Hyoliths and small shelly fossils from the Lower Cambrian of North-East Greenland

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The hyolith assemblage from the Lower Cambrian Bastion Formation of North-East Greenland is significant in that it contains several hyolith taxa that possess traits of both orders Hyolithida and Orthothecida. They possess morphological traits that seem to be characteristic of the ancestral forms of both groups. In addition, many hyolith taxa from this interval are globally distributed, supporting the notion that these fossils have potential as stratigraphic indicators. This assemblage contains genera and/or species seen in Australia, North America, the Siberian Platform, and South China. Hyoliths identified include the hyolithids *Parkula bounites*, *Hyptiotheca karraculum*, *Microcornus eximius*, *M. petilus*, *Paracornus poulseni* gen. et sp. nov., as well as *Similotheca similis*?, *S. bastionensis* sp. nov., and *S. groenlandica* sp. nov.; two opercula remain in open nomenclature. Orthothecids from this assemblage are one unnamed species each of *Contitheca* and *Gracilitheca*. Large, macro-sized hyoliths from the same formation described by Poulsen (1932) are mostly unidentifiable, although an operculum formerly identified as *Hyolithes* (*Orthotheca*) *communis* is reassigned to *Hyptiotheca*. Problematic organisms of uncertain affinity include *Cupitheca holocyclata*, *Conotheca australiensis*, an unnamed species of *Coleolus*, and the cap-shaped *Cassitella baculata* gen. et sp. nov. that may be an operculum of some as yet unknown organism. Missarzhevsky (1969) used *Hyolithes* (*Orthotheca*) *bayonet* var. *groelandicus* and *H.* (*O.*) *bayonet* var. *longus* as the basis for *Lenatheca*, but the specimens on which that genus is based are too poorly known for a proper diagnosis of *Lenatheca*.

Key words: Hyolitha, Hyolithida, Orthothecida, Botomian, Lower Cambrian, Bastion Formation, Greenland.

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Introduction

Hyoliths have long been recognized as a component of faunal assemblages from the Lower Cambrian of North-East Greenland. Poulsen (1932) described six species represented by twelve specimens from the Bastion Formation, and recent discoveries of micro-sized individuals from acid resistant residues from the same unit have substantially increased the number of specimens known. Poulsen's (1932) specimens have not been revised until now, nor were they integrated into the newly emerging taxonomic system in Russia in the late 1950s and early 1960s (Syssoiev 1958, 1962). Most specimens are incompletely preserved, and the taxa they represent cannot be properly diagnosed by the standards established by Marek (1967) in his seminal work on Ordovician hyoliths from Bohemia. The newly discovered specimens provide the impetus for a re-evaluation of Poulsen's (1932) material, and overall serve to increase knowledge of hyolith diversity as well as the geographic and stratigraphic distribution of these organisms in the Lower Cambrian. Many Lower Cambrian hyoliths from Siberia (Missarzhevsky 1989 and references therein) and from China (Qian 1989 and references therein) appear to be incompletely preserved, and thus not recognizable by modern standards. In contrast, the majority of the newly discovered specimens from Greenland are much better preserved. The purpose of this work is to evaluate all hyolith specimens from the Bastion Formation of Greenland for taxonomic purposes and then integrate them into current taxonomic, geographic, and stratigraphic frameworks.

The hyolith fauna of the Bastion Formation is unique in several respects. Certain taxa, such as *Hyptiotheca* Bengtson, 1990a and opercula A and B, possess traits characteristic of both the orders Hyolithida and Orthothecida. In the case of *Hyptiotheca*, clavicles on the interior of the operculum are absent, making this the only hyolithid species known to lack this feature. Opercula A and B on the other hand possess cardinal processes and clavicles, but lack the dorso-ventral differentiation normally associated with hyolithid opercula. Furthermore, each has an outline that approaches a circular or sub-circular shape. These features ordinarily are observed among Orthothecida. Even though the Bastion Formation hyoliths are not the oldest hyoliths known, perhaps the seeming combination of hyolithid and orthothecid traits in certain individuals resembles the ancestral individuals that through time evolved into the two well-differentiated hyolith orders seen in this same and in younger intervals.

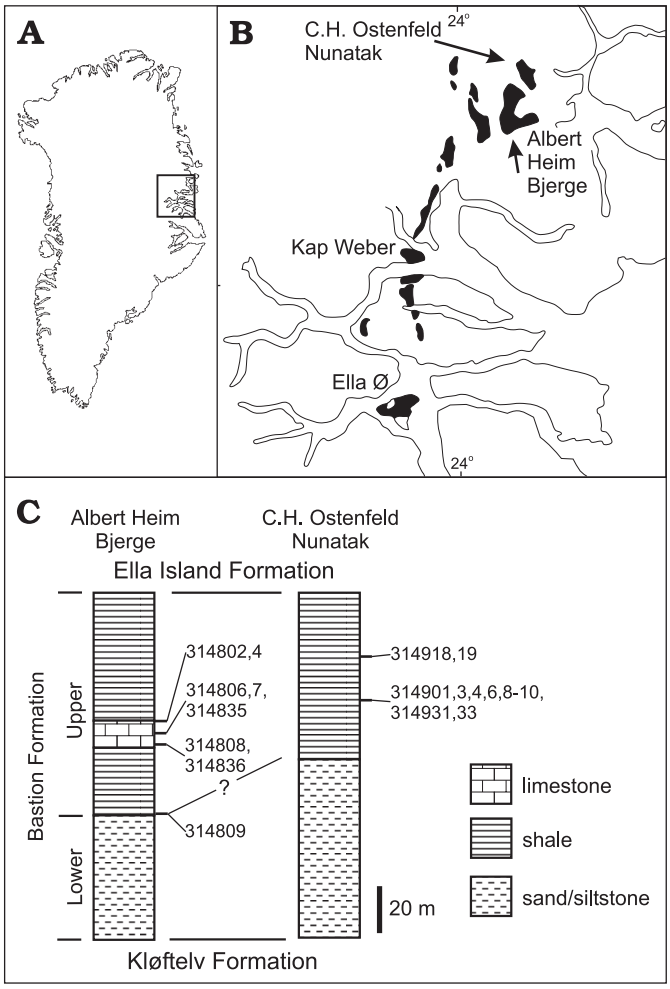


Fig. 1. Stratigraphy and locality map. **A**. Map of Greenland with area of study marked. **B**. Generalised map of study area with outcrops of Lower Palaeozoic rocks in black. The position of hyolith localities indicated. **C**. Generalised stratigraphy of the Bastion Formation of Hudson Land with position of samples yielding hyoliths in acid resistant residues. Modified from Skovsted and Holmer (in press).

Bergström and Gee (1985) discussed faunal provincialism in the Cambrian, and Cowie (1971, 1974) distinguished three faunal provinces in the Cambrian based on the distribution of trilobites, with Australia, China, and Siberia located within the same province. Faunal provincialism, however, apparently did not extend to the hyoliths or to certain other small shelly fossils; the record of taxa presented herein makes clear that many of these fossils have a widespread geographic range. Perhaps the planktic larval forms of these organisms were long-lived, and therefore became widely distributed by prevailing ocean currents. It was not until the Ordovician that the hyoliths occurred in well-differentiated palaeobiogeographical provinces (Marek 1976a). Affinities to assemblages in Australia, Antarctica, South China, North American, Scandinavia, Kazakhstan, and Siberia are clear for much of the assemblage of the Bastion Formation. The hyolithids *Hyptiotheca* Bengtson, 1990a, *Parkula* Bengtson, 1990a, and *Microcornus* Mambetov, 1972, the orthothecid *Gracilitheca* Syssoiev, 1968, and the problematic *Conotheca* Missarzhevsky, 1969 are common to Australia, Antarctica, Greenland and Siberia. Further connection with the Siberian Platform is suggested by the possible occurrence of *Burithes* Missarzhevsky, 1969 in Greenland (as *Hyolithes americanus* Billings, 1872 herein). The orthothecid *Contitheca* Syssoiev, 1972 was initially described from the Middle Cambrian of Sweden; it has subsequently been recognized in the Middle Cambrian of North Africa (Marek et al. 1997) and Antarctica (Shergold et al. 1976), and is probably present also in Korea (Saito 1936). *Similotheca* Malinky, 1988 and *Coleolus* Hall, 1879 also occur in eastern North America, and *Cupitheca* Duan, 1984 is a component of small shelly fossil assemblages in China as well as Australia and Antarctica. *Paracornus poulseni* gen. et sp. nov. thus far is known only from Greenland. Similar patterns of distribution have been observed for molluscs (Gubanov et al. in press; Skovsted in press), brachiopods (Skovsted and Holmer in press) and various problematic fossils (Brock et al. 2000). Gubanov (2002) explained the marked similarities among Early Cambrian faunal assemblages across the modern continents as a result of the close proximity of all major cratonic basins in the form of a supercontinent at the start of the Cambrian. The widespread distribution of the hyolith and small shelly fossil taxa seen in North-East Greenland lends support to this view.

Institutional abbreviations.—USNM, Natural History Museum, Smithsonian Institution, Washington, D.C., USA; GGU, Geological Survey of Denmark, Copenhagen, Denmark; MGUH, Geological Museum, Copenhagen, Denmark; SAMP, South Australian Museum, Adelaide, Australia; SH, Tianjin Institute of Geology and Mineral resources, People's Republic of China; and GIN, Geological Institute, Russian Academy of Sciences, Moscow, Russia.

Geological setting

Cambrian rocks in North-East Greenland unconformably overlie a thick sequence of Late Proterozoic shelf sediments (Hambrey and Spencer 1987; Stouge et al. 2001). The Cambrian succession begins with sandstones of the Kløftelv Formation and continues with glauconitic siltstones of the lower Bastion Formation, followed by shales with minor carbonate beds and nodules of the upper Bastion Formation (Cowie and Adams 1957; Stouge et al. 2001). The overlying Ella Island Formation is dominated by limestone, and deposition of carbonate sediments continued throughout the Cambrian period and into the Late Ordovician (Cowie and Adams 1957; Hambrey et al. 1989; Stouge et al. 2001). Acritarchs are known from the Upper Proterozoic and from the lower Bastion Formation (Vidal 1979) and trace fossils have been described from the Kløftelv and lower Bastion Formations (Hambrey and Spencer 1987; Pickerill and Peel 1990). However, the first metazoan body fossils occur in the richly

fossiliferous upper Bastion Formation (Poulsen 1932; Cowie and Adams 1957; Stouge et al. 2001) which was probably deposited below wave base in an offshore shelf environment (H. Tirsgaard in Pickerill and Peel 1990). Many of the carbonate layers yielding shelly fossils probably represent influx of material from areas closer to the shore line, as is evident from their common clastic texture.

Hand specimens of hyoliths collected from the Upper Bastion Formation on the south coast of Ella Ø and from Hyolithus Creek and Tillite Canyon on the north coast of Andrée Land and described in this paper were loaned from the Geological Museum in Copenhagen. This material was collected in 1929 by Christian Poulsen and described by him in 1932. Hyoliths were also found in the residues following acetic acid digestion of limestone samples collected from the Bastion Formation by John S. Peel and M. Paul Smith during fieldwork organised by the Geological Survey of Greenland in 1988. Limestone samples were collected from a section through the upper Bastion Formation described by Cowie and Adams (1957: 53–58) in the Albert Heim Bjerge region and from two previously unknown sections on C.H. Ostenfeld Nunatak to the north of Albert Heim Bjerge. The section at Albert Heim Bjerge was correlated with the upper Bastion Formation of Ella Ø by Cowie and Adams (1957), but the sections on C.H. Ostenfeld Nunatak are incompletely exposed and can not be correlated in detail with other sections through the formation. The stratigraphic position of the fossiliferous samples is shown in Fig. 1. All specimens are deposited in the MGUH.

In addition to hyoliths, the shelly fauna of the upper Bastion Formation contains a wide range of fossils including brachiopods (Poulsen 1932; Holmer et al. 2002; Skovsted and Holmer 2003, in press), molluscs (Gubanov et al. in press, Skovsted in press), and bradoriid arthropods (Poulsen 1932), as well as problematic forms such as *Mongolitubulus* (Skovsted and Peel 2001), *Discinella* (Skovsted 2003) and currently undescribed coeloscleritophorans and lapworthellids. Trilobites and various other elements of the fauna were identified by Cowie and Adams (1957) but not described. Although differences in faunal composition between outcrop areas in North-East Greenland were documented by Skovsted (in press), there appears to be no vertical differentiation of the fossil fauna within the Upper Bastion Formation.

Systematic palaeontology

Class Hyolitha Marek, 1963

Order Hyolithida Syssoiev, 1957

Family Similothecidae Malinky, 1988

Genus *Similotheca* Malinky, 1988 emended

Type species: *Hyolithes similis* Walcott, 1890, Lower Cambrian, Newfoundland.

Diagnosis.—Similothecid having flattened venter, grading into keel-like lateral edges, which in turn pass into dorsal flanks, which are convex near the lateral edges but become concave close to the middle of the dorsum.

Remarks.—This genus was based on material described by Walcott (1890a, b) from the Brigus Formation (formerly Smith Point Formation; see Landing and Benus 1988). Diagnostic traits include the keel-like dorsal ridge, concavo-convex flanks of the dorsum and longitudinal elements of sculpture on the dorsum. The concept of *Similotheca* is broadened herein to encompass forms with a reduced concavity adjacent to the dorsal ridge and less steeply dipping dorsal flanks.

Stratigraphic range and distribution.—Lower Cambrian; southeastern Newfoundland and Greenland.

Similotheca similis? (Walcott, 1890)

Fig. 2A.

