The operculum and mode of life of the lower Cambrian hyolith

Cupitheca from South Australia and North China

By Christian B. Skovsted¹, Bing Pan^{2, 3}, Timothy P. Topper¹, Marissa J. Betts⁴, Guoxiang Li² & Glenn A. Brock⁴

¹ Christian B. Skovsted, Timothy P. Topper [christian.skovsted@nrm.se; timothy.topper@nrm.se]; Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

² Bing Pan, Guoxiang Li [bpan@nigpas.ac.cn; gxli@nigpas.ac.cn]; State Key Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

³ Bing Pan; University of Chinese Academy of Sciences, Beijing 100049, China

⁴ Marissa J. Betts; Glenn A. Brock [marissa.betts@mq.edu.au; glenn.brock@mq.edu.au]; Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Abstract

The operculum of the problematic tubular fossil *Cupitheca holocyclata* Bengtson in Bengtson et al. 1990 is described for the first time based on collections from South Australia and North China. The phosphatized sub-circular operculum exhibits well defined cardinal processes and a narrow cardinal shield unequivocally demonstrating that *Cupitheca* is a hyolith, probably an orthothecid. *Cupitheca holocyclata* has an almost global distribution in Cambrian Stage 3-4. The apical structure of the operculum is an elevated, disc-shaped platform with a concave base and a marginal rim that could represent the scar of a specialized larval attachment structure, perhaps anchoring the larval hyolith

to a sediment grain, algae or other benthic substrate. *Cupithec*a probably had a pelagic larval stage and settled on the seafloor by attachment of the apical disc to suitable substrates before developing a free-living benthic adult lifestyle. This contrasting mode of life compared to other hyolith genera suggests that the group had already evolved a range of distinct lifestyles in the Cambrian, providing significant clues into their ecology and distribution.

Key words: *Cupithec*a; *Operculum*; Lower Cambrian; South Australia; North China; Hyolitha; Orthothecida.

Introduction

*Cupithec*a Duan in Xing et al., 1984 was originally described from cup-shaped fossils with blunt, rounded apical terminations from the early Cambrian of China (Xiao & Zhou 1984; Xing et al. 1984; see discussions in Bengtson et al. 1990 and Pan et al. 2015). After studying well preserved specimens from South Australia, Bengtson (in Bengtson et al. 1990) concluded that these fossils were likely to represent elongate tubes, with the characteristic rounded terminations representing moulds of transverse septa. According to the interpretation developed by Bengtson (in Bengtson et al, 1990) the apical portion of the tubes were periodically lost by decollation in connection with the formation of septa in a manner similar to that of the recent gastropod *Caecum* (Fretter & Graham 1978; Bandel 1996). The seemingly incomplete nature of the aperture has been a significant hindrance in understanding the taxonomy and mode of life of *Cupithec*a. The tubes have been compared to hyoliths, despite the unusual decollating growth mode and the lack of an identifiable operculum (Xiao & Zhou 1984; Xing et al. 1984; Bengtson in Bengtson et al. 1990) and although *Cupithec*a has not formally been placed in the Hyolitha, these fossils have generally been described together with hyoliths (Demidenko in Gravestock et al. 2001; Wrona 2003; Malinky & Skovsted 2004; Topper et al. 2009).

Hyoliths are a group of Palaeozoic skeletal fossils combining an elongate, tubular shell (conch) with a lid-like operculum (Marek 1963). Two Orders are recognized, the Hyolithida Syssoiev, 1957 and the Orthothecida Marek, 1966. The Hyolithida have conchs characterized by triangular cross-sections and elongate ventral ligula, opercula divided into distinct conical and cardinal shields (Marek 1967). The skeleton of hyolithids also includes additional skeletal elements in the form of narrow, spine shaped helens of uncertain function. Hyolithids are often reconstructed as epibenthic suspension feeders (Marti-Mus et al. 2014). The Orthothecida are characterized by conchs with circular or rectangular cross sections with planar apertures and flat or conical opercula that were likely retractable into the conch (Marek 1966). Orthothecids appear to lack helens and based on their sediment-filled guts are usually reconstructed as infaunal or semi-infaunal deposit feeders (Devaere et al. 2014). However, this strict division of hyoliths into hyolithids and orththecids is difficult to apply to some Cambrian hyolith taxa that seem to possess traits of both orders (Malinky and Skovsted 2004).

Bengtson (in Bengtson et al. 1990) discussed the possible presence of an operculum in *Cupitheca* and illustrated circular objects occurring together with *Cupitheca holocyclata* (Bengtson in Bengtson et al., 1990) as possible opercula (Bengtson et al. 1990, fig. 138). However, the illustrated objects exhibit no morphological features that unequivocally connect them to *Cupitheca* and they lack structures comparable to the clavicles and cardinal processes typical of hyolith opercula. Herein we report new collections of well-preserved specimens of *Cupitheca* from the lower Cambrian Ajax and Wilkawillina limestones of Mt Scott and Bunyeroo Gorge in the Flinders Ranges, South Australia and from the basal part of the lower Cambrian Xinji Formation at Shangwan section of Luonan County in Shannxi Province, and Sanjianfang section of Yexian County in Henan Province, North China Platform. The new material from Australia and China, for the first time combines phosphatized tubes of *Cupitheca* with well-preserved opercula with characteristic hyolith features and thus confirming the hyolith affinity of *Cupitheca*. The opercula differ in several respects from the circular objects described by Bengtson (in Bengtson et al. 1990), and the latter are likely to be unrelated to

Cupitheca. Given the biological importance of the opercula to the genus, we also investigate the mode of life of *Cupitheca*, providing insights into the ecological diversity and significance of the Hyolitha in the Cambrian.

