. Terreneuvian orthothecid (Hyolitha) digestive tracts from northern Montagne Noire, France; taphonomic, ontogenetic and phylogenetic implications. *PLoS One* 9 (2), e88583.
- Dzik, J., 1980. Ontogeny of *Bactrotheca* and related hyoliths. *Geologiska Föreningen i Stockholm Förhandlingar* 102 (3), 223–233.
- Dzik, J., 1994. Evolution of 'small shelly fossils' assemblages of the early Paleozoic. *Acta Palaeontol. Pol.* 39 (3), 247–313.
- Fisher, D.W., 1962. Small conoidal shells of uncertain affinities. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part W. Geological Society of America, New York, University of Kansas Press, Lawrence*, pp. 98–140.
- Galle, A., Parsley, R.L., 2005. Epibiont relationships on hyoliths demonstrated by Ordovician trepostomes (Bryozoa) and Devonian tabulates (Anthozoa). *Bull. Geosci.* 80 (2), 125–138.
- Harvey, T.H., Butterfield, N.J., 2011. Great Canadian Lagerstätten 2. Macro and microfossils of the Mount Cap Formation (early and middle Cambrian, Northwest Territories). *Geosci. Can.* 38 (4).
- He, T.G., Pei, F., Fu, G.H., 1984. Small shelly fossils from the lower Cambrian Xinji Formation in Fangcheng County, Henan Province. *Acta Palaeontol. Sin.* 23, 350–357 (In Chinese with English summary).
- Hou, X.G., Bergström, J., Wang, H.F., et al., 1999. The Chengjiang Fauna: Exceptionally Well-Preserved Animals from 530 Million Years Ago. Yunnan Science and Technology Press, Kunming, pp. 1–80 (In Chinese with English summary).
- Hou, X.G., Aldridge, R.J., Bergström, J., et al., 2004. The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life. Blackwell Publishing, Oxford 233 pp.
- Hou, X.G., Siveter, D.J., Siveter, D.J., et al., 2017. The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life. John Wiley & Sons.
- Hu, S.X., Luo, H.L., Zhu, M.Y., et al., 2013. The Guanshan Biota. Yunnan Science and Technology Press, Kunming.
- Jacquet, S.M., Betts, M.J., Huntley, J.W., et al., 2019. Facies, phosphate, and fossil preservation potential across a Lower Cambrian carbonate shelf, Arrowie Basin, South Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 533, 109200.
- Kimmig, J., Pratt, B.R., 2018. Coprolites in the Ravens Throat River Lagerstätte of Northwestern Canada: implications for the middle Cambrian food web. *Palaios* 33 (4), 125–140.
- Kouchinsky, A., Bengtson, S., Runnegar, B., et al., 2012. Chronology of Early Cambrian biomineralization. *Geol. Mag.* 149, 221–251.
- Kouchinsky, A., Bengtson, S., Clausen, S., et al., 2015. An early Cambrian fauna of skeletal fossils from the Emyaksin Formation, northern Siberia. *Acta Palaeontol. Pol.* 60 (2), 421–513.
- Landing, E.D., 1993. In situ earliest Cambrian tube worms and the oldest metazoan-constructed biostrome (Placentian Series, southeastern Newfoundland). *J. Paleontol.* 67 (3), 333–342.
- Landing, E.D., Kröger, B., 2012. Cephalopod ancestry and ecology of the hyolith "*Allatheca*" *degeeri* s.l. in the Cambrian Evolutionary Radiation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 353–355, 21–30.
- Li, L.Y., Zhang, X.L., Skovsted, C.B., et al., 2019. Homologous shell microstructures in Cambrian hyoliths and molluscs. *Paleontology* 62 (4), 515–532.
- Liu, F., Skovsted, C.B., Topper, T.P., et al., 2020. Are hyoliths Palaeozoic lophophorates? *Natl. Sci. Rev.* 7, 453–469.
- Luo, H., Li, Y., Hu, S., et al., 2008. Early Cambrian Malong Fauna and Guanshan Fauna From Eastern Yunnan, China. 134 Yunnan Science and Technology Press, Kunming, China (in Chinese with English summary).