Hyolithes similis Walcott; Walcott 1890a: 38.
Hyolithes similis Walcott; Walcott 1890b: 622, pl. 75: 3a–d.
Hyolithes similis Walcott; Sinclair 1946: 80.
Similotheca similis (Walcott); Malinky 1988: 225, figs. 1.1–1.6, 1.8.

Lectotype.—USNM 18319-A (see Malinky 1988).

Material.—MGUH 3535 (Fig. 2A = Poulsen 1932: pl. 4: 1).

Description.—Conch with generally small apical angle creating slender appearance; dorsum seemingly high with ridge marked by blunt keel-like termination; adjacent flanks dip steeply away from the dorsal keel; flanks are flat to very slightly concave near the middle of the dorsum, and then become inflated and convex toward the lateral edges. Aperture orthogonal with shallow indentation in the middle of dorsal rim. Shell has three low and faint, widely spaced longitudinal ribs on each flank; ribs subdivide slightly more prominent transverse ribs to create a cancellate pattern on dorsum.

Remarks.—This species is represented by one specimen from the Bastion Formation which is an external mould of the dorsum; the apical and apertural ends are missing, and no traces of the venter remain. Poulsen (1932) referred it to Walcott's species with question, owing largely to the ornament on the shell. The slightly concavo-convex dorsal flanks noted above, which is considered to be a diagnostic trait of the genus (Malinky 1988), further support this assignment. However, the species' identification remains in question due to the incomplete nature of the specimen. As noted by Poulsen (1932) the number of longitudinal ribs on the flanks of the dorsum of the Greenland specimen differs from the type material, in which four ribs are present. The concavity near the dorsal keel is also less developed than that seen among the types, but this may also be attributed to intraspecific variation until additional specimens from Greenland demonstrate otherwise.

The synonymy list given for a particular taxon ordinarily is taken to denote which specimens belong to that taxon. Herein the list is intended to indicate how widespread were the reports of a particular taxon, and not necessarily which specimens belong to it.

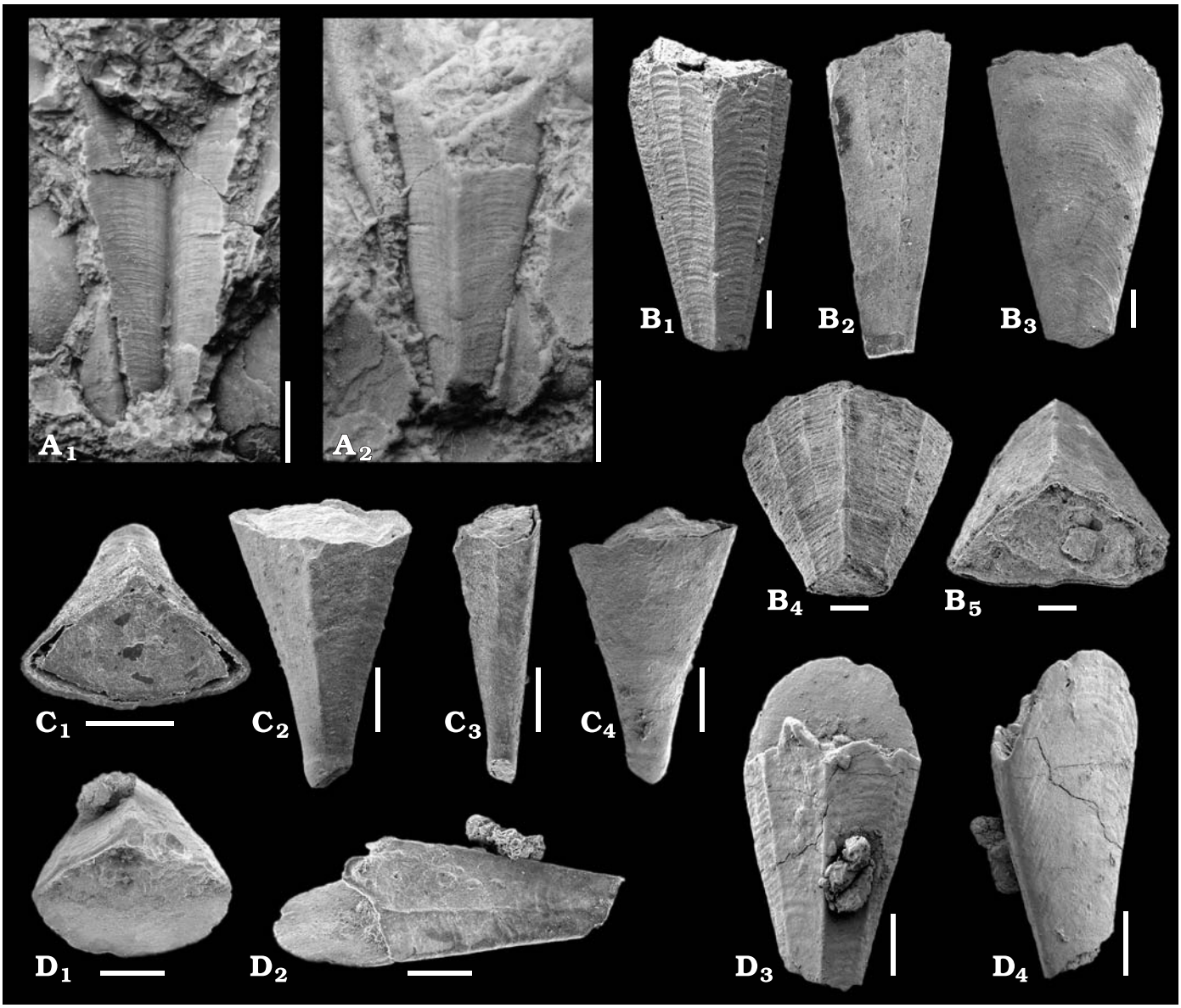


Fig. 2. **A**. *Similotheca similis*? (Walcott, 1890), MGUH 3535 from the collections of C. Poulsen; A_1, external mould of dorsum; A_2, latex cast of dorsum. **B**, **C**. *Similotheca bastionensis* sp. nov. **B**. MGUH 27082, holotype; B_1, dorsum; B_2, right lateral edge; B_3, venter; B_4, view of dorsum from apex; B_5, cross-section and view of dorsum from aperture. **C**. MGUH 27083; C_1, cross-section and view of dorsum from aperture; C_2, dorsum; C_3, right lateral edge; C_4, venter. **D**. *Similotheca groenlandica* sp. nov., MGUH 27084, holotype; D_1, cross-section and view of dorsum from aperture; D_2, left lateral edge; D_3, dorsum; D_4, oblique view of venter. All, except A, from GGU sample 314835. Scale bars 0.2 mm, except A_1 and A_2 which are 0.5 mm.

Stratigraphic range and distribution.—Lower Cambrian, southeastern Newfoundland and North-East Greenland.

Similotheca bastionensis sp. nov.

Fig. 2B, ?C.

Holotype: MGUH 27082 from GGU sample 314835.

Type horizon: Bastion Formation, Lower Cambrian.

Type locality: North-East Greenland.

Etymology: From the Bastion Formation in North-East Greenland where the type material was discovered.

Material.—MGUH 27082–27083 and six additional specimens from GGU samples 314807 and 314835.

Diagnosis.—*Similotheca* having coarse transverse rugae on the dorsum and narrow longitudinal concavities immediately adjacent to the dorsal keel.

Description.—Conch orthoconic with large apical angle such that conch has wide appearance; venter flat, grading into sharp, bluntly rounded lateral edges; dorsum low with prominent, well-developed median ridge; side of ridge marked by prominent ribs; each dorsal flank has a narrow, shallow longitudinal concavity adjacent to the median ridge, and the flanks overall are only slightly inflated, with a gentle slope away from the ridge. Venter flat, with faint transverse growth lines on shell; ligula seemingly long and rounded at anterior edge, with steeply dipping sides.

Dorsum with two prominent longitudinal ridges on each flank that subdivide the flanks into three discrete parts of about the same width. Transverse growth ribs are convex toward aperture and are subdivided into distinct segments by longitudinal ribs. Aperture apparently orthogonal but with slight median indentation in middle of dorsal rim. Cross-section with pronounced triangular shape.

Remarks.—The concavo-convex dorsal flanks and longitudinal elements of sculpture on the dorsum support assignment to *Similotheca*. *Similotheca similis* possesses a distinctly concavo-convex dorsum, with a well-developed longitudinal concavity adjacent to the median dorsal ridge, and has much fainter transverse ornament on the dorsum. In contrast, *S. bastionensis* sp. nov. has a narrower dorsal concavity and much coarser transverse dorsal sculpture.

A specimen (Fig. 2C) with a large apical angle bears limited resemblance to *Similotheca bastionensis*, but its venter is slightly more inflated and convex, creating a more rounded triangular cross-section (Fig. $2C_1$). In addition the apical angle is not constant, but increases toward the apertural region, giving the conch a flaring appearance. There is no sculpture on the specimen, but whether this is a biological or taphonomic trait cannot be determined. Thus, its assignment to *S. bastionensis* can only be tentative. Specimens with a similar cross-section and apical angle from Australia were assigned by Bengtson (1990a) to "*Hyolithes*" *conularioides* Tate, 1892 but that taxon has a distinct dorsal indentation in the centre of the apertural rim, which is lacking in C_1–C_4. "*Hyolithes*" *conularioides* is similar to the Lower Cambrian *Yankongovitus* Qian, 1978 from South China and India, and the Middle Ordovician *Sulcavitus* Syssoiev, 1958 from Sweden and Estonia, in having a longitudinal depression in the centre of the dorsum.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Similotheca groenlandica sp. nov.

Fig. 2D.

Holotype: MGUH 27084 from GGU sample 314835.

Type horizon: Bastion Formation, Lower Cambrian.

Type locality: North-East Greenland.

Etymology: Occurring in Greenland.

Diagnosis.—*Similotheca* with dorsum having one narrow, keel-like ridge on each flank and coarse, widely spaced rugae.

Description.—Conch seemingly orthoconic with large apical angle such that conch expands rapidly; venter inflated into broad, rounded surface; lateral edges sharp and keel-like; dorsum high and inflated with median ridge marked by central longitudinal keel-like rib and one similar keel in the middle of each flank; surface of flank is concave next to both the central rib and the rib in the middle of each flank, whereas elsewhere the flank is convex. Dorsal apertural rim orthogonal but with very shallow median indentation, and lateral sinuses broad though shallow; ligula long and curved at anterior edge with steeply dipping sides. Cross-section has rounded triangular shape.

Dorsum covered with transverse rugae that are widely separated and irregularly spaced; each is rounded on top with gently dipping sides such that interspaces are curved on both sides; combination of rugae and keels defines cancellate pattern on dorsum. Venter with faint growth lines only.

Remarks.—This species is based on one specimen that is well-preserved in the apertural region but lack the apical termination. Inclusion under *Similotheca* is warranted by the longitudinal ribs that create the cancellate pattern on the dorsum and by the concavity adjacent to the dorsal keel. This species differs from *S. similis* (Walcott, 1890) and *S. bastionensis* sp. nov. in having on the dorsum only one longitudinal keel-like rib on each flank and coarser rugae, which intersect to define a cancellate pattern of ornament on the dorsum. In addition the venter is more inflated, thereby giving rise to a more rounded triangular cross-section.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Family uncertain

Remarks.—Use of the heading above for all hyolithids discussed below is not meant to imply that all belong to the same family, but merely that further study of earlier diagnosed families and the taxa on which they are based is required before the genera herein can be placed confidently at the familial level.

Genus *Microcornus* Mambetov, 1972

Type species: *Microcornus parvulus* Mambetov, 1972, Lower Cambrian, Kazakhstan.

Diagnosis.—Shell small, dorsal side with pronounced median ridge and flattened flanks, ventral side weakly convex, transverse cross-section rounded triangular. Dorsal apertural edge straight or with slight median sinus, ligula semi-circular. Initial part bulbous, delineated from adult part by constriction, and usually recurved towards dorsal side. Surface sculpture fine wrinkles parallel to apertural margin. Operculum with narrow cardinal shield (from Bengtson 1990a).

Remarks.—The diagnosis of this genus given by Mambetov (1972) emphasized the bulbous protoconch, whereas that of Bengtson (1990a) also included a variety of other features of the conch. Marek (1976b, personal communication 1993) regarded use of the protoconch in hyolith taxonomy at the generic or specific level, and the use of apparently early juvenile specimens for types, as unwise, given the morphologic changes he documented in the course of hyolith ontogeny among an assemblage from the Lower Cambrian of Nevada (Marek 1976b). It is unfortunate and indeed remarkable that there are no specimens either from Greenland or Malyy Karatau that are intermediate in size between the *Microcornus*-sized specimens from both areas, and the much larger individuals reported by both Poulsen (1932) and Missarzhevsky (1969) respectively. None of the larger conchs of

those authors can be positively identified as belonging to the same taxa as any of the micro-sized individuals. At least part of the difficulty in this situation arises from the incomplete preservation of many of the larger and presumably adult individuals. Despite the large number of micro- and macro-sized hyoliths documented from Siberia and South China, and now herein, it still remains impossible to determine even whether the illustrated specimens of *Microcornus* are juveniles or adults. In contrast, Marek (1976b) possessed individuals of a variety of different sizes which he interpreted as a series of different ontogenetic stages of *Nevadalites palmeri* Marek, 1976. Marek's (1976b) specimens, and one small and presumably juvenile representative of *Nevadotheca tenuistriata* (Linnarsson, 1871; see Berg-Madsen and Malinky 1999) from the Middle Cambrian of Sweden, indicate that adult morphologic features develop early in ontogeny.