Geological setting and Materials and Methods

South Australia

The majority of investigated specimens of *Cupitheca holocyclata* from South Australia were derived from acid resistant residues of limestone samples collected in 2006 from the Ajax Limestone (Hawker Group) at section AJX-M in the Mt Scott Range in the Flinders Ranges, South Australia (Fig. 1A). The stratigraphic range of *C. holocyclata* at this section spans the *Abadiella huoi* and *Pararaia tatei* trilobite zones, which correlates with unnamed Cambrian Series 2, Stage 3 (Betts et al. 2015). For detailed geographical and stratigraphical information on this section see Brock et al (2006), Topper et al. (2011) and Skovsted et al. (2012, 2015). A single operculum of *C. holocyclata* was also recovered from a sample (BUN3*), collected from the Wilkawillina Limestone at Bunyeroo Gorge (Fig. 1A) by the late Brian Daily. Whilst, Daily did not provided exact stratigraphic information for this sample, but the shelly fossil assemblage recovered from this sample includes abundant *D. macroptera* which indicates a level below the Flinders Unconformity, probably equivalent to the *A. huoi* trilobite Zone (Skovsted et al. 2015).

Collected samples were processed by digestion in 10% acetic acid at Macquarie University in Sydney, Australia. Fossils were manually picked from the residues under stereo microscope and selected specimens were placed on carbon-stubs, coated by gold and depicted using the Scanning Electron Microscopy facility (SEM) at the Swedish Museum Natural History in Stockholm, Sweden. All illustrated specimens are housed in collections of the South Australian Museum, Adelaide (acronym SAMP).

Figure 1

Maps outlining the location of sampled sections in Australia and China. A, Map of the Arrowie Basin in South Australia with sampled localities AJX-M (Mt. Scott) and BUN (Bunyerroo Gorge) indicated. A, AJX-M section at Mt. Scott. B, Location of Shangwan section in Shaanxi Province, China. C, Location of Sanjianfang section in Henan Province. D, Map of mainland China with sampled locations in B and C indicated. For more detailed geographic and stratigraphic information on South Australian sections see Skovsted et al. 2012, 2015. For more detailed geographic and stratigraphic information on Chinese sections see Li et al. 2014 and Pan et al. 2015.

North China

The opercula of *Cupithecra holocyclata* from China were recovered from the Xinji Formation of two sections (Shangwan [Zhangwan], Shimen Town, Luonan County, Shaanxi Province and Sanjianfang,

Baoan Town, Yexian County, Henan Province) on the south margin of the North China platform (Fig. 1B-D). At the Shangwan section, *C. holocyclata* occur in the 0.8 m thick basal bed of the Xinji Formation. For detailed stratigraphical and palaeontological information on this section see Li et al. (2014). At the Sanjianfang section, the Xinji Formation is about 100 m thick. The 90 m lower part consists mainly of siltstone, quartz sandstone and shales. The 10 m upper part consists mainly of argillaceous limestones and sandy dolomite. The opercula of *C. holocyclata* were collected from the 2-m-thick argillaceous limestones with abundant small shelly fossils at the base of the upper part. The Xinji Formation has been correlated with the *Drepanuloides* Biozone of the middle Tsanglangpuan stage (Cambrian Stage 4) on the Yangtze platform (Li et al. 2014).

Fossils were recovered through acetic acid (~10%) maceration of sandy limestone and argillaceous limestone samples and picked from the residues under stereo microscope. The selected specimens were placed on metal stubs, coated by gold and depicted using the Scanning Electron Microscopy facility (SEM) at the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (acronym NIGPAS), Nanjing. All the illustrated specimens are housed in NIGPAS.

Taxonomic notes

The taxonomic history of the name *Cupitheca* is complicated with similar fossils described under different names more or less simultaneously in two Chinese publications (Xiao & Zhou 1984; Xing et al. 1984). The generic name *Actinotheca* Xiao & Zhou, 1984 was preferred by Bengtson (in Bengtson et al. 1990) but this name is a junior homonym of the tabulate coral genus *Actinotheca* Frech, 1889; see Demidenko in Gravestock et al. 2001). The next available junior synonym is *Cupitthea* Duan in Xing et al., 1984, but this name was considered by Wrona (2003) as an inadvertent misspelling of *Cupitheca* Duan in Xing et al., 1984 and the latter was chosen as the valid name for this genus in accordance with the rules of the ICZN (Wrona 2003, p. 200). As it can not presently be confirmed that

all fossils that have been described as *Cupitheca* (or its many synonyms; see discussion below) are closely related, *Cupitheca* may prove to represent a form taxon. However, at the present time we consider the morphology of the countersunk rim with tubules around the transverse septum, distinctive enough to uphold the generic uniqueness.

