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Cephalopod ancestry and ecology of the hyolith "*Allatheca*" *degeeri* s.l. in the Cambrian Evolutionary Radiation

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ABSTRACT

Pyritized, elongate, conical conchs of "*Allatheca*" *degeeri* s.l. are common in dysoxic, dark gray mudstone intervals in the Early Cambrian (upper Terreneuvian–Series 2 boundary interval) Cuslett Formation at Keels, eastern Newfoundland. Wave-oriented, horizontal specimens are most abundant in this cool-water, high latitude, off-shore shelf facies of the Early Palaeozoic Avalon microcontinent. Based on conch morphology, shell microstructure, and the operculum, the species is an orthothecid hyolith. Comparison with the sizes of the early shells of planktic gastropods indicates a non-planktic life mode of "*A.*" *degeeri* s.l. hatchlings, although buoyancy calculations show that small juveniles with septate conchs to ca. 17 mm long could have been nektic/planktic. If smaller "*A.*" *degeeri* s.l. individuals had a non-benthic mode of life, they and pseudoconodonts were the oldest skeletalized pelagic/nektic animals in the Cambrian Evolutionary Radiation. Most "*A.*" *degeeri* s.l. conchs at Keels are horizontally embedded and show a bimodal, wave-determined orientation, but about 10% of the large conchs are vertically embedded with their aperture down. As larger shells were not neutrally buoyant, the vertical orientations of about 10% of the conchs suggests an infaunal, likely detritivore, life mode suggestive of a scaphopod. Available morphologic and taphonomic evidence suggests that the vertically embedded conchs are in situ remains of dead benthic animals that colonized the bottom in better oxygenated intervals. Based on the current knowledge of Early Palaeozoic hyolith and cephalopod larval and adult morphologies, existing hypotheses of a planktic origin of cephalopods from hyolith ancestors are evaluated, and no evidence for such an evolutionary relationship is concluded to exist.

1. Introduction

A number of high-level skeletalized metazoan groups (i.e., cephalopods, euconodonts, polyplacophorans, and bryozoans) seemingly "missed" the early stages of the Cambrian Evolutionary Radiation. These groups have their oldest-known record in the middle Late Cambrian as harbingers of the "Great Ordovician Diversification" (e.g. Landing et al., 2010).

Cephalopods, important macropredators of Late Cambrian–Recent marine faunas, provide relatively little palaeontological information to reconstruct their pre-Late Cambrian origins or ancestors. Two main hypotheses exist for the origin of cephalopods: a benthic origin with a monoplacophoran-like mollusk ancestor (Yochelson et al., 1973; Webers and Yochelson, 1989; Peel, 1991; Brock, 2004) and a pelagic origin that derives cephalopods from a small, tube-shaped planktic/nektic ancestor that was likely an orthothecid ancestor (Dzik, 1981, 2010). A third phylogenetic origin (Smith and Caron, 2010) with a coleoid-like animal without a shell, such as *Nectocaris pteryx* Conway Morris, 1976, as a cephalopod ancestor was rejected by Mazurek and Zaton (2011) and Kröger et al. (2011).

This report presents new data on the taphonomy and depositional environment of the tube-shaped, septate Early Cambrian problematicum "*Allatheca*" *degeeri* Holm, 1893, s.l. The data do not support a planktic/nektic early life stage of this animal and also do not support a cephalopod phylogeny similar to the planktic/nektic origin model. In a review of the evidence that seemingly supported the latter phylogenetic model, the ancestry of cephalopods is discussed. (In this report, "Lower"/"Early," "Middle"/"Middle" and "Upper"/"Late" Cambrian are proposed subsystem- and subperiod-level divisions that correspond to the Terreneuvian + Series/Epoch 2, Series/Epoch 3, and Furongian, respectively (Landing, 2007)).