It is also worth noting that undescribed hyolithids of a small size similar to *Microcornus* from the Devonian of the Prague Basin may have an elongated, bullet-shaped or tubular protoconch (Malinky, unpublished) whereas those from Upper Carboniferous (Pennsylvanian) cyclothems of Midcontinent North America have no apparent protoconch (Malinky and Mapes 1983; Malinky et al. 1986). Inclusion of tubular protoconchs in the diagnosis of *Microcornus* could thus extend the range of the genus from Lower Cambrian into the Lower Devonian. Qian (1989) and Demidenko (2001) each implied a highly modified concept of *Microcornus* when they established species of that genus that lacked the bulbous protoconch. Both *Microcornus breviligulatus* Qian, 1989 and *M. egregius* Demidenko, 2001 have a tubular protoconch, but otherwise the conchs are similar in overall form to *Microcornus.* The report of *Microcornus* sp. from the upper Lower Cambrian upper Ludwigsdorf Member of the shallow marine Charlottenberg Formation near Görlitz in eastern Germany extends the range of this genus into central Europe (Elicki and Schneider 1992).

Stratigraphic range and distribution.—Upper Lower Cambrian (equivalent to Atdabanian–Botomian); Mongolia, Kazakhstan, South China, England, Australia, Germany, and North-East Greenland.

Microcornus eximius Duan, 1984

Fig. 3A, B.

Microcornus eximius Duan, 1984: 153, pl. 1: 5; see Bengtson 1990a: 221 for synonymy to date.

?*Microcornus eximius* Duan, 1984; Wrona 2003: 193, fig. 7A–C.

Holotype: Tianjin Institute of Geology and Mineral Resources, People's Republic of China SH 1001.

Material.—MGUH 27085–27086 and 17 additional specimens from GGU samples 314804, 314807, and 314835.

Description.—Conch orthoconic although with slight apical curvature toward right when viewed from dorsum; apical angle large such that conch has wide appearance; venter slightly inflated, grading into rounded lateral edges which in turn pass into nearly flat, only slightly inflated dorsal flanks; flanks meet in high, almost keel-like median ridge. Cross-section has rounded triangular shape. Aperture appears orthogonal with long ligula having steeply dipping sides toward aperture; anterior edge of ligula rounded; lateral sinuses well-developed, as is sinus in centre of dorsal apertural rim. Surface of shell covered with fine, equally spaced growth lines that are most prominent next to aperture but become fainter in direction of apex. Distinct bulbous protoconch separated from remainder of conch by shallow constriction.

Remarks.—This species is represented by two generally well-preserved and 17 fragmentary individuals. Overall proportions of the conch and ornament on the shell indicate placement of these specimens under *M. eximius* Duan, 1984, from South China and Australia. It is distinguished from *M. petilus* Bengtson, 1990a with which it co-occurs, by a larger apical angle and generally finer ornament on the shell. *Microcornus breviligulatus* Qian, 1989 and *M. egregius* Demidenko, 2001 have tubular protoconchs with no apparent growth lines or other ornament on the shell, and on that basis are easily distinguishable from both Greenland species of *Microcornus*. Specimens of questionable affinity to *M. eximius* were recently described from Antarctica by Wrona (2003).

Stratigraphic range and distribution.—Lower Cambrian; Australia, South China, North-East Greenland, and possibly Antarctica.

Microcornus petilus Bengtson, 1990a

Fig. 3C, D.

Microcornus petilus Bengtson, 1990a: 217, figs. 145–147.
Microcornus petilus Bengtson, 1990a; Wrona 2003: 194, fig. 8A–H.

Holotype: South Australian Museum, Adelaide SAMP30887.

Material.—MGUH 27087–27088 from GGU sample 314835.

Description.—Orthoconic to slightly cyrtoconic conch with curvature toward dorsum; apical angle small creating narrow appearance for conch; venter slightly inflated, grading into tightly rounded lateral edges and then into straight flanks; flanks meet at prominent dorsal ridge; dorsum low, giving conch depressed triangular cross-section. Aperture amblygonal, defined by very broad though shallow lateral sinuses; central portion of dorsal apertural rim rises to form low protuberance on that side.

Shell varies from nearly smooth on both dorsum and venter to having prominent well-developed ribs on either or both sides; spaces between ribs equal to diameter of between 1–3 ribs; protoconch generally bulbous, tapering to a bluntly rounded apex.

Remarks.—Specimens from North-East Greenland assigned to this species match well the descriptions and illustrations of this species given by Bengtson (1990a) and Wrona (2003).

Stratigraphic range and distribution.—Lower Cambrian; Australia, Antarctica, and North-East Greenland.

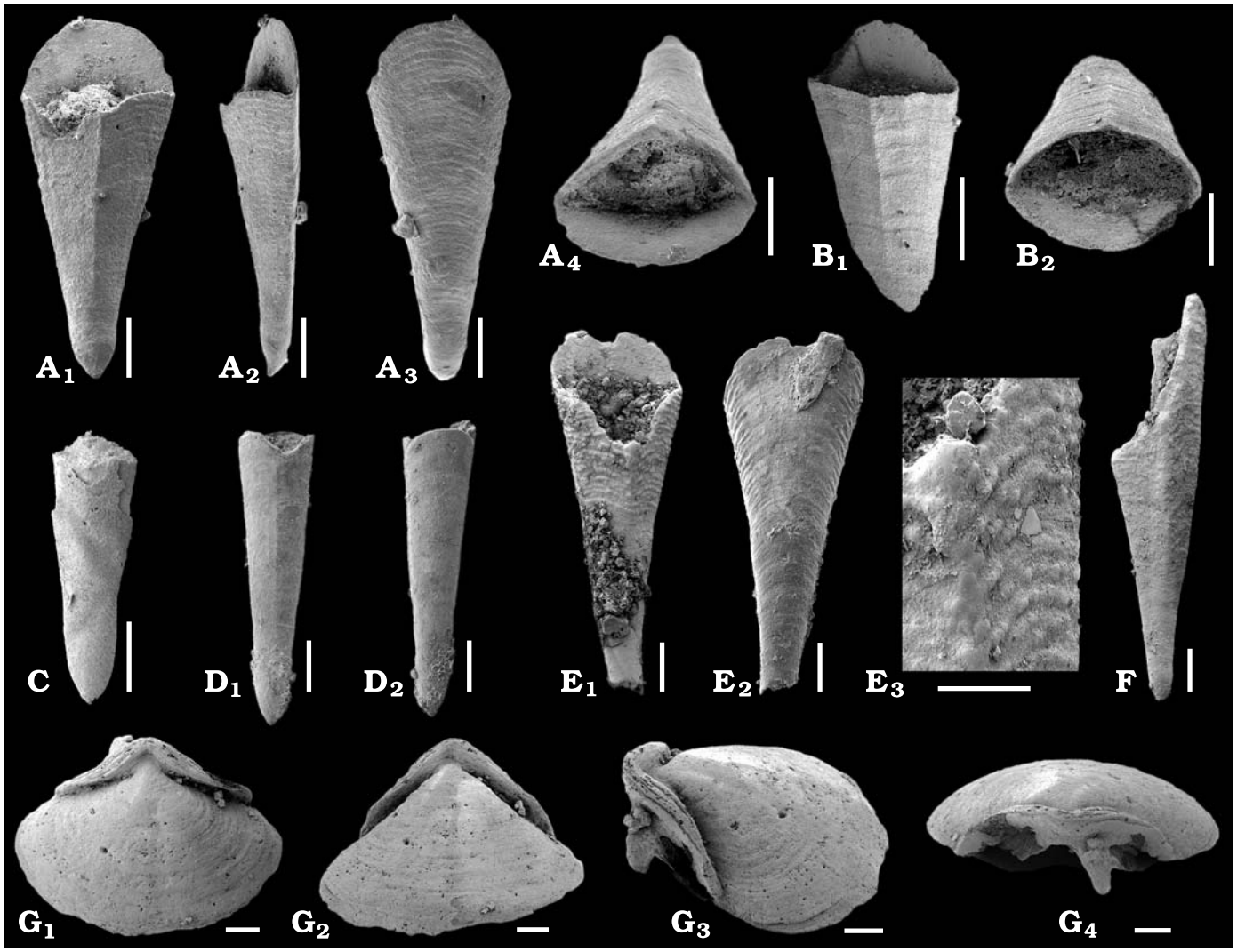


Fig. 3. **A**, **B**. *Microcornus eximius* Duan, 1984. **A**. MGUH 27085; A_1, dorsum; A_2, right flank of dorsum; A_3, venter; A_4, cross-section and view of dorsum from aperture. **B**. MGUH 27086; B_1, dorsum; B_2, cross-section and view of dorsum from aperture. **C**, **D**. *Microcornus petilus* Bengtson, 1990a. **C**. MGUH 27087, venter. **D**. MGUH 27088; D_1, dorsum; D_2, venter. **E**, **F**. *Paracornus poulseni* gen. et sp. nov. **E**. MGUH 27089, holotype; E_1, dorsum; E_2, venter; E_3, enlarged view of ornament at right lateral edge (venter to right). **F**. MGUH 27090, dorsum. **G**. *Parkula bounites* Bengtson, 1990a, MGUH 27091; G_1, exterior of operculum from above; G_2, exterior of operculum from conical shield; G_3, lateral view of operculum with conical shield to right; G_4, exterior of operculum with cardinal shield in foreground. A, D–G, from 314835; B, from GGU sample 314906; C, from GGU sample 314904. Scale bars 0.2 mm, except E_3 which is 50 μm.

Genus *Paracornus* nov.

Type species: *P. poulseni* gen. et sp. nov.

Etymology: From Greek *para*, by, close to, and the generic name *Microcornus*.

Diagnosis.—Hyolithid having small apical angle and therefore narrow conch with gradual increase in apical angle beginning at approximately half the distance between apex and aperture; ornament on dorsum consist of rows of low rounded knobs that follow pattern of growth lines.

Remarks.—The change in apical angle and unusual ornament on the dorsum separate this form from all other Lower Cambrian hyolithids. The former trait is known from one species of *Parakorilites* He and Pei, in He et al.1984 from the Meischucunian of South China, and from *Tizilites* Marek, Malinky, and Geyer, 1997 from the Middle Cambrian of Morocco. In the former, the transformation from smaller to larger apical angle is more subtle and occurs much closer to the aperture than in *Paracornus*. In contrast, the change in *Tizilites* is far more abrupt and the resulting flaring of the aperture more pronounced. The rows of knobs that constitute the ornament on *Paracornus* are unknown in any other hyolithid. The protoconch of *Paracornus* is unknown at present, although should this genus prove to have a bulbous protoconch similar to *Microcornus* Mambetov, 1972 or *Parkula* Bengtson, 1990a, the change in angle and ornamentation would still suffice to separate it from those genera.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