Bengtson (in Bengtson et al. 1990) described *Cupitheca holocyclata* and *C. clathrata* (Bengtson in Bengtson et al., 1990) as separate species occurring at different stratigraphic levels in the lower Cambrian section at Horse Gully, South Australia and also reported indeterminate specimens of *Cupitheca* (as *Actinotheca* sp.) from the Ajax Limestone at Mt. Scott. Morphologically, *C. holocyclata* and *C. clathrata* were exclusively distinguished by differences in ornamentation, with simple transverse ornament in *C. holocyclata* combined with longitudinal ribs in *C. clathrata*. Specimens of *Cupitheca* from the Ajax Limestone in our collection show an ornament more or less intermediate between that of the two morphospecies from Horse Gully, displaying a weakly expressed longitudinal ornament superimposed on the more strongly developed transverse ribs (Fig. 2A, B). This suggests that the two forms described by Bengtson (in Bengtson et al. 1990) represent variations of a single species and we refer our material to the first named species, *C. holocyclata*.

Conchs of *Cupitheca* from the Xinji Formation at Shangwan section in Shaanxi Province, North China has recently been described by Pan et al. (2015) who recognized two distinct co-occurring species; *Cupitheca holocyclata* with distinctive transverse ornament and *C. costellata* (Xiao & Zhou, 1984) with longitudinal ornament only. The co-occurrence of these forms at Shangwan in Shaanxi Province and at Sanjianfang in Henan Province suggests that they, unlike the Australian species discussed above may represent different biological species (Pan et al. 2015). Although the external surface is often partly covered by diagenetic minerals, the opercula from Shangwan and Sanjianfang documented herein appear to differ slightly in external surface ornament. However, the majority of specimens appear to combine radial and concentric ornament as in the Australian opercula referred to *C. holocyclata*. Consequently, we refer the Chinese opercula to *C. holocyclata*, although we

acknowledge that the Australian and Chinese specimens may differ slightly in age and that it may be difficult to distinguish opercula of closely related species such as *C. holocyclata* and *C. costellata*.

Tubular specimens of *Cupitheca holocyclata*

The majority of specimens of *Cupitheca holocyclata* in our samples from both South Australia and North China are short tube segments terminating in a gently convex septum. As suggested by Bengtson (in Bengtson et al. 1990), these specimens probably represent individual conch segments that were decollated during the life of the organism. Septate hyoliths of differing morphology are also common in the Cambrian (Malinky & Berg-Madsen 1999; Landing & Kröger 2012) and moulds of individual segments between septa in such tubes are a common constituent in SSF faunas (CBS pers. obs.). Tubes referred to *Cupitheca* differ from other septate hyoliths by the presence of characteristic structures along the circumference of the conch wall close to the septum, interpreted by Bengtson (in Bengtson et al. 1990) as specific adaptations to facilitate dissolution and decollation of the tube along a transverse zone close to a previously formed internal septum. These adaptations include a countersunk rim around the septum and tubules through the shell arranged along the rim (see discussion by Bengtson in Bengtson et al. 1990, p. 204-208, fig. 136).

Figure 2

Conch and operculum of *Cupitheca holocyclata* (Bengtson in Bengtson et al., 1990) from Mt. Scott, Flinders Ranges, South Australia. A-C, SAMPXXXX1 from sample AJAX-M/371; A, lateral view of complete specimen presumably representing the living chamber; B, Detail of A showing apertural region with ornament and commissure of conch; C, detail of A showing abapical termination of conch with apical septum and countersunk rim with traces of tubules. D, SAMPXXXX6 from sample AJAX-M/305 (see also Fig. 4L-M); lateral view of operculum arranged to fit the apertural opening of conch in B (obs. image is horizontally flipped). Scale bars equal 1 mm in A and 200µm in B-D.

Bengtson (in Bengtson et al. 1990, fig. 139) also illustrated apparently more complete specimens of *Cupitheca* that may represent the living chamber of the animal. One such well preserved specimen is also present in our material from the Ajax Limestone, Mt. Scott (Fig. 2). The gently curved conch is about 2 mm long, gently tapering with terminal diameters of 300 µm and 650 µm respectively (Fig. 2A). The cross section is almost circular and the narrow end terminates in a convex septum with countersunk rim preserving traces of tubules (Fig. 2C). The external ornament reveals a combination of strong, transverse growth-lines and finer, longitudinal ribs resulting in a weakly reticulate pattern (Fig. 2B). The aperture is not planar and circumscribe a gently undulating curve which is mirrored by the transverse growth lines (Fig. 2B).