2. Systematic position of "*Allatheca*" *degeeri* s.l

2.1. Morphology and systematic paleontology of "Allatheca" degeeri s.l

Elongate, generally straight to weakly dorsally curved calcareous conchs that reach a 12 cm length are one of the most abundant fossils in the Lower Cambrian of the Early Palaeozoic Avalon microcontinent (e.g. Landing, 2004). These conchs have a variable angle of expansion

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(5–10°); variable, weakly dorsoventrally compressed cross section (broadly oval, often with less convex to rarely flattened or slightly concave venter); weak transverse annulations; apical septa; and short, fusiform protoconch with circular cross section and pointed apex (e.g. Landing, 1988, figs. 7.1?, 7.2?, 7.3, 7.4, 7.9, 7.11?, 8.1.,8.2, 9.6, 9.8). Brasier (1984) and Landing (1988) compared conchs from the upper part of the sub-trilobitic Lower Cambrian of the British and American successions of Avalonia with those of *Hyolithus* (*Orthotheca*) *degeeri* Holm, 1893, from the Baltica palaeocontinent, and termed the form, respectively, Allatheca degeeri and "A." degeeri s.l.

The naming of the form reflects taxonomic problems associated with Missarzhevsky's (in Raaben, 1969) and Holm's (1893) typological diagnoses of the genus and species *Allatheca degeeri*. In particular, the conch cross sections of the Avalonian forms are not uniformly oval, and the development of less convex to slightly concave venters means the conchs have a wider range of variability than that described for *Allatheca* Missarzhevsky, 1969, and *Hyolithus* (*Orthotheca*) *degeeri* Holm, 1893, and its synonym *H.* (*O.*) *johnstrupi* Holm, 1893 (Landing, 1988). These concerns and the presently undetermined range of morphologic variation of topotype *A. degeeri* from Baltica explain the tentative identification of "*A.*" *degeeri* s.l. from Avalon. For instance, Malinky and Berg-Madsen (1999) described but did not illustrate a concave venter of the small number (5) of topotype *Orthotheca degeeri* specimens, while Holm (1893, fig. 26) figured a flat venter. By comparison, Landing (1988) reported a transition of conch cross sections from oval to rounded–triangular with convex, flat, and gently concave venters in a large collection from Avalonian Massachusetts. Missarzhevsky (1969, p. 139) also noted a concave venter near the aperture for the form in Siberia. Further taxonomic uncertainty derives from the variable measurements taken of the conch. Thus, apical angles are variously reported as 8–9° (Holm, 1893) or 7° (Malinky and Berg-Madsen, 1999) on the same topotype specimens and 5–10° on Avalonian and 10–15° on Siberian specimens (Missarzhevski, 1969; Brasier, 1984; Landing, 1988).

Holm (1893) described an operculum in his two "species" of *Hyolithus* (*Orthotheca*) *degeeri* and its synonym *H.* (*O.*) *johnstrupi* that has two strongly developed, elliptical cardinal processes. These processes diverge from the dorsal margin and extend across most of the ventral surface of the operculum. Despite all of the work on the Lower Cambrian of Avalon and Siberia, this type of operculum has rarely been recovered from crack-out or acid-disaggregated residues that yield phosphatized or limonite-replaced skeletal fossils. Indeed, most authors have not reported an operculum in association with "*Allatheca*" *degeeri* s.l. conchs in Avalonia (Shaler and Foerste, 1888; Grabau, 1900; Brasier, 1984). Landing (1988, 1993a) illustrated the exterior of broken opercula, but could not determine whether they belonged to "*A.*" *degeeri* s.l. or to the hyolithid *Hyolithes tenuistriatus* Linnarsson, 1871. Matthew (1899) associated opercula in the Fosters Point Formation of southeastern Newfoundland (Fig. 2) with conchs of his "*Orthotheca pugio*," a junior synonym of "*A.*" *degeeri* s.l. (see synonymy in Landing, 1988). These opercula show the visceral surface and show large cardinal processes that "should" be present in an orthothecid hyolith identified as "*A.*" *degeeri* (see Malinky, 2006).

"*Allatheca*" *degeeri* and its junior synonyms are variably classified within the Orthothecidae Syssoiev, 1958; Orthothecida Marek, 1966; or Orthothecimorpha Syossiev, 1968 (Fisher, 1962; Malinky, 1987; Landing, 1988). Orthothecids are operculate conical-shelled organisms that are assigned to the class Hyolitha Marek, 1963. The Early Devonian genus *Orthotheca* Novák, 1886, was revised by Malinky (2009) and identified as a characteristic orthothecid.