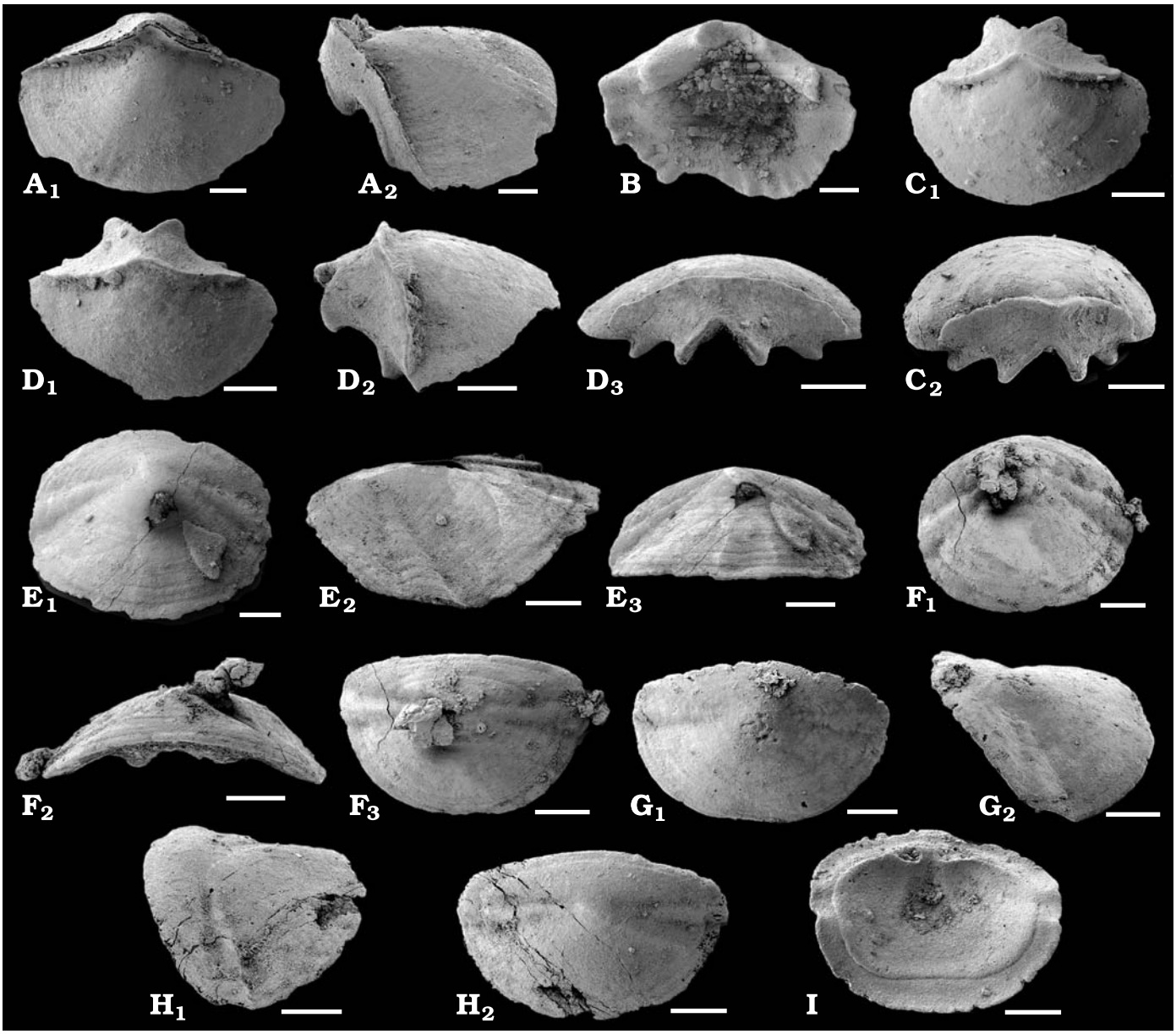


Fig. 4. **A**, **B**. *Parkula bounites* Bengtson, 1990a. **A**. MGUH 27092; A_1, exterior of operculum from above; A_2, lateral view of operculum with conical shield to right. **B**. MGUH 27093, interior of operculum with cardinal processes and clavicles (top of the picture). **C**, **D**. *Parkula*? sp. **C**. MGUH ZZZ13; C_1, exterior of operculum from above; C_2, view from cardinal shield showing enlarged cardinal processes. **D**. MGUH 27095; D_1, exterior of operculum from above; D_2, lateral view of operculum with conical shield to right; D3, view from cardinal shield showing enlarged cardinal processes. **E–I**. *Hyptiotheca karraculum* Bengtson, 1990a. **E**. MGUH 27096; E_1, exterior of operculum from above; E_2, lateral view with conical shield to right, showing no change in angle between conical and cardinal shields; E_3, view from edge of conical shield. **F**. MGUH 27097; F_1, oblique view from above of exterior of operculum from above; F_2, view from edge of conical shield; F3, exterior of operculum from above. **G**. MGUH 27098; G_1, oblique view from above of exterior of operculum from above; G_2, lateral view of operculum with conical shield to right, showing abrupt change in angle between cardinal and conical shields. **H**. MGUH 27099; H_1, lateral view of operculum with conical shield to right, showing abrupt change in angle between cardinal and conical shield; H_2, exterior of operculum from above. **I**. MGUH 27100, interior view showing weakly developed depressions along edges only, corresponding to rooflets on exterior. All from GGU sample 314835. Scale bars 0.2 mm.

Paracornus poulseni gen. et sp. nov.

Fig. 3E, F.

Holotype: MGUH 27089 from GGU sample 314835.

Type horizon: Bastion Formation, Lower Cambrian.

Type locality: North-East Greenland.

Etymology: In honour of Christian Poulsen, in recognition of his work on the faunas and stratigraphy of Greenland.

Diagnosis.—Same as for genus.

Material.—MGUH 27089–27090 and a single fragment from GGU sample 314835.

Description.—Seemingly orthoconic conch with apical curvature slightly to right when viewed from dorsum; sides of conch nearly parallel to each other in apical region with sides diverging due to increase in apical angle at approximately half the

distance between apex and aperture; dorsum high with blunt median ridge; flanks adjacent to it seem to be straight, and lateral edges tightly rounded; aperture seems to be orthogonal but with broad shallow median indentation along dorsal rim, and lateral sinuses poorly developed to non-existent. Ligula apparently long with flattened anterior edge and gently dipping sides. Cross-section has rounded triangular shape.

Shell on dorsum covered with series of knob-like projections that are aligned to create what appear to be ribs; ribs follow pattern of growth lines; width of knobs equal to width of space between each row of knobs. Venter has widely and evenly spaced ribs which are most pronounced near lateral edges beginning where apical angle changes to become fainter both near the middle of venter and toward apex. Protoconch appears to be elongate and tubular.

Remarks.—Knowledge of this species is derived from a generally well-preserved holotype and two less well-preserved paratypes. The rows of knobs provide details of the aperture on the holotype because part of the apertural rim is broken on that individual. No other hyolith species reported from the Bastion Formation or elsewhere in the Lower and Middle Cambrian resemble *Paracornus poulseni* gen. et sp. nov. in apical angle or ornament.

Stratigraphic range and distribution.—Same as for genus.

Genus *Parkula* Bengtson, 1990a

Type species: *P. bounites* Bengtson, 1990a.

Diagnosis.—Straight conchs with lenticular cross-section, faint dorsal median ridge, and semi-elliptical ligula. Surface sculpture of transverse striations and irregular longitudinal wrinkles. Opercula with strongly convex conical shield, short cardinal processes, and one pair of short clavicles ending in blade-like projections (from Bengtson 1990a).

Stratigraphic range and distribution.—Lower Cambrian; Australia, Antarctica, and North-East Greenland.

Parkula bounites Bengtson, 1990a

Figs. 3G, 4A, B, 5.

Parkula bounites Bengtson, 1990a: 223, figs. 149–151.

Parkula bounites Bengtson, 1990a; Demidenko 2001: 101, pl. 9: 12, 13.

Parkula bounites Bengtson, 1990a; Wrona: 197, fig. 5F.

Holotype: South Australian Museum, Adelaide SAMP30892.

Material.—MGUH 27091–27093, MGUH 27101 and 116 additional specimens from GGU samples 314807, 314835, and 314908.

Diagnosis.—As for genus.

Description.—Operculum having broad, rounded conical shield with a relatively high profile; summit is rounded to flattened on surface; furrows are deep and well-developed although associated rooflets appear nonexistent; cardinal shield small with sides adjacent to summit also curved to be convex toward conical shield. Operculum monoclaviculate, with one pair of short cardinal processes that expand toward distal end, to terminate in blade-like projections; clavicles diverge at angle of approximately 70°. Edge of conical shield may have series of low, widely spaced radial ridges with spaces between them equal to width of ridge. Exterior may have widely spaced, generally indistinct concentric growth lines; interior smooth except for ridges at edge of conical shield.

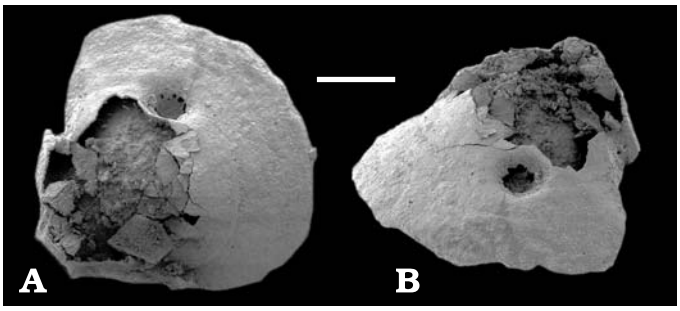


Fig. 5. Exterior view of operculum of *Parkula bounites* Bengtson, 1990, MGUH 27101, showing possible borehole. From GGU sample 314807. Scale bar 0.2 mm.

Remarks.—Opercula from the Bastion Formation of North-East Greenland match well those of *Parkula bounites Bengtson, 1990a* from Australia, although there is much variability in the width of the operculum (see Bengtson 1990a: fig. 150A and E and herein). The conch of this species has not yet been identified in Greenland. Its absence supports the notion of a hydrodynamically sorted accumulation of fossils in the bed that yielded the specimens. Its absence could also be explained by differential preservation, as initially suggested by Holm (1893) for some hyolith species from Denmark, and later expanded by Malinky and Berg-Madsen (1999) to explain general disparities in the numbers of hyolith conchs versus opercula from the same levels. However in this instance, because the conch of *Parkula* is known from other localities, sorting provides a better explanation.

A single specimen from Greenland (Fig. 5) shows a circular perforation on the right hand side of the conical shield. Its diameter is about 100 μm and the sides slope slightly inwards. Perforations of similar size and morphology in shells of Early and Middle Cambrian phosphatic brachiopods and problematic fossils were interpreted by Conway Morris and Bengtson (1994) as evidence of the activity of some as yet unidentified predator.

Stratigraphic range and distribution.—Lower Cambrian; Australia, Antarctica, and North-East Greenland.

Parkula? sp.

Fig. 4C, D.

Material.—MGUH ZZZ13-27095 and ten additional specimens from GGU sample 314835.

Description.—Low and broad conical shield of generally low profile, grading into shallow and poorly defined furrows with no identifiable rooflets; summit low and indistinct; cardinal shield low, curving by summit to become convex toward conical shield. Interior with cardinal processes having broad base that originates at edges of operculum and progres-

sively expands to form wide, blade-like processes at center of cardinal shield that have blunt, rounded terminations with very slightly curvature and indentation at distal end of processes. Operculum monoclaviculate, and cardinal processes diverge at angle of 80°. Exterior of operculum smooth.

Remarks.—This taxon is known from two specimens in which the edge of the conical shield is broken, and no details remain of the exterior. The most distinctive feature is the massive cardinal processes with the broad base that attaches them to the cardinal shield. The seemingly small size of the cardinal shield itself is worthy of note, although the amount removed by breakage cannot be known with certainty. These features clearly distinguish this taxon from all others reported by Bengtson (1990a) and Demidenko (2001) from Australia, and no Early Cambrian opercula of similar morphology have been reported from elsewhere.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Genus *Hyptiotheca* Bengtson, 1990a

Type species: *H. karraculum* Bengtson, 1990a.

Diagnosis.—Conchs with ovoid cross-section and ventrally directed longitudinal curvature. Ligula semi-elliptical, at 120° to dorsal apertural margin. Surface sculpture of distinct growth lines and faint longitudinal striations. Opercula with broad cardinal shield, well-defined tectula, cardinal processes about 3 lengths of the operculum width, thickened central field on inner surface, and no clavicles (from Bengtson 1990a).

Stratigraphic range and distribution.—Lower Cambrian; Australia, Antarctica, Siberia, South China, Nova Scotia, New York State, and North-East Greenland.

Hyptiotheca karraculum Bengtson, 1990a

Figs. 4E–I, 6A, B.

Hyptiotheca karraculum Bengtson, 1990a: 228, figs. 152–155.

part. *Insolitotheca communis* (Billings, 1972); Landing and Bartowski 1996: 758, figs. 7.18, 7.19, 7.21, 7.22, non 7.14–7.17, 7.20.

Hyptiotheca karraculum Bengtson, 1990a; Demidenko 2001: 102, pl. 10: 3–6.

Hyptiotheca karraculum Bengtson, 1990a; Wrona 2003: 197, figs. 9A, B, 10A–E.

Holotype: South Australian Museum, Adelaide SAMP30902.

Material.—MGUH 3522 (Fig. 6A = Poulsen 1932: pl. 2: 12), MGUH 27096–27100, MGUH 27102 and 115 additional specimens from GGU samples 314804, 314835, 314918 and 314919.

Diagnosis.—As for genus.

Description.—Operculum of generally elliptical shape with conical shield only slightly more curved than cardinal shield along the edge; conical shield gently curved with low profile grading into indistinct summit; furrows and rooflets well defined though furrows shallow; cardinal shield may intersect conical shield at angle of about 20°, or it may grade smoothly without any change in angle into cardinal shield, such that operculum when viewed from lateral edge has profile of gently curving line; surface of operculum with widely spaced concentric grooves.

Interior of operculum has thickened central region that has a distinct sharp boundary with edge of the operculum; shallow depressions that mark the sites of the rooflets on the exterior may be present only along the edges of the operculum in the thinner region, or they may be present only in the thicker region, or they may be lacking entirely; interior of operculum smooth and apparently lacking any evidence of clavicles.

Remarks.—This taxon is known from the Bastion Formation only from the operculum, but the generally fine preservation of most individuals confirms their affinity to *Hyptiotheca*. This taxon is highly unusual for a hyolithid in two ways. First, the transition between cardinal and conical shields is smooth without any change in angle on some individuals (Fig. $4E_2$), whereas on others there may be an abrupt boundary between shields (Fig. $4G_2$, H_1). The latter type of operculum with an angular break between shields is normal for hyolithids. Second, all opercula of this species from Greenland and Australia (Bengtson 1990a: figs. 5I, $8B_1$–B_3) lack clavicles on the interior. The presence of these structures is one of the defining traits of the order Hyolithida (Marek 1963), and their absence certainly raises questions about the concept of that group, as well as the functional morphology and palaeobiology of this particular species. Perhaps the clavicles were not mineralized in *Hyptiotheca*, or their role in this taxon was assumed by some other structure. Possibly the mode of life of this taxon was different such that clavicles were not needed. This is the only species identified thus far in which clavicles are lacking, but given that opercula are far less common in the fossil record than hyolith conchs, the absence of clavicles may be more widespread than is generally realized. A final possibility is that *Hyptiotheca karraculum* may represent a short-lived experiment in the evolution of hyoliths, in which differences in mode of life and/or functional morphology ultimately proved to be only of limited adaptive value, and the animal quickly became extinct. A similar short-lived experiment in hyolith evolution may have been represented by *Polylopia* Clark, 1925 from the Middle Ordovician of Tennessee, which Yochelson (1968) suggested was a hyolith that adopted a vagrant mode of life, carrying its shell in the manner of a gastropod.

Conchs of *H. karraculum* are not known from Greenland but Bengtson (1990a) reported 15 conchs and nine opercula from Australia. The conch possesses a short ligula which is a diagnostic trait of the Hyolithida, but the strongly amblygonal nature of the aperture causes the dorsal and ventral rims of the aperture to be nearly the same height. *Patholites* Marek, Malinky, and Geyer, 1997 from the Middle Cambrian of Morocco is similar in terms of apertural morphology to *Hyptiotheca*, but its operculum remains unknown.