202 **Opercula of *Cupitheca holocyclata***

203 South Australia

204 Tubular fossils, both decollated segments and more or less complete conchs, of *Cupitheca*
205 *holocyclata* occur in our samples together with low, sub-circular to sub-triangular hyolith opercula
206 with a characteristic external ornament of fine radiating and concentric ribs (Fig. 3). These ribs match
207 the transverse and longitudinal striations of the associated *C. holocyclata* conchs in size, amplitude
208 and distribution (Fig. 3E). In plan external view, the opercula are sub-circular to sub-triangular with a
209 flattened ventral margin. The external surface of the opercula exhibit a low, sloping conical shield
210 and a narrow hemi-circular cardinal shield along the dorsal margin (Fig. 3A-F). The furrow between
211 conical and cardinal shields is poorly defined. The raised apex is situated on the conical shield, close
212 to the dorsal margin (Fig. 3A, E, G). In lateral view, it is apparent that the edge of the operculum
213 follows a gently undulating curve, which closely matches the outline of transverse growth-lines on
214 the associated conchs (Figs 2C, D, 3M). The internal surface of the opercula exhibits a narrow distal
215 ridge along the dorsal and lateral margins (Fig. 3I-L). Two well defined, blade-like cardinal processes
216 extends almost perpendicularly from the inner slope of the marginal ridge close to the dorsal margin
217 (Fig. 3I, L). The angle formed by the processes is close to 60° and they terminate in smoothly rounded
218 edges (Fig. 3K). The internal surface is otherwise smooth and no traces of clavicles can be observed.

219 The apex of the operculum of *Cupitheca holocyclata* is characterized by a transversely oval
220 structure with a diameter of about 150 µm, which is raised (by up to 50 µm) above the conical shield
221 (Fig. 3G, H). The apical structure is a flat or gently convex plate encircled by a 5-10 µm high wall (Fig.
222 3H). The central part of the apical structure of the best preserved specimen exhibits a weakly defined
223 circular depression about 25 µm across (Fig. 3G).

Figure 3: Opercula of *Cupithea holocyclata* (Bengtson in Bengtson et al., 1990); from the Flinders Ranges, South Australia; all except A-B from Mt. Scott. A-B, SAMPXXXX2 from sample BUN3*, Bunyeroo Gorge; A, external view; B, oblique lateral view. C, SAMPXXXX3 from sample AJX-M/282, external view. D-H, SAMPXXXX4 from sample AJX-M/323.5; D, oblique lateral

view; E, external view; F, oblique dorsal view showing presence of cardinal processes; G, detail of D showing apical structure in lateral view; H, detail of apical structure viewed from the ventral side. I-K, SAMPXXX5 from sample AJX-M/281; I, internal view; J, oblique lateral view of internal surface; K, detail of cardinal processes in oblique ventral view. L-M, SAMPXXX6 from sample AJX-M/305 (see also Fig. 3D), L, internal view; M, lateral view. Scale bars equal 200µm in A-F, I-J, L-M, 100µm in G-H and 250µm in K.

North China

The opercula associated with *Cupitheca* conchs at Shangwan and Sanjianfang in North China are very similar to the Australian specimens described above in outline and gross morphology (Fig. 4). The Chinese specimens are partly fragmentary and most are strongly covered by diagenetic minerals. However, they appear to exhibit a greater variation in shape and external surface ornament compared to the Australian specimens. Opercula of similar size may be either subtriangular (Fig. 4A, D, G) or sub-circular (Fig. 4B, H, K, L) and either the radial or the concentric ornament may be more strongly developed (compare figs 4A and 4B). However, to what degree this is a consequence of preservation is not clear. Minor morphological differences between the Australian and Chinese forms exist in the slightly thicker cardinal processes of the Chinese specimens (Fig. 4F, M) and in the less strongly undulating margin of the operculum in lateral view (Fig. 4I).

The apical structures of the Chinese opercula appear to be identical to those of the Australian specimens, except that the average diameter of the raised area is smaller (about 100 µm; Fig. 4C, F, J). The relatively poor preservation obscures such details as the presence of a raised rim around the apical structure or a central circular depression which could not be observed.

250

251 **Figure 4:** Opercula of *Cupithecina holocyclata* (Bengtson in Bengtson et al., 1990); from North China Platform; A, B, C, D, G, K
 252 from Shangwan section, Luonan County, Shannxi Province; E, F, H, I, J, L, M from Sanjianfang section, Yexian, Henan
 253 Province; A, NIGPAS163151 from sample LNSW-1, external view. B-C, NIGPAS163152 from sample LNSW-1; B, external
 254 view; C, detail of B showing apical structure. D, NIGPAS 163153 from sample, external view. E-F, NIGPAS163156 from
 255 sample SJF-3/0.2; E, oblique view from dorsal side; F, detail of E showing apical structure. G, NIGPAS163154 from sample
 256 LNSW-1, external view. H, NIGPAS163157 from sample SJF-3/0.2, external view. I-J, NIGPAS163158 from sample SJF-5/1.0; I,

257 lateral view; J, detail of I showing apical structure. K, NIGPAS163155 from sample LNSW-1, internal view. L-M,
 258 NIGPAS163159 from sample SJF-3/0.2; L, internal view; M, detail of L showing apical processes. Scale bars equal 200µm in
 259 A-B, D-E, G-I, K-L and 100µm in C, F, J, M.