Historically, the term "orthothecid hyolith" was a catch-all designation for phylogenetically unrelated Early Paleozoic conical-shelled organisms with circular or oval cross-sections Malinky (2009). As consequence, the term "orthothecid" may refer to hyoliths, polycheates, or other phylogenetically unrelated organisms with conoidal conchs (e.g., Bandel, 1986; Landing, 1993b). Indeed, earlier classifications of "*A.*" *degeeri* s.l. as an orthothecid should not be regarded as definitive for the hyolith relationships of this form.

However, one important result of Malinky's (2009) revision of orthothecids is the demonstration of hyolithid hyolith-like opercula in the type species of *Orthotheca*; which means that orthothecids are a subgroup of hyoliths. Malinky (2009, p. 590) evaluated the morphology of the orthothecid operculum, which is characterized by a pair of diverging cardinal processes on the interior, as the "the single most important item that unites this array of morphologies under Orthothecida, and a diagnostic feature of the group."

The early line drawing of an operculum of "*Allatheca*" *degeeri* s.l. (Matthew, 1899, pl. 6, fig. 5e) shows a bilaterally symmetrical sclerite with structures suggestive of a pair of cardinal processes. The shell of "*A.*" *degeeri* s.l. was aragonitic (Landing and Benus, 1988), which is in accordance with other known orthothecids (Kouchinsky, 2000). Based on this evidence, "*A.*" *degeeri* s.l. is best classified as an orthothecid hyolith.

3. Geologic setting

3.1. Avalonian inner platform

The large syncline on the north side of Keels village at the tip of the Bonavista Peninsula features the northernmost exposure of Cambrian rock in the Avalon zone of eastern Newfoundland (Fig. 1). Siliciclastic-dominated, terminal Ediacaran–Ordovician rocks unconformably overlie and form a cover sequence on volcaniclastic-rich, uppermost Cryogenian–Ediacaran rocks of the Avalonia microcontinent (e.g. Landing, 1996, 2003, 2004, 2005). As the tidalites of the Lower Cambrian Random Formation are the oldest cover sequence rocks in the Bonavista and Avalon peninsulas, these peninsulas were part of the Avalonian inner platform (Landing, 1996; Figs. 1, 2). Syndepositional, transtensional faulting after Random Formation deposition led to accumulation of the thickest deposits of the uppermost sub-trilobitic Lower Cambrian along the Placentia–Bonavista axis. The syncline at Keels lies right on this axis, and has the thickest known, albeit incomplete, succession of the Bonavista Group in North American Avalonia (Landing, 1988; Figs. 1, 2).

3.2. Keels succession

A gently dipping, slaty, siliciclastic mudstone-dominated Bonavista Group succession forms shore outcrops on both limbs of the Keels syncline (Landing et al., 1988, stops 8a, b; Landing and Benus, 1988, fig. 35). The mudstones include red, purple, and green gray mesoscale alternations, which represent, respectively, a spectrum from near-shore to more distal and less oxygenated muddy shelf facies in Avalon. Carbonates are limited to diagenetic nodules and to several peritidal highstand carbonates that cap the Bonavista Group formations (Landing et al., 1988, 1989; Myrow and Landing, 1992; Landing, 1993a; Landing and Westrop, 2004).

The Petley and West Centre Cove formations (38 m and 79 m thick, respectively, at Keels), are the lowest Bonavista Group formations (Fig. 2). These two formations have highstand carbonate caps (algal mud-mound and fossil hash packstone with limonitic SH-V stromatolites at their very top). Sparse trace fossils occur in the Petley and West Centre Cove formations. *Sunnaginia imbricata* Zone small shelly fossil assemblages occur in the highstand carbonates of the Petley and West Centre Cove formations (Landing, 1988), and a "*Ladatheca*" *cylindrica* worm reef caps the West Centre Cove Formation at Keels (Landing, 1993a). The *S. imbricata* Zone assemblage is middle Lower Cambrian, and is a Tommotian Stage-equivalent when correlated into the Siberian Platform (Landing, et al., 1989; Brasier et al., 1992; Landing, 1994)