Conchs of *H. karraculum* have a distinct apical curvature toward the venter, which Bengtson (1990a) noted was unusual for a hyolith. He suggested that the animal lived with dorsum

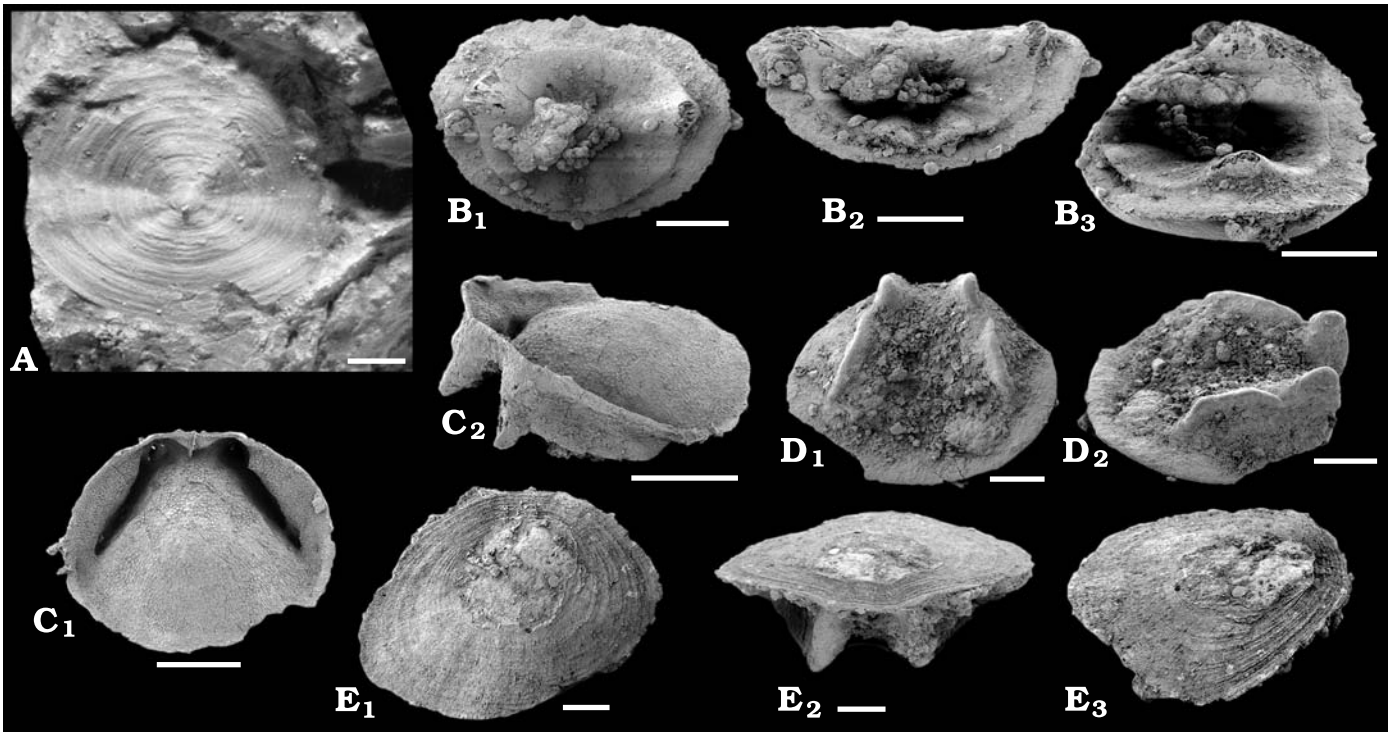


Fig. 6. **A**, **B**. *Hyptiotheca karraculum* Bengtson, 1990a. **A**. MGUH 3522, exterior view of operculum from above. **B**. MGUH 27102; B_1, interior view with ridges emanating from central raised region and terminating at edge of raised region; B_2, lateral view; B_3, lateral view showing edge of ridge. **C**–**E**. Operculum A. **C**. MGUH 27103; C_1, internal mould of interior of operculum showing semi-circular cardinal processes and elongate clavicles; C_2, lateral view with conical shield to right. **D**. MGUH 27104; D_1, interior of operculum with clavicles in foreground; D2, interior of operculum with cardinal processes at right edge of photograph. **E**. MGUH 27105; E_1, exterior view of operculum from above; E_2, oblique view from dorsal edge showing cardinal processes; E_3, oblique exterior view. A, from the collections of C. Poulsen; B–D, from GGU sample 314835; E from GGU sample 314807. Scale bars 0.2 mm, except A which is 1 mm and B_1–B_3 which are 0.5 mm.

down against the sediment. While the function of ventral curvature is not well understood, it seems unlikely that the animal could survive in that orientation. The most stable orientation would have been with the flattened venter down, whereas with the dorsum against the sediment the animal probably would have tilted on its side or sank into the sediment, thereby causing suffocation. The ligula has been interpreted as a platform on which the animal could extend its soft tissue without fouling the inside of the conch with sediment. With the dorsum down, the ligula would have served as a roof over the animal's head instead of as a platform under the head. Malinky and Sixt (1990) documented an assemblage of 76 hyoliths from the Lower Mississippian of Iowa in which some individuals curved dorsally, others ventrally and others either to the left or right when viewed from the dorsum. The function of such curvature is not understood, although it seems unlikely that within one species at one locality there would be such variability in mode of life. Probably apical curvature represents an adaptation to highly localized conditions in which the shell curved so that the animal could shift its center of buoyancy without sinking into the sediment.

Landing and Bartowski (1996) illustrated three opercula assigned to the ill-founded taxonomic wastebasket "*Insolitotheca*" *communis* (Billings, 1972) from the Browns Pond Formation of the Taconic Allochthon in New York State (Landing and Bartowski 1996: figs. 7.18, 7.19, 7.21, 7.22). The poor preservation of the illustrated material makes the relationship between the conchs of "*I.*" *communis* and the alleged opercula difficult to address. The lack of a depressed marginal rim on the opercula was used to separate them from *Hyptiotheca*, but this feature appears to be the consequence of abrasion, and the specimens are here included in *H. karraculum*. Landing (1995) also reported an unequivocal occurrence of *Hyptiotheca* from Nova Scotia. Opercula that bear some resemblance to *Hyptiotheca* were illustrated by Poulsen (1932: pl. 2:12, as *Hyolithus* (*Orthotheca*?) *communis* Billings, 1872); by Missarzhevsky (1969: pl. 11: 4), as *Allatheca* sp., and later one under *Allatheca*? *concinna* (Missarzhevsky, 1989: pl. 3: 12). Sokolov and Zhuravleva (1983: pl. 22: 7b) also illustrated a probable specimen of *Hyptiotheca* that they referred to *Majatheca tumefacta* Missarzhevsky, 1969 while Qian (1989) illustrated an operculum (Qian 1989: pl. 19: 1) that bears limited resemblance to *Hyptiotheca*. These specimens are not formally re-assigned until their morphology becomes better known. These possible occurrences would extend the geographic range of this taxon to Siberia and the stratigraphic range to the *D. lenaicus–M. tumfacta* Zone. The large size of the operculum recorded by Poulsen (1932) suggests that it represents an adult or at least a much later ontogenetic stage than the smaller opercula re-

ported herein. Poulsen's operculum strongly supports the notion that the amount of ontogenetic change in this species is minimal.

Stratigraphic range and distribution.—Same as for genus.

Class Hyolitha *incertae sedis*

Operculum A

Fig. 6C–E.

Material.—MGUH 27103–27105 and 67 additional specimens from GGU samples 314807, 314835, 314904, 314906, 314908, 314910, and 314933.

Description.—Operculum of either sub-circular (Fig. 6D) to rounded trapezoidal outline (Fig. 6E) with the dorsal edge approximately three times the width of the ventral edge; ventral edge is slightly elevated above dorsal part, but otherwise there is no indication of clear dorso-ventral differentiation; faint rounded summit is offset toward ventral edge but exact location uncertain. Exterior has concentric ribs that are best developed along ventral edge but yet remain visible around entire surface. Interior with prominent extended cardinal processes with rounded summit and steeply dipping sides; processes are slightly higher than clavicles and diverge at an angle of approximately 50°; extending in ventral direction from cardinal processes are flattened, blade-like clavicles with steeply dipping sides although the sides facing the middle of the operculum dip more gently than those on the opposite side. The interior appears to be smooth, lacking any indication of muscle scars or ornament.

Remarks.—This taxon is represented by opercula with similar clavicles on the interior but with a slightly differing outline. These opercula are unusual in that they possess certain traits associated with the Hyolithida but lack others thought to be critical in defining and recognizing that group. The structures that resemble clavicles and cardinal processes are elements that partly define the Hyolithida, but the lack of any dorso-ventral differentiation and the rooflets and furrows that are associated with the boundaries between these sides are lacking. This trait is a common feature among the Orthothecida Marek, 1966. *Hyolithes communis* Billings, 1872 from the Lower Cambrian of New York has a tubular conch, but its operculum, which otherwise resembles the Greenland taxon in some aspects, can be subdivided into dorsal and ventral portions, and it has demonstrable rooflets and furrows, even though they are faint and not well-developed. The conch of Operculum A is unknown. Given that only the operculum is available, these individuals are best left in open nomenclature, although retained provisionally under Hyolithida.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Operculum B

Fig. 7.

Material.—MGUH 27106–27107 and 16 additional specimens from GGU samples 314809, 314836, 314901, 314906, 314908, and 314933.

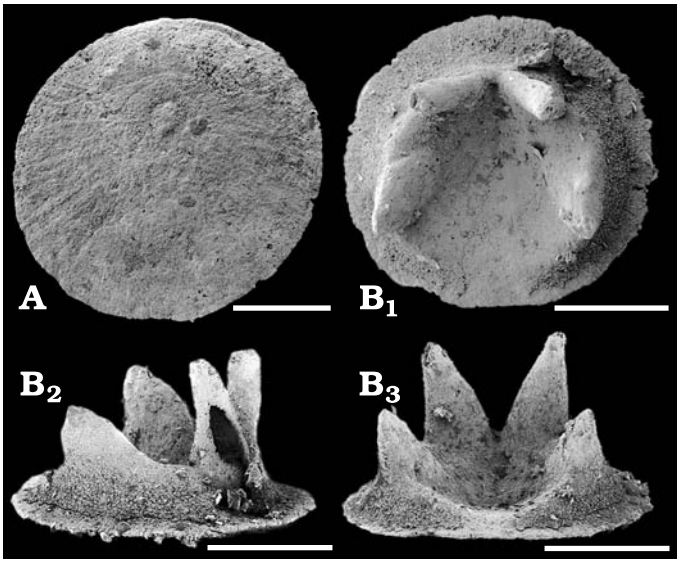


Fig. 7. Operculum B. **A**. MGUH 27106; exterior view of operculum from above. **B**. MGUH 27107; B_1, interior view from above; B_2, lateral view; B_3, interior view showing distal edges of clavicles. Both from GGU sample 314933. Scale bars 0.2 mm.

Description.—Nearly circular operculum with summit located two fifths of the distance from the dorsal edge; surface of exterior with apparent faint radial lines at least in some places; interior has large, rod-like, straight and widely diverging clavicles joined at base, that separate from each other at angle of nearly 60°; near proximal end nearest cardinal processes, processes diverge at angle of approximately 45°; clavicles are low, but the upper surface curves steeply upward to terminate in blunt point oriented toward ventral edge; beyond termination the edge of clavicles drops vertically toward interior surface of operculum. When viewed from above, clavicles have a massive compacted appearance with widest portion at proximal end, progressively thinning toward distal termination; surfaces of clavicles that face each other dip more steeply than those facing away; clavicles form slightly elevated ridge that connects the two at the distal termination.

Remarks.—This taxon is known from 18 specimens, which are here left in open nomenclature because the conch is unknown. The morphology of this species blurs the distinction between Hyolithida and Orthothecida owing to the lack of dorso-ventral differentiation of the exterior, as is seen among many orthothecids, yet it possesses clavicles on the interior which normally characterize hyolithids (but see *Hyptiotheca*). A nearly circular operculum such as this would ordinarily be an ideal candidate for inclusion under one of the many supposed orthothecid hyolith taxa based on tubular conchs from the Lower Cambrian, such as *Turcutheca* Missarzhevsky, 1969 from Siberia. To ascribe this operculum to a taxon such as that implies a seemingly unusual functional morphology for this animal. Perhaps it was from such an animal that hyolithids and orthothecids differentiated into the two better defined groups seen later in the Palaeozoic. However, given the ab-