260

261 Discussion

262 *Hylolithid or orthothecid?*

263 The cone-shaped conch and sub-circular operculum with well defined cardinal process clearly
 264 establishes that *Cupitheca* is a hylolith. However, *Cupitheca* appears to exhibit a mixture of hylolithid
 265 and orthothecid characteristics; the presence of a narrow cardinal shield in the operculum is
 266 reminiscent of the Hylolithida while the rounded cross-section and the lack of clavicles is more typical
 267 of the Orthothecida. There is no evidence that *Cupitheca* possessed helens. Consequently this hylolith
 268 is most closely comparable to orthothecids. The combination of hylolithid-like and orthothecid-like
 269 characters is not unique to *Cupitheca* (Dzik 1994). A number of Cambrian hyloliths exhibit similar
 270 character combinations. Examples include *Triplicatella* (Skovsted et al. 2004, 2012) and *Hyptiotheca*
 271 (Malinky & Skovsted 2004). The conventional division of hyloliths into hylolithids and orthothecids is
 272 based mainly on post-Cambrian taxa (Marek 1966, 1967) and the high frequency of unusual
 273 character combinations in early Cambrian hyloliths, suggests that the diversity of hyloliths in the
 274 Cambrian was higher than later in the Palaeozoic.

275

276 *Palaeogeography of C. holocyclata*

277 The palaeogeography of hyloliths is best known for the Ordovician (Marek 1976) and was most
 278 recently studied by Valent (2010). In the latter analysis, Valent (2010) documented an increasing
 279 diversity of hyloliths and established that the distribution of hyloliths is highly endemic with unique
 280 taxa dominating each palaeogeographic province. The biostratigraphy and palaeogeography of

Cambrian hyoliths is less well understood although some regional stratigraphic schemes have been proposed (Val'kov 1987; Jiang 1992; Kruse 2002). However, at least in the early part of the Cambrian (Stages 2-4), a number of hyolith genera and species appear to have a wide geographical distribution (Malinky & Skovsted 2004), and these include *Cupithec**a holocyclata*. A similar pattern has been identified for other Cambrian shelly fossils such as molluscs (Gubanov 2002; Gubanov et al. 2004), brachiopods (Skovsted & Holmer 2005) and diverse problematic fossils (Skovsted 2006). However, many of these fossils may have very long stratigraphic ranges and their taxonomy is often too poorly understood for accurate intercontinental correlation.

*Cupithec**a holocyclata* has so far been reported from rocks of Cambrian Series 2 (Stage 3-4) of several different Cambrian palaeocontinents including east Gondwana (South Australia; Bengtson et al., 1990; Gravestock et al., 2001; herein and Antarctica; Wrona, 2003), South China (Duan 1984; Xing et al. 1984), North China Platform (Xiao & Zhou 1984; Pan et al. 2015; herein), and Laurentia (Greenland; Malinky & Skovsted 2004 and western Newfoundland; Skovsted & Peel 2007). Other relatively well preserved species of *Cupithec**a* (i.e. where external ornament is known) appear to have more restricted distributions (Malinky & Skovsted 2004; Pan et al. 2015). The almost global distribution of *C. holocyclata* may suggest that this species could be useful for intercontinental correlation in Cambrian Series 2, although its stratigraphical range is not fully known and may span both Cambrian stages 3 and 4. However, it is worth noting that species identification in *Cupithec**a* relies on preservation of external ornament (Bengtson et al. 1990) and that the genus *Cupithec**a* itself has a wider range both geographically and stratigraphically than *C. holocyclata*.

Apex of operculum and life history

The most unusual feature of the operculum of *Cupithec**a* from Australia and China is the raised sub-circular apical structure. The operculum of hyoliths often exhibits a small, apical structure on the conical shield of the operculum, which probably represents the initial growth stage, possibly

corresponding to the protoconch of the associated conchs (Dzik 1978). In both hyolithids and orthothecids this structure is typically a sub-circular or circular convex plate (Dzik 1980). The diameter of the apical structure of the operculum is usually not reported although Dzik mentioned a diameter of 85 μm for the Ordovician *Bactrotheca* sp. (Dzik 1980). Based on published images of hyolith opercula, a similar size range (60-100 μm) of the apical structures seems to be characteristic for most hyoliths of both orders (cf. Dzik 1978; Bengtson et al. 1990; Malinky & Skovsted 2004). The diameter of the operculum is thought to correspond to the diameter of the protoconch of the main shell which typically exhibits a similar size range (Dzik 1978, 1980). However, it is not clear that the initial conch and operculum formed at the same time.

Based on the size and morphology of hyolith protoconchs, Dzik (1978, 1980) suggested that hyoliths had a planktic larval “veliger” stage with different taxa exhibiting evidence of planktotrophic and lecithotrophic development. Dzik (1994) also noted that most Cambrian hyoliths exhibit larval shells of the minute bullet-shaped “mucronate” type with visible growth lines, which he interpreted as evidence of planktotrophy. However, Landing & Kröger (2012) showed that the protoconch in one of the oldest known hyoliths, “*Allatheca*” *degeeri* Holm, 1893 from southeastern Newfoundland (Terreneuvian-Cambrian Stage 2) is substantially larger than in later hyoliths (400 μm in diameter) and suggested that this hyolith may not have had a planktic larval life stage at all.