- Malinky, J.M., 2009a. Permian hyolithida from Australia: the last of the hyoliths? *J. Paleontol.* 83 (1), 147–152.
- Malinky, J.M., 2009b. First occurrence of *Orthotheca* Novák, 1886 (Hyolitha, Early Devonian) in North America. *J. Paleontol.* 83 (4), 588–596.
- Malinky, J.M., Skovsted, C.B., 2004. Hyoliths and small shelly fossils from the Lower Cambrian of North-East Greenland. *Acta Palaeontol. Pol.* 49 (4).
- Malinky, J.M., Yochelson, E.L., 2007. On the Systematic Position of the Hyolitha (Kingdom Animalia). *Memoirs of the Association of Australasian Paleontologists*. 34. pp. 521.
- Maloof, A.C., Porter, S.M., Moore, J.L., et al., 2010. The earliest Cambrian record of animals and ocean geochemical change. *Bulletin* 122 (11–12), 1731–1774.
- Marek, L., 1963. New Knowledge on the Morphology of Hyolithes. *Sborník geologických věd, řada Paleontologie*. 1. pp. 53–72.
- Marek, L., 1966. New hyolithid genera from the Ordovician of Bohemia. *Časopis Národního Muzea* 135, 89–92.
- Marek, L., 1967. The Class Hyolitha in the Caradoc of Bohemia. *Sborník geologických věd*. 9. pp. 51–112.
- Marek, L., Parsley, R.L., Galle, A., 1997. Functional morphology of hyoliths based on lumina studies. *Věstník Českého geologického ústavu* 72 (4), 277–283.
- Martí Mus, M., 2016. A hyolithid with preserved soft parts from the Ordovician Fezouata Konservat-Lagerstätte of Morocco. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 460, 122–129.
- Martí Mus, M., Bergström, J., 2005. The morphology of hyoliths and its functional implications. *Paleontology* 48, 1139–1167.
- Martí Mus, M., Bergström, J., 2007. Skeletal microstructure of helens, lateral spines of hyoliths. *Paleontology* 50, 1231–1243.
- Martí Mus, M., Jeppsson, L., Malinky, J.M., 2014. A complete reconstruction of the hyolithid skeleton. *J. Paleontol.* 88, 160–170.
- Missarzhevsky, V.V., 1989. Drevnishiye Skeletnye Okamenelosti I Stratigrafija Pogranichnykh Tolsch Kembrija I Dokembrija. [The Oldest Skeletal Fossils and Stratigraphy of Precambrian and Cambrian Boundary Beds]. 237 pp. Trudy Geologicheskogo Instituta Akademii Nauk SSSR 443. (In Russian).
- Moore, J.L., Porter, S.M., 2018. Plywood-like shell microstructures in hyoliths from the middle Cambrian (Drumian) Gowers Formation, Georgina Basin, Australia. *Paleontology* 61 (2).
- Moysiuk, J., Smith, M.R., Caron, J.B., 2017. Hyoliths are Palaeozoic lophophorates. *Nature* 541, 394–397.
- Orłowski, S., Waksmundzki, B., 1986. The oldest hyolitha in the lower Cambrian of the Holy cross mountains. *Acta Geol. Pol.* 36 (1–3), 225–232.
- Pan, B., Skovsted, C.B., Sun, H.J., et al., 2019. Biostratigraphical and palaeogeographical implications of Early Cambrian hyoliths from the North China Platform. *Alcheringa* 43, 351–380.
- Peel, J.S., 2010. Articulated hyoliths and other fossils from the Sirius Passet Lagerstätte (early Cambrian) of North Greenland. *Bull. Geosci.* 85 (3), 385–394.
- Qian, Y., 1978. The early Cambrian hyoliths of central and southwest China and their stratigraphical significance. In: *Memoir of the Nanjing Institute of Geology and Palaeontology*. 11. pp. 1–43 (in Chinese).
- Qian, Y., Zhang, S.B., 1983. Small shelly fossils from the Xihaoing Member of the Tongying Formation in Fangxian County of Hubei Province and their stratigraphical significance. *Acta Palaeontol. Sin.* 22, 82–94 (in Chinese with English abstract).