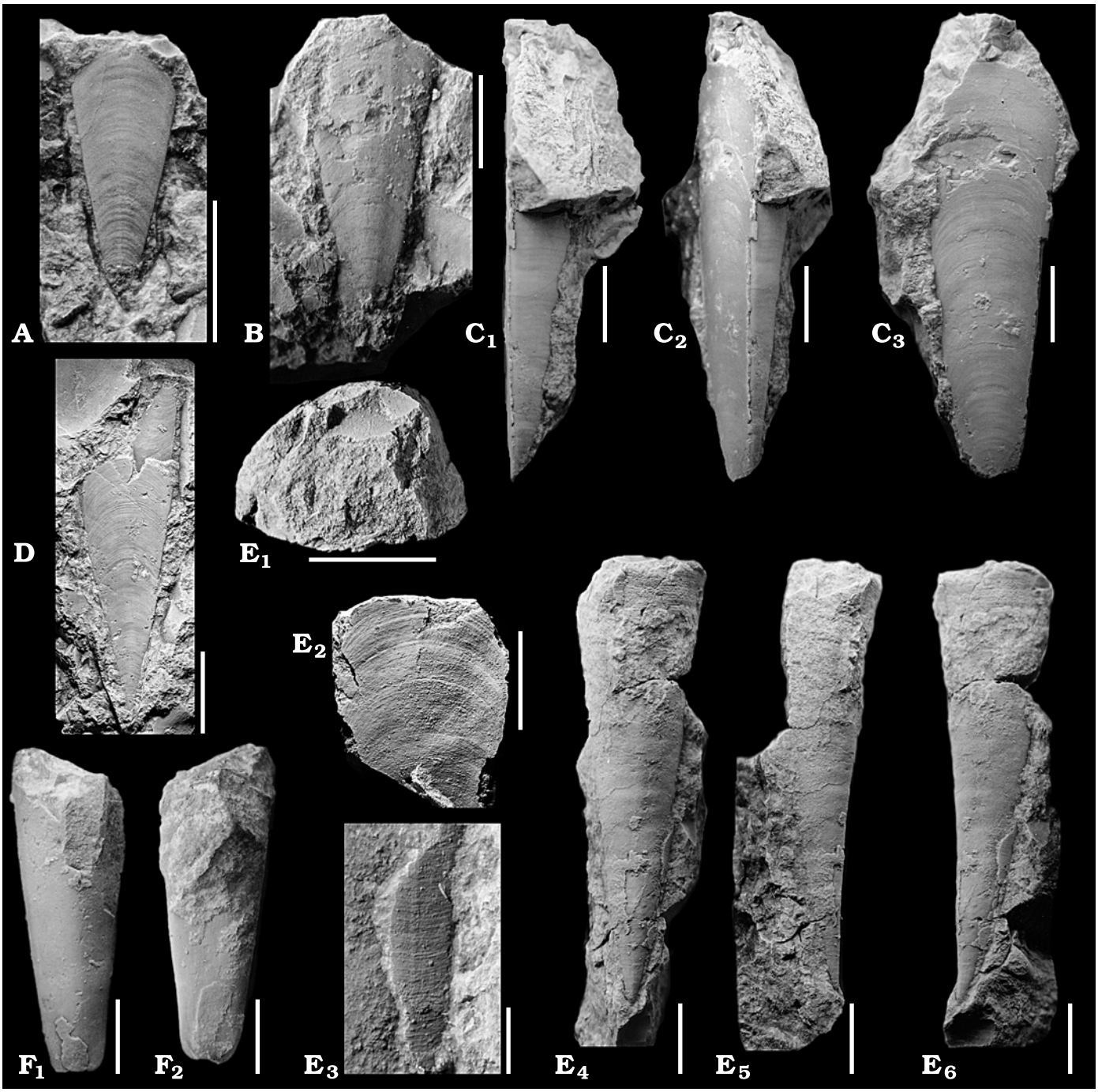


Fig. 8. **A**–**D**. "*Hyolithus* (*Hyolithus*) *americanus* Billings, 1872". **A**. MGUH 3531, venter. **B**. MGUH 3530, venter. **C**. MGUH 3532; C_1, left lateral edge; C_2, oblique view of left lateral edge with venter on left; C_3, venter. **D**. MGUH 3529, venter, with apex of smaller hyolith protruding from conch. **E**. "*Hyolithus* (*Hyolithus*) *mutatus* Poulsen, 1932", MGUH 3534; E_1, cross-section; E_2, venter in apertural region; E_3, magnified view of shell on right flank of dorsum; E_4, dorsum; E_5, left flank of dorsum; E_6, right flank of dorsum. **F**. "*Hyolithus* (*Hyolithus*) sp." MGUH 3536; F_1, dorsum; F_2, venter. All from the collections of C. Poulsen. Scale bars 5 mm, except E_3 which is 1 mm.

sence of a direct association of conch and operculum, it is unwise at this time to place this operculum in any established taxon, although it is provisionally included under order Hyolithida.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Hyolithus* (*Hyolithus*) *americanus* Billings, 1872"

Fig. 8A–D.

Hyolithus (*Hyolithus*) *americanus* Billings; Poulsen 1932: 21, pl. 3: 7–11.

Material.—MGUH 3531 (Fig. 8A = Poulsen 1932: pl. 3: 9); MGUH 3530 (Fig. 8B = Poulsen 1932: pl. 3: 8), MGUH

3526 (Fig. 8C = Poulsen 1932: pl. 3: 10), MGUH 3529 (Fig. 8D = Poulsen 1932: pl. 3: 7).

Description.—Conch seemingly orthoconic with small apical angle; venter flat or slightly raised along mid-line; ligula short and rounded at anterior edge with gently sloping sides; all else unknown.

Remarks.—This species was listed and illustrated by Poulsen (1932) but not described, other than to say that some specimens show traces of longitudinal lines on the venter. Specimens MGUH 3531 (Fig. 8A) and MGUH 3530 (Fig. 8B) retain faint, low longitudinal ribs on the venter which are probably the lines to which Poulsen (1932) referred. The original designation of *Hyolithes americanus* is *Theca triangularis* Hall, 1847 from the Lower Cambrian of New York. It was reassigned when the name *Theca* fell out of favour in the 19th century, abetted by Barrande's (1867) promotion of the name *Hyolithes*. The species' name *americanus* was substituted when Billings (1872) thought that the name *triangularis* was preoccupied by another hyolith species, *Theca triangulare* Portlock, 1843 from Ireland, but the Irish species subsequently was recognized as a cephalopod, and reassigned to *Orthoceras*. *Hyolithes americanus* was revised by Malinky (1989) and shown to be an unrecognizable taxon, because preservation of the surviving specimens, as casts in sandstone, is incomplete. The Greenland species cannot be compared in detail to the much better preserved specimens assigned to *H. americanus* by Shaw (1955) from the Lower Cambrian of Vermont. There is limited resemblance in conch form between the Greenland specimens and two species of the Siberian genus *Burithes* Missarzhevsky, 1969. Fig. 8A and B resemble *B. erum* Missarzhevsky, 1969, and the others are somewhat similar to *B. elongatus* Missarzhevsky, 1969. *Burithes* is based on internal moulds (Malinky unpublished), thus comparison between the two is limited.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Hyolithus* (*Hyolithus*) *mutatus* Poulsen, 1932"

Fig. 8E.

Hyolithus (*Hyolithus*) *mutatus* Poulsen, 1932: 23, pl. 3: 12–17.

Material.—MGUH 3534.

Description.—Cyrtoconic conch with apical curvature toward dorsum; conch has narrow tapering appearance due to low apical angle; venter seemingly flat, grading into sharp lateral edges; flanks of dorsum inflated and rounded, intersecting to create rounded central ridge; ligula apparently short and rounded on anterior edge with gently dipping sides; cross-section triangular; shell on dorsum and venter with faint, closely spaced transverse lines; internal mould of dorsum with widely and irregularly spaced transverse rugae.

Remarks.—This species is known from one internal mould of a large conch with a minute fragment of shell adhering to the dorsum, and shell on the venter, but only the apertural region of the venter is free of matrix. This individual is distinctive because it is much larger than Poulsen's other material and the new material documented herein. It also has a strong apical curvature toward the dorsum, a feature widely shared among Ordovician hyoliths of Baltica but rarely seen among other individuals.

The few longitudinal elements of sculpture seen on the shell suggest resemblance to *Lovenedolithes araneus* (Holm, 1893; see Berg-Madsen and Malinky 1999) from the Middle Cambrian of Sweden, and to *L. groenwalli* (Poulsen, 1967) from the Lower Cambrian of Denmark. Both species of *Lovenedolithes* possess much smaller conchs than does *H. (H.) mutatus* Poulsen, 1932, assuming that *Lovenedolithes* is represented by normal-sized adults. *Doescherina clarkei* Malinky, 1989 from the Middle Cambrian of Montana likewise has longitudinal elements of sculpture, but it too is smaller and as with both species of *Lovenedolithes*, the apical angles of the conchs are much larger. Owing to generally incomplete preservation, *H.* (*H.*) *mutatus* Poulsen, 1932 cannot be further assigned to genus.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Hyolithus* (*Hyolithus*) sp."

Fig. 8F.

Hyolithus (*Hyolithus*) sp.; Poulsen 1932: 23, pl. 4: 2–5.

Material.—MGUH 3536.

Description.—Orthoconic conch with small apical angle and therefore narrow appearance; internal mould of venter seemingly flat, grading in tightly rounded, blunt lateral edges; dorsum high with tightly rounded median ridge; flanks adjacent to it also inflated to create high triangular cross-section. Surface of internal mold smooth; all else unknown.

Remarks.—This taxon is known from one incompletely preserved internal mould which lacks any features that could reasonably be used to identify it to genus or species. Even its affinity to the Hyolithida is open to question because no trace of a ligula or any other apertural features remain. The triangular cross-section seen in this species is a common feature among hyolithids, but it is seen even among some orthothecids, such as *Novitatus tarynicus* Syssoiev, 1972. However, no good purpose is served in transferring this form to Orthothecida owing to incomplete preservation, and the species is retained under its original designation.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Order Orthothecida Marek, 1966

Remarks.—This order of hyoliths was defined to encompass individuals that have either a planar aperture or one with a broad indentation usually on the ventral side. Within this concept, a ligula would therefore be lacking. In addition, the orthothecid operculum lacks not only clavicles but also a furrow and rooflets.

Orthothecids fall into two broad groups based on cross-sectional shape: the first with a poor- to well-developed kidney or heart shape, and a second with either a circular, sub-circular, lenticular or elliptical cross-section. The former are readily identifiable as orthothecids because opercula that match in outline those cross-sections have cardinal processes typically seen among hyoliths. The second group is more problematic because opercula are unknown for most such tubular fossils, and the tubular morphology is a trait seen in other groups of calcareous organisms, such as *Coleolus* and *Coleoides* (Fisher 1962). *Circotheca* Syssoiev, 1958 is a tubular hyolith with an operculum that clearly possesses cardinal processes (Berg-Madsen and Malinky 1999), thus its affinity to the Hyolitha is beyond question. However, many tubular fossils particularly from the Lower Cambrian of Siberia and South China, such as *Turcutheca* Missarzhevsky, 1989 and *Paracircotheca* Qian, 1989 have been referred to Orthothecida, and many others to *Circotheca* itself (Syssoiev 1960; Meshkova 1974; Kerber 1988) even though the operculum is unknown. Relatively few calcareous tubular fossils are known from Greenland, although some do occur (Figs. 10G, 11–13) but without an operculum their affinity to the Hyolitha cannot be demonstrated.

It is also worth noting that apical curvature has not been documented among any undoubted adult orthothecid hyoliths with a heart- or kidney-shaped cross-section except for *Contitheca*? sp. and "*Orthotheca bayonet* var. *groenlandica* (Poulsen, 1932)" below. In contrast, many small, strongly curved tubular fossils of circular or sub-circular cross-section are assigned to *Circotheca* (Kerber 1988: pl. 1: 10, 11, 14), even though such curvature has not been seen among larger and presumably adult individuals of *Circotheca* (Berg-Madsen and Malinky 1999).

Stratigraphic range.—Lower Cambrian–Middle Devonian.

Family Gracilithecidae Syssoiev, 1972

Genus *Gracilitheca* Syssoiev, 1968

Diagnosis.—Orthothecid hyolith with shallow ventral furrow, grading into blunt lateral edges that extend to form a distinct protrusion along the entire length of the lateral edges of the conch (emended from Syssoiev 1968: 39).

Remarks.—Representatives of this genus are distinguished by a conch with a pronounced triangular cross-section that includes longitudinal protuberances extending from each lateral edge, and extending for the entire length of the conch. The type species, *G. ternata* Syssoiev, 1968 is known only from an impression of the venter, but the presence of the protuberances is beyond question.

Stratigraphic range and distribution.—Lower Cambrian; eastern Canada (Matthew 1899), England (Cobbold 1921), Siberian Platform (Syssoiev 1968; Val'kov 1975, 1987), Morocco (Marek et al. 1997), and North-East Greenland.

Gracilitheca sp.

Fig. 9A.

Material.—MGUH 27108 and 27 additional specimens from GGU sample 314807, 314835, and 314908.

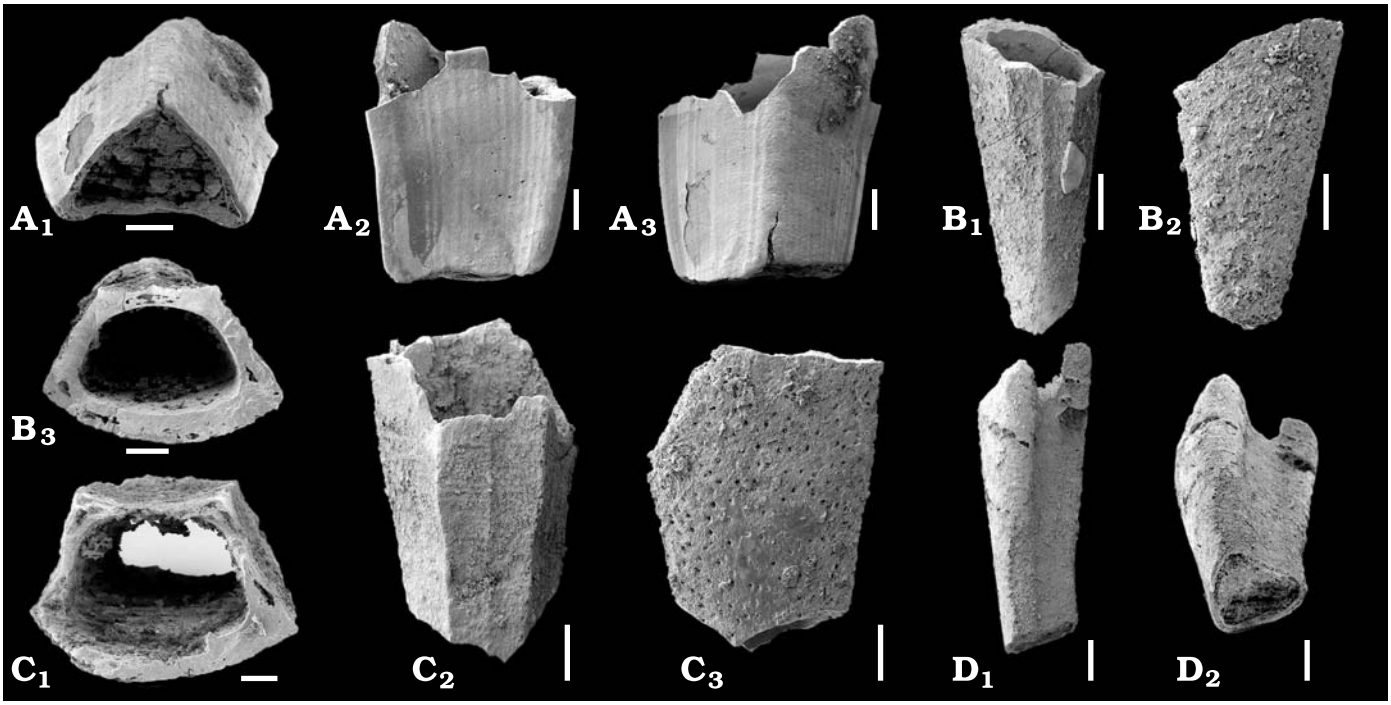


Fig. 9. **A**. *Gracilitheca* sp. MGUH 27108. From GGU sample 314908; A_1, cross-section viewed from apical region with dorsum above; A_2, venter; A_3, dorsum. **B**, **C**. Orthothecid? sp. B. MGUH 27109; B_1, oblique view of dorsum; B_2, venter; B_3, cross-section. **C**. MGUH 27110; C_1, cross-section; C_2, oblique view of dorsum; C_3, venter. **D**. *Contitheca*? sp. MGUH 27111; D_1, oblique view with venter to right. D_2, cross-section viewed from apical region with dorsum on top. All except A from GGU sample 314809. Scale bars 0.2 mm.