Due to the decollating growth mode it has not been possible to identify the earliest growth stage of the conch in *Cupitheca*. However, the associated opercula described here preserve the initial growth stage of the operculum. In diameter, the apical structure of the *Cupitheca* operculum is slightly larger than in most other hyoliths (100-150 μm) but is substantially smaller than the diameter of the larval shell in “*Allatheca*” *degeeri* (400 μm). Its slightly variable diameter fits well with the diameter of the protoconch of supposedly planktic hyolith larvae, as well as with those of fossil and recent planktotrophic gastropods (Dzik 1978, 1980; Jablonski & Lutz 1983; Nützel et al. 2006; Landing & Kröger 2012, Table 1).

Both adult hyolithids and orthothecids, are thought to be free living, benthic animals, although at least some orthothecids may be partly or completely infaunal (Landing & Kröger 2012) deposit feeders (Devaere et al. 2014 and references therein). Like other benthic invertebrates with a planktic larval stage, hyoliths must have gone through a settling stage and evidence for metamorphic changes in growth associated with settling were described by Dzik (1978, 1980). Although increased weight during shell growth in itself could facilitate settling of planktic larvae, selective settling by attachment of the larva on suitable substrates may have been beneficial to the survival of the individual. The apical structure of the operculum in *Cupitheca* could represent specialized attachment structures, perhaps anchoring the larval hyolith to a sediment grain, algae or other anchored substrates.

The apical disc of the operculum in *Cupitheca holocyclata* differ from the initial shell of all other known hyolith opercula by being raised significantly above the level of the cardinal shield, in its concave shape and in the presence of a raised marginal rim. The apical disc of the operculum of *Cupitheca holocyclata* is reminiscent of apical attachment scars (cicatrix) in ventral valves of palaeozoic craniiform brachiopods (Popov et al. 2010) and thecideidine brachiopods (Baker 1983) as well as the attachment scar formed by the pedicle tube of polytechoid strophomenates (Popov et al. 2007). The craniiform cicatrix, the thecideidine apical attachment and the polytechoid pedicle tube all constitute scars, formed at settlement of the planktic brachiopod larvae and represents the physical attachment of the ventral valve to the substrate (Baker 1983; Popov et al. 2007, 2010). Although most craniids and thecideidines remain attached to their substrate throughout ontogeny, adult polytechoids were free living benthic brachiopods.

Besides brachiopods, attachment of the larva at settling is known to happen in many different benthic invertebrates that are free living as adults. Other well known fossil examples include the rugose coral *Calceola* where juveniles attach to algae (Stolarski 1993) and the bivalve *Gryphaea* where the juveniles attach to small shell fragments or other sediment grains (Swinnerton 1964). In these cases, as well as in polytechoid strophomenates, the connection to the substrate is either

broken at a later growth stage or rendered meaningless as the shell outgrow the grain it is initially attached to. We suggest that a similar process of larval attachment is possible in *Cupitheca*. The concave apical structure of *Cupitheca* represents an attachment scar formed by the tissues secreting the initial operculum and firmly attaching the larva to a selected grain or other suitable substrate. The adult life mode of *Cupitheca* is not well known but as the attachment surface is small compared to the size of the complete shell and do not appear to grow during ontogeny, the link to the initial substrate is likely broken during later growth stages. This study further adds to the diversity of life modes and benthic niches occupied by members of the Hyolitha in the 'early' Cambrian.

Acknowledgements

The authors thank Graham and Laura Ragless of Beltana Station for access to localities in the Mt Scott Range. James B. Jago (University of South Australia, Adelaide), John R. Paterson (University of New England, Armidale), Peter Cockle and Rebecca Smart (both Macquarie University, Sydney) are thanked for assistance in the field in Australia. Luyi Zhang (Xi'an Institute of Geology and Mineral Resources) is thanked for assistance in the field in China. Johanna E. Skovsted assisted in the construction of figures. Financial support from Australian Research Council Discovery Project #120104251 (to GAB) and from the Swedish Museum of Natural History to CBS and TPT as well as from the National Natural Science Foundation of China (41372021), and the Ministry of Science and Technology of China (2013CB835000) to GXL are gratefully acknowledged.

References

BAKER, P. 1983. The diminutive thecideidine brachiopod *Enallothecidea pygmaea* (Moore) from the Middle Jurassic of England. *Palaeontology*, 26, 663-669.