- Qian, Y., Xie, Y.S., He, T.G., 2001. Hyoliths of the lower Cambrian Chingchussuan Stage in South Shaanxi Province. *Acta Palaeontol. Sin.* 40 (1), 37–43 (in Chinese with English abstract).
- Rozanov, A.Y., Missarzhevsky, V.V., Volkova, N.A., et al., 1969. The Tommotian Stage and the Cambrian lower boundary problem. In: *Transactions of the Academy of Sciences of the USSR Nauka*. 206. pp. 1–380.
- Runnegar, B., Pojeta, J., Morris, N.J., et al., 1975. Biology of the hyolitha. *Lethaia* 8 (2), 181–191.
- Sepkoski Jr., J.J., Bambach, R.K., Raup, D.M., et al., 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293 (5832), 435.
- Skovsted, C.B., 2006. Small Shelly fauna from the upper Lower Cambrian Bastion and Ella Island formations, north-east Greenland. *J. Paleontol.* 80 (6), 1087–1112.
- Skovsted, C.B., Peel, J.S., 2007. Small shelly fossils from the argillaceous facies of the Lower Cambrian Forteau Formation of western Newfoundland. *Acta Palaeontol. Pol.* 52 (4).
- Skovsted, C.B., Topper, T.P., Betts, M.J., et al., 2014. Associated conchs and opercula of *Triplicatella disdona* (Hyolitha) from the early Cambrian of South Australia. *Alcheringa* 38 (1), 148–153.
- Skovsted, C.B., Pan, B., Topper, T.P., et al., 2016. The operculum and mode of life of the lower Cambrian hyolith *Cupitheca* from South Australia and North China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 443, 123–130.
- Stachacz, M., 2012. Ichnology of Czarna shale formation (Cambrian, Holy cross mountains, Poland). *Ann. Soc. Geol. Pol.* 82 (2), 105–120.
- Sun, H.J., Babcock, L.E., Peng, J., et al., 2016. Three-dimensionally preserved digestive systems of two Cambrian hyoliths (Hyolitha). *Bull. Geosci.* 91 (1).
- Sun, H.J., Babcock, L.E., Peng, J., Kastigar, J.M., 2017. Systematics and palaeobiology of some Cambrian hyoliths from Guizhou, China, and Nevada, USA. *Alcheringa* 41 (1), 79–100.
- Sun, H.J., Smith, M.R., Zeng, H., et al., 2018a. Hyoliths with pedicles illuminate the origin of the brachiopod body plan. *Proc. R. Soc. Biol. Sci.* 285, 20181780.
- Sun, H.J., Zhao, F.C., Wen, R.Q., et al., 2018b. Feeding strategy and locomotion of Cambrian hyoliths. *Paleoworld* 27 (3), 334–342.
- Sysoev, V.A., 1957. To the morphology, systematics and systematic position of the hyoliths. In: *Akademiâ Nauk SSSR, Doklady*. 116. pp. 304–307 (in Russian).
- Valent, M., Fatka, O., Marek, L., 2017. Slapylitidae: a new family of hyoliths (Cambrian–? Devonian; Baltica, Laurentia, Gondwana). *PalZ* 91 (4), 497–505.
- Yu, W., 1974. Cambrian Hyoliths. In: *Handbook of Stratigraphy and Palaeontology of Southwest China*; Edited by Nanjing Institute of Geology and Palaeontology. Academia Sinica, Science Press, Beijing, pp. 111–112.
- Zhang, Z.L., Skovsted, C.B., Zhang, Z.F., 2018. A hyolithid without helens preserving the oldest hyolith muscle scars; palaeobiology of *Paramicrocornus* from the Shujingtu Formation (Cambrian Series 2) of South China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 489, 1–14.
- Zhao, F.C., Smith, M.R., Yin, Z.J., et al., 2017. *Orthozanclus elongata* n. sp. and the significance of sclerite-covered taxa for early trochozoan evolution. *Sci. Rep.* 7, 16232.