Description.—Conch with bluntly rounded central dorsal ridge that grades into adjacent flanks that are slightly inflated; the flanks grade into blunt lateral edges that protrude slightly to form a longitudinal ridge along each edge; the venter has a shallow median furrow bounded on each side by a low rounded longitudinal ridge. Cross-section has a generally triangular shape. Surface of shell on dorsum with faint longitudinal lines best seen near lateral edges, becoming fainter near middle of dorsum.

Remarks.—This taxon is known from 29 specimens, all of which only preserve a portion of the mid-region of the conch. Nonetheless, the cross-section and lateral protuberances are sufficiently distinct to indicate placement within *Gracilitheca* Syssoiev, 1968, although identification to species is not possible. The Greenland specimens have lateral protuberances that are most similar to those of *Gracilitheca gratuita* Val'kov, 1987 from Siberia. In contrast, *G. excavata* (Val'kov, 1975) has a much deeper ventral longitudinal furrow but otherwise the shape of the protuberances and dorsum is similar to that of the Greenland forms. *Gracilitheca bayonet* (Matthew, 1899) also resembles the Greenland species in terms of shape of the protuberances, but it lacks any longitudinal ornament. *Gracilitheca ternata* Syssoiev, 1968, *G. argasalaica* Val'kov, 1987, and *G. destombesi* Marek, Malinky, and Geyer, 1997 may be distinguished from *Gracilitheca* sp. from Greenland by the shape of the protuberances.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Orthothecid? gen et. sp.

Fig. 9B, C.

Material.—MGUH 27109–27110 from GGU sample 314809.

Description.—Seemingly cyrtoconic conch with slightly inflated venter, grading into sharp, keel-like lateral edges, which in turn pass into flat, steeply dipping dorsal flanks. Dorsum is flat, with sharp intersection with lateral edges, and with one distinct longitudinal ridge in middle. Faint transverse lines on dorsum, remainder of shell seemingly smooth. Cross-section has quadrate shape.

Remarks.—This species is known from two fragmentary specimens, neither of which has the apex or aperture intact. Referral to order is especially difficult because these individuals possess a generally quadrate cross-section, seen thus far only among Orthothecida. They also display, however, an inflated venter which ordinarily is more characteristic of Hyolithida. Known orthothecids that have a cross-section somewhat resembling that of the Greenland specimens are *Obliquatheca acostae* Syssoiev, 1968 (pl. 2: 9b) and *Trapezotheca aemula* (Holm, 1893; see Malinky 2002: text-fig. 3N) but in both of these taxa the venter has a shallow longitudinal furrow, creating a slightly kidney-shaped cross-section, whereas the venter of the Greenland specimens is inflated. *Sokolovitheca sokolovi* Syssoiev, 1972 has a variable cross-section although one individual (Syssoiev 1972: pl. 2: 1e) resembles the Greenland species. However, the dorsal morphology of *S. sokolovi* does not match that of the Greenland individuals. No traces of growth lines or any other surface ornamentation remain, and the nature of the aperture, in particular whether a ligula was present, is obscure.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Genus *Contitheca* Syssoiev, 1972

Type species: *Hyolithus* (*Orthotheca*) *cor* Holm, 1893, Middle Cambrian, Sweden.

Diagnosis.—Orthothecid having prominent longitudinal ventral furrow and prominent well-developed keel-like median ridge on dorsum, creating a distinctive heart-shaped cross-section.

Stratigraphic range and distribution.—Middle Cambrian; Sweden (Holm 1893; Berg-Madsen and Malinky 1999), Morocco (Marek et al. 1997), Antarctica (Shergold et al. 1976), Korea (Saito 1936), and possibly North-East Greenland.

Contitheca? sp.

Fig. 9D.

Material.—MGUH 27111 and 15 additional specimens from GGU samples 314809, 314906, 314908, 314909, and 314933.

Description.—Seemingly slightly cyrtoconic conch with curvature toward venter; apical angle small, giving conch tubular appearance, venter has pronounced, deep longitudinal furrow which is bounded on both sides by well-developed high-standing longitudinal ridges having sides steeply dipping toward furrow; dorsum with high median ridge and steeply dipping flanks adjacent to it, to creating a decidedly heart-shaped cross-section. Surface of conch seems smooth.

Remarks.—This taxon is only known from incomplete specimens, yet its most distinctive features, the deep longitudinal furrow on the venter and resulting heart-shaped cross-section, are easily discernible (Fig. $9D_2$). It clearly resembles *Contitheca* Syssoiev, 1972 from the Middle Cambrian of Sweden, Morocco, Korea and Antarctica, and is referred to it with question, owing to incomplete preservation. The high dorsum with slightly inflated flanks and pronounced heart-shaped cross-section suggest that the Greenland material may represent a new species, but given the fragmentary nature of all specimens, assignment to species is not advisable at this time. If better preserved material bears out the contention that *Contitheca* is present in the Lower Cambrian of North-East Greenland, this genus now ranges into the Lower Cambrian, and its geographic distribution includes North-East Greenland. It is worth noting that the two surviving specimens of *Lenatheca groenlandicus* (Poulsen, 1932) from among the Siberian material of Missarzhevsky (1969) resemble *Contitheca*? sp. in the depth of the ventral furrow, but because the dorsum is unknown, they cannot be compared further with *Contitheca*? sp.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Orthotheca bayonet* var. *groenlandica* (Poulsen, 1932)"

Fig. 10A–C.

Hyolithus (*Orthotheca*) *bayonet* var. *groenlandicus* Poulsen, 1932: 20, pl. 3: 1–3.

Material.—MGUH 3526 (Fig. 10C_3 = Poulsen 1932: pl. 3: 3); MGUH 3521 (Fig. 10A_3 = Poulsen 1932: pl. 3: 2); MGUH 3523 (Fig. 10B = Poulsen 1932: pl. 3: 1).

Description.—Apical region of conch cyrtoconic, venter appears flat but has very shallow longitudinal furrow; lateral edges bluntly rounded grading into relatively high dorsum with inflated flanks that terminate in pronounced median ridge; crest of ridge nearly angular, and cross-section nearly triangular with slight depression on ventral side. Aperture apparently planar without indentations on either dorsal or ventral rim. Surface of shell has distinct transverse ribs of slightly unequal spacing and intensity on both dorsum and venter.

Remarks.—The planar aperture and shallow longitudinal furrow on the venter indicate that this species belongs within the Order Orthothecida. It is therefore designated "*Orthotheca*", not because it represents the genus *Orthotheca* Novák, 1886 from the Lower Devonian of the Barrandian, but because of its affinity to the order Orthothecida. Poulsen (1932) assigned it to *H.* (*O.*) *bayonet* Matthew, 1899 but placed it into the subspecies *groenlandicus* because the dorsal flanks are slightly inflated. Matthew's (1899) species is distinctive because the lateral edges are developed into elongate protuberances which extend away from the shell.

Fig. 10A and C appear to represent the same species based especially on the dorsal morphology in which growth lines, indicating the presence of a short projection on that side, are present. The venter of Fig. 10C is not well enough preserved to meaningfully compare it to Fig. 10A. Fig. 10B in contrast appears to belong to a different taxon based on the narrower conch, and deep, narrower longitudinal ventral furrow.

Missarzhevsky (1969) designated Poulsen's species as type species of *Lenatheca*. Given the poor preservation of

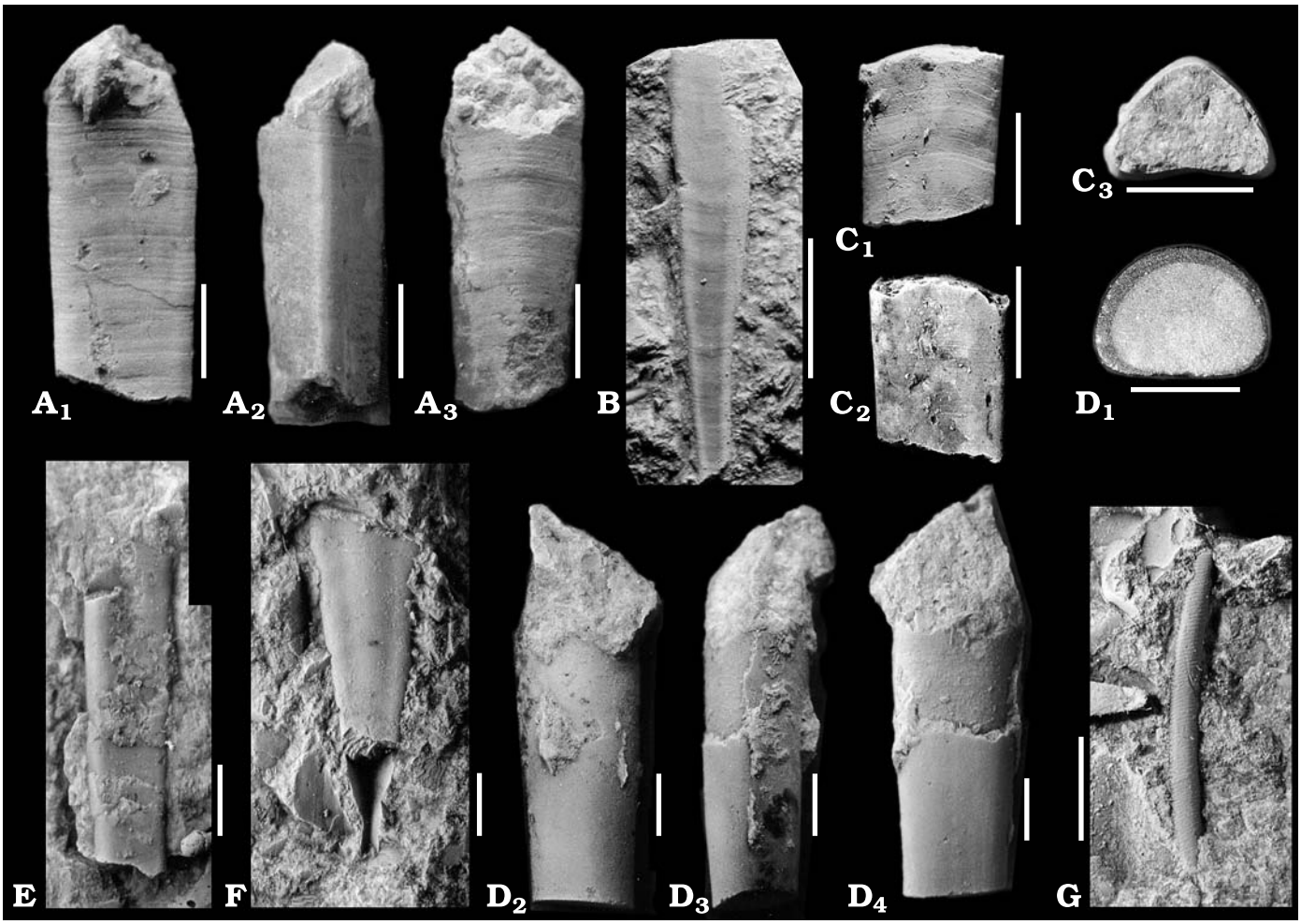


Fig. 10. **A–C**. "*Orthotheca bayonet* var. *groenlandica* (Poulsen, 1932)". **A**. MGUH 3521; A_1, venter; A_2, right lateral edge; A_3, dorsum. **B**. MGUH 3523, venter. **C**. MGUH 3525; C_1, dorsum; C_2, venter; C_3, cross-section. **D**. "*Orthotheca communis* (Billings, 1872)", MGUH 3524; D_1, cross-section; D_2, dorsum; D_3, right lateral edge with venter to right; D_4, venter. **E**. "*Orthotheca bayonet* var. *longa* (Poulsen, 1932)", MGUH 3526, venter. **F**. "*Orthotheca billingsi* (Walcott, 1886)", MGUH 3528, venter. **G**. *Coleolus* sp.? MGUH 3517. All specimens from the collections of C. Poulsen. Scale bars 2 mm.