- 379 BANDEL, K. 1996. Some heterostrophic gastropods from Triassic St. Cassian Formation with a
 380 discussion on the classification of the Allogastropoda. *Paläontologische Zeitschrift*, 70, 325-
 381 365.
- 382 BENGTON, S., MORRIS, S. C. & COOPER, B. 1990. Early Cambrian fossils from South Australia.
 383 *Memoir of the Association of Australasian Palaeontologists*, 9, 1-364.
- 384 BETTS, M. J., BROCK, G. A., PATERSON, J. R., JAGO, J. B. & ANDREW, A. S. 2015. Integrated Shelly
 385 Fossil Biostratigraphy and Carbon and Oxygen Chemostratigraphy: Applying a Multi-proxy
 386 Toolkit to Correlating the Lower Cambrian of South Australia. *AAPG/SEG International*
 387 *Conference and Exhibition, Melbourne, Australia. Abstracts with Programs*.
- 388 BROCK, G., ALEXANDER, E. M., PATERSON, J. R., JAGO, J. B. & GATEHOUSE, C. G. 2006. Mt. Scott
 389 Range and Ajax Mine. In: JAGO, J. B. & ZANG, W. L. (eds.) *XI International Conference of the*
 390 *Cambrian Stage Subdivision Working Group Field Guide*. South Australia: International
 391 Subcommittee on Cambrian Stratigraphy.
- 392 DEVAERE L, CLAUSEN S, JAVIER ÁLVERO J, PEEL JS, VACHARD D. 2014. Terreneuvian Orthothecid
 393 (Hyalitha) digestive tracts from Northern Montagne Noire, France; taphonomic, ontogenetic
 394 and phylogenetic implications. *PLoS ONE* 9, e88583
- 395 DUAN, C. H. 1984. Small shelly fossils from the Lower Cambrian Xihaoping Formation in the
 396 Shennongjia District, Hubei Province—hyoliths and fossil skeletons of unknown affinities.
 397 *Bulletin of the Tianjin Institute of Geology and Mineral Resources*, 7, 143-188.
- 398 DZIK, J. 1978. Larval development of hyolithids. *Lethaia*, 11, 293-299.
- 399 DZIK, J. 1980. Ontogeny of *Bactrotheca* and related hyoliths. *GFF*, 102, 223-233.
- 400 DZIK, J. 1994. Evolution of 'small shelly fossils' assemblages of the early Paleozoic. *Acta*
 401 *Palaeontologica Polonica*, 39, 247-313.
- 402 FRETTER, V. & GRAHAM, A. 1978. The prosobranch Molluscs of Britain and Denmark. *Journal of*
 403 *Molluscan Studies Supplement 6(4) Marine Rissocacea*, 153-241.

- 404 FRECH, F. 1889. Anthozoa. In Holzapfel E. ed. Carbon von Erdbach-Breitschheid bei Herborn.
 405 *Paläontologische Abhandlungen, Neue Folge* I (1): 1-74.
- 406 GRAVESTOCK, D. I., ALEXANDER, E. M., DEMIDENKO, Y. E., ESAKOVA, N. B., HOLMER, L. E., JAGO, J. B.,
 407 LIN, T.-R., MELNIKOVA, N., PARKHAEV, P. Y., ROZANOV, A. Y., USHATINSKAYA, G. T., SANG,
 408 W.-L., ZHEGALLO, E. A. & ZHURAVLEV, A. Y. 2001. The Cambrian biostratigraphy of the
 409 Stansbury Basin, South Australia. *Transactions of the Palaeontological Institute of the Russian*
 410 *Academy of Sciences*, 282, 1-341.
- 411 GUBANOV, A. P. 2002. Early Cambrian palaeogeography and the probable Iberia–Siberia connection.
 412 *Tectonophysics*, 352, 153-168.
- 413 GUBANOV, A. P., SKOVSTED, C. B. & PEEL, J. S. 2004. *Anabarella australis* (Mollusca, Helcionelloida)
 414 from the Lower Cambrian of Greenland. *Geobios*, 37, 719-724.
- 415 JABLONSKI, D. & LUTZ, R. A. 1983. Larval ecology of marine benthic invertebrates: paleobiological
 416 implications. *Biol. Rev.*, 58, 21-89.
- 417 JIANG, Z. 1992. The Lower Cambrian fossil record of China. In: LIPPS, J. H. & SIGNOR, P. W. (eds.)
 418 *Origin and Early Evolution of the Metazoa*. New York: Plenum Press.
- 419 KRUSE, P. D. 2002. Biostratigraphic potential of Middle Cambrian hyoliths from the eastern Georgina
 420 Basin. *Alcheringa*, 26, 353-398.
- 421 LANDING, E. & KRÖGER, B. 2012. Cephalopod ancestry and ecology of the hyolith “*Allatheca*” degeeri
 422 sl in the Cambrian Evolutionary Radiation. *Palaeogeography, Palaeoclimatology,*
 423 *Palaeoecology*, 353, 21-30.
- 424 LI, G., ZHANG, Z., HUA, H. & YANG, H. 2014. Occurrence of the enigmatic bivalved fossil *Apistoconcha*
 425 in the lower Cambrian of southeast Shaanxi, North China Platform. *Journal of Paleontology*,
 426 88, 359-366.
- 427 MALINKY, J. M. & BERG-MADSEN, V. 1999. A revision of Holm's Early and early Mid Cambrian hyoliths
 428 of Sweden. *Palaeontology*, 42, 25-65.

- 429 MALINKY, J. M. & SKOVSTED, C. B. 2004. Hyoliths and small shelly fossils from the Lower Cambrian of
430 North-East Greenland. *Acta Palaeontologica Polonica*, 49, 551-578.
- 431 MAREK, L. 1963. New knowledge on the morphology of Hyolithes. *Sborník Geol. Véd, paleontologie*,
432 řada P, I, 53-73.
- 433 MAREK, L. 1966. New hyolithid genera from the Ordovician of Bohemia. *Časopis Národního muzea*,
434 oddíl přírodovědný, 135, 89-92.
- 435 MAREK, L. 1967. The Class Hyolitha in the Caradoc of Bohemia. *Sborník geologických věd*,
436 *Paleontologie*, 9, 51-113.
- 437 MAREK, L. 1976. On the ontogeny in Hyolithida. *Čas. Mineral. Geol.*, 21, 277-283.
- 438 MARTÍ MUS, M., JEPSSON, L. & MALINKY, J. M. 2014. A complete reconstruction of the hyolithid
439 skeleton. *Journal of Paleontology*, 88, 160-170.
- 440 NÜTZEL, A., LEHNERT, O. & FRÝDA, J. Í. 2006. Origin of planktotrophy—evidence from early molluscs.
441 *Evolution & development*, 8, 325-330.
- 442 PAN, B., MIAO, L., YANG, h. & LI, G. 2015. Enigmatic tubular fossil *Cupithea* from the lower Cambrian
443 Xinji Formation of Luonan, Shaanxi Province. *Acta Micropalaeontologica Sinica* (in press)
- 444 POPOV, L. E., BASSETT, M. G., HOLMER, L. E., SKOVSTED, C. B. & ZUYKOV, M. A. 2010. Earliest
445 ontogeny of Early Palaeozoic Craniiformea: implications for brachiopod phylogeny. *Lethaia*,
446 43, 323-333.
- 447 POPOV, L. E., EGERQUIST, E. & HOLMER, L. E. 2007. Earliest ontogeny of Middle Ordovician
448 rhynchonelliform brachiopods (Clitambonitoidea and Polytoechioidea): implications for
449 brachiopod phylogeny. *Lethaia*, 40, 85-96.
- 450 SKOVSTED, C. B. 2004. Mollusc fauna of the Early Cambrian Bastion Formation of north-east
451 Greenland. *Bulletin of the Geological Society of Denmark*, 51, 11-37.
- 452 SKOVSTED, C. B. 2006. Small Shelly Fauna From The Upper Lower Cambrian Bastion And Ella Island
453 Formations, North-East Greenland. *Journal of Paleontology*, 80, 1087-1112.

- 454 SKOVSTED, C.B., BETTS, M.J., TOPPER, T.P. & BROCK, G.A. 2015. The early Cambrian tommotiid genus
 455 *Daliyatia* from South Australia. *Memoirs of the Association of Australasian Palaeontologists*
 456 48, 1-116.
- 457 SKOVSTED, C. B., BROCK, G. A. & TOPPER, T. P. 2012. First occurrence of a new *Ocruranus*-like
 458 helcionelloid mollusc from the Lower Cambrian of east Gondwana. *Gondwana Research*, 22,
 459 256-261.
- 460 SKOVSTED, C. B. & HOLMER, L. E. 2005. Early Cambrian brachiopods from north-east Greenland.
 461 *Palaeontology*, 48, Part 2, 325-345.
- 462 STOLARSKI, J. 1993. Ontogenetic development and functional morphology in the early growth-stages
 463 of *Calceola sandalina* (Linnaeus, 1771). *Courier Forschungsinstitut Senckenberg*, 164, 169-
 464 177.
- 465 SWINNERTON, H. H. 1964. The early development of *Gryphaea*. *Geological magazine*, 101, 409-420.
- 466 SYSSOIEV, V. A. 1957. About the morphology, systematic position and systematics of Hyolithoidea.
 467 *Dokl. Akad. Nauk. USSR*, 116, 304-307.
- 468 TOPPER, T.P., BROCK, G.A., SKOVSTED, C.B & PATERSON, J.R. 2009. Shelly fossils from the lower
 469 Cambrian *Pararaia bunyeroensis* Zone, Flinders Ranges, South Australia. *Memoirs of the*
 470 *Association of Australasian Palaeontologists* 37, 199-246.
- 471 TOPPER, T. P., BROCK, G. A., SKOVSTED, C. B. & PATERSON, J. R. 2011. *Microdictyon* plates from the
 472 lower Cambrian Ajax Limestone of South Australia: Implications for species taxonomy and
 473 diversity. *Alcheringa* 35, 427-443.
- 474 VAL'KOV, A. K. 1987. Biostratigrafiya nizhnego kembriya vostoka Sibirskoj Platformy (Yudoma-
 475 Olenyokskij region) [Lower Cambrian biostratigraphy of the eastern part of the Siberian
 476 Platform (Yudoma-Olenyok region)]. *Moskva: Nauka*, 136pp.
- 477 VALENT, M. 2010. Palaeogeographic distribution of Ordovician hyoliths. *Journal of the National*
 478 *Museum (Prague), Natural History Series*, 179, 179-182.

- 479 WRONA, R. 2003. Early Cambrian molluscs from glacial erratics of King George Island, West
480 Antarctica. *Polish Polar Research*, 24, 181-216.
- 481 XIAO LIGONG & ZHOU BENHE, 1984. Early Cambrian Hyolitha from Huainan and Huoqiu County in
482 Anhui Province. *Professional Papers on Stratigraphy and Palaeontology* 13, 141-151.
- 483 XING YUSHENG, DING QIXIU, LUO HUILIN, HETINGGUI & WANG YANGENG, 1984. The Sinian-
484 Cambrian boundary of China. *Bulletin of the Institute of Geology, Chinese Academy of*
485 *Geological Sciences* 10, 1-262.