Poulsen's (1932) material, the genus cannot be considered well-founded, and specimens from Siberia included under it by Missarzhevsky (1969) add little to the concept of the taxon. The surviving specimens of *Lenatheca* (GIN 3593/197 = Missarzhevsky 1969: pl. 10: 17 and GIN 3593/42 = Missarzhevsky 1969: pl. 13: 12, 13) are themselves poorly known. The former is an exposed venter, and the latter exposes the venter and the right lateral edge, but that specimen appears to have been weathered, and no details remain except for the overall shape of the conch. Poulsen's (1932) material is markedly different from the Siberian *Lenatheca* in having a larger apical angle. Furthermore, Poulsen's specimens which are largely incomplete seem to represent two different taxa, neither of which appears to be the same as any Siberian specimen. Thus further use of the name *Lenatheca* for orthothecid hyoliths is to be discouraged.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Orthotheca bayonet* var. *longa* (Poulsen, 1932)"

Fig. 10E.

Hyolithus (*Orthotheca*) *bayonet* var. *longus* Poulsen, 1932: 20, pl. 3: 4.

Material.—MGUH 3526.

Description.—Conch seemingly orthoconic with small apical angle, giving conch narrow, gently tapering appearance; venter with shallow median longitudinal furrow bounded on each side by very low longitudinal ridges; surface of shell seemingly smooth without any transverse or longitudinal elements of sculpture.

Remarks.—Comments above under the previous species apply here as well regarding the assignment to *H.* (*O.*) *bayonet* Matthew, 1899. Poulsen (1932) accorded subspecies status to this specimen because of its smaller apical angle. It also is referred to "*Orthotheca*" for the same reasons as the previous species. Because so little of this specimen is known, confident assignment to any species is impossible. Poulsen (1932: 20) said that he had five specimens of this taxon, but thus far only the illustrated specimen has been located.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Orthotheca billingsi* (Walcott, 1886)"

Fig. 10F.

Hyolithus (*Hyolithus*) *billingsi* Walcott; Poulsen 1932: 22, pl. 3: 6.

Material.—MGUH 3528.

Description.—Orthoconic conch with small apical angle; venter with two shallow longitudinal depressions near each edge with region between depressions slightly convex and inflated; shell smooth; all else unknown.

Remarks.—This species is known from one individual that has the dorsum embedded in matrix. The absence of any apparent growth lines or other elements of sculpture on the shell suggest affinity to the Orthothecida, although the middle of the venter is inflated slightly, owing to the presence of two longitudinal furrows on each side. The morphology of the conch may be accommodated under either Hyolithida or Orthothecida, and confident assignment at this time is impossible due to limited knowledge of this taxon.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

"*Orthotheca communis* (Billings, 1872)"

Fig. 10D.

Hyolithus (*Orthotheca*?) *communis* Billings; Poulsen 1932: 20, pl. 2: 10–11.

Material.—MGUH 3524 (Poulsen 1932: fig. 10 = Fig. 10D$_3$, fig. 11 = Fig. 10D$_1$).

Description.—Orthoconic conch with venter nearly flat having only shallow longitudinal depression; lateral edges tightly rounded grading into inflated dorsal flanks which meet in broad median ridge; surface of shell and internal mould smooth.

Remarks.—One specimen represents this taxon and it appears to have smooth shell entirely lacking growth lines or any other ornament. The generally featureless quality of this specimen suggests that it is preserved as an internal mold, but without doubt this individual possesses shell on the dorsum and part of the venter, because the shell has been broken away partly on the venter to expose a smooth internal mold. The apical end has been cut and polished to reveal the cross-section (Fig. 10D$_1$). *Hyolithes communis* Billings, 1872 has a tubular conch, but its affinity to the Hyolitha is beyond question, owing to the ventral ligula and interior of the operculum with clavicles and cardinal processes in place. Furthermore, the shell is covered with transverse rugae, which are lacking in the Greenland species. It is unlikely that the Greenland species and *H. communis* Billings, 1872 from New York belong to the same taxon.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Phylum, class, and order uncertain

Family Cupithecidae Duan, 1984

Genus *Cupitheca* Duan in Xing et al., 1984

Type species: *Paragloborilus mirus* He in Qian, 1977, Lower Cambrian, South China.

Diagnosis.—Conch straight or curved, with circular to oval cross-section, low angle of divergence. Older parts of conch successively aborted during ontogeny in connection with formation of secondary transverse wall sealing off apical end. Operculum, if present, a simple disc (from Bengtson 1990b).

Remarks.—Demidenko (2001: 97) pointed out that the generic name *Actinotheca* Xiao and Zhou, 1984 used earlier (Bengtson 1990b) for decollating, hyolith-like tubular fossils from the Lower Cambrian is occupied by a genus of tabulate

corals (*Actinotheca* Frech, 1884), and should be replaced by the next valid junior synonym, *Cupitheca* Duan in Xing et al., 1984 (*Cupittheca* of Demidenko 2001: 96). The generic name was spelled "*Cupittheca*" by Duan (in Xing et al. 1984: 152) but this appears to be a printing error (see Wrona 2003: 200). Specimens from North-East Greenland are assigned to this genus based on the tubular conch with an apical termination created by a septum and the transverse sculpture on the shell. Bengtson (1990b) pointed out that species of this genus may be difficult to distinguish from one another, including the type species, because the type and several other species are founded upon internal moulds in which surface sculpture is lacking. Surface ornamentation, however, is considered to be a distinguishing feature of some species, including *C. hemicyclata* and *C. holocyclata* herein.

The biology of this organism, particularly as related to the development of septae and decollation of the conch was discussed by Bengtson (1990b). Owing to the separation of the apical region from the remainder of the conch as the animal grew, fragments of this taxon are common but complete specimens are rare. Affinity between North-East Greenland and Australian Lower Cambrian assemblages of shelly fossils is strongly supported by the occurrence of *Cupitheca* in both regions, although a third Australian species of this genus, *C. clathrata* (Bengtson, 1990b) has yet to be identified from Greenland. *Cupitheca* is very widespread in the Early Cambrian, and ranges into the lower Middle Cambrian of Morocco and possibly England as well (*Cephalopyge notabilis* Zone of Morocco and "*Protolenus* limestone" of Comley, Shropshire; Gerd Geyer, personal communication 2004).

Stratigraphic range and distribution.—Lower Cambrian, South China, Australia, Antarctica, and North-East Greenland, possibly Kazakhstan. Lower Middle Cambrian of southern Morocco and possibly England.

Cupitheca hemicyclata (Bengtson, 1990b)

Fig. 11.

Actinotheca hemicyclata Bengtson, 1990b: 210, fig. 140.

Holotype: South Australian Museum, Adelaide SAMP30864.

Material.—MGUH 27112–27113 from GGU sample 314835.

Description.—Slightly cyrtoconic tubular conch with circular cross-section with the apex terminating in a poorly developed convex inflated septum. Side of conch toward which apex bends possesses coarse annular half rings; rings have steeply dipping sides and stand high; spaces between half rings have concave surfaces, and width of spaces equal is to about 2–3 times the width of one ring. Opposite side of conch smooth due to disappearance of co-marginal ornament about midway between opposing sides of the conch.

Remarks.—This species is represented by two fragmentary individuals in the Greenland collections, although the distinctive half rings confirm the specific identity. It is referred to *Cupitheca hemicyclata* based on the annular rings are seen on only one side of the conch. In *C. holocyclata* the rings encircle the conch.

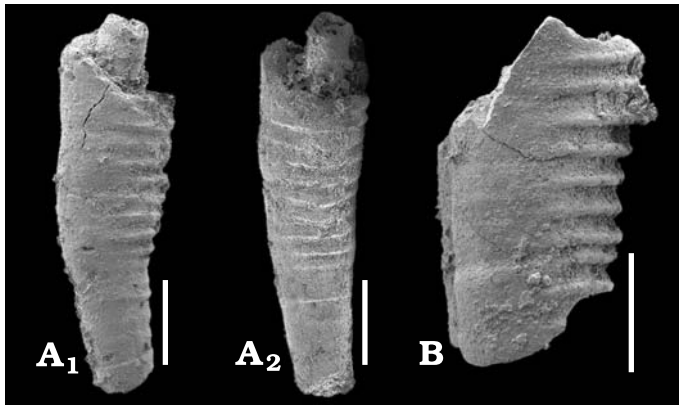


Fig. 11. *Cupitheca hemicyclata* (Bengtson, 1990b). **A**. MGUH 27112. **B**. MGUH 27113. Both specimens from GGU sample 314835. Scale bars 0.2 mm.

Stratigraphic range and distribution.—Lower Cambrian, Australia and North-East Greenland.

Cupitheca holocyclata (Bengtson, 1990b)

Fig. 12.

Actinotheca holocyclata Bengtson, 1990b: 204, figs. 134–136.

Cupittheca holocyclata (Bengtson, 1990b); Demidenko 2001: 97, pl. 9: 1a, b.

Cupitheca holocyclata (Bengtson, 1990b); Wrona 2003: 200, fig. 11A–F, G_3.

Holotype: South Australian Museum, Adelaide SAMP30845.

Material.—MGUH 27114–27118 and 59 additional specimens from GGU samples 314807, 314835, 314904, 314906, 314908, 314918, 314919, 314931 and 314933.

Description.—Straight to slightly tapering tubular conch with circular cross-section; apical region with shallow though well-developed constriction that separates the septum-like wall from remainder of conch. Septum convex toward apex. Constriction may be either perpendicular to, or at an oblique angle to the longitudinal axis of the conch. Wall of conch seems to consist of distinct tubular or rod-like structure. Shell with very faint, widely spaced, shallow depressions with spaces in between equal to width of 2–5 depressions; areas between depressions are flat or slightly concave.

Remarks.—This taxon ordinarily is represented by short segments whose length may be only several times the width. Most specimens of *Cupitheca holocyclata* illustrated by Bengtson (1990b: fig. 134I, P) possess coarse annular rings, but in some the rings are much finer, resembling those on the specimens recorded herein. Thus these specimens are assigned to *C. holocyclata* because of the generally fine transverse sculptural elements that completely encircle the shell. *Cupitheca hemicyclata* has much coarser elements though only one on side of the shell, and *C. clathrata* (Bengtson, 1990b) has a distinctive cancellate ornamentation not seen in any material from Greenland.

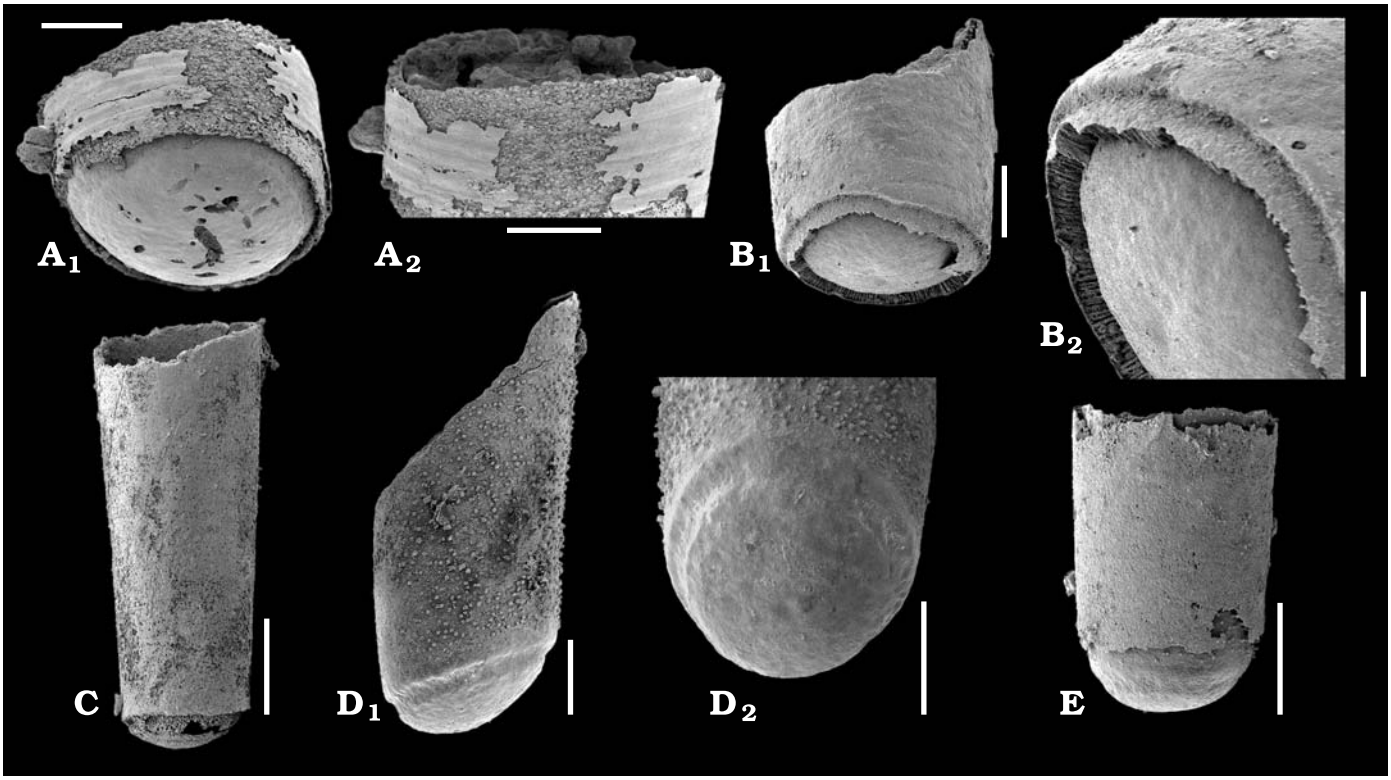


Fig. 12. *Cupitheca holocyclata* (Bengtson, 1990b). **A**. MGUH 27114; A_1, apical view showing septum; A_2, lateral view showing shell with ornamentation. **B**. MGUH 27115; B_1, B_2, oblique views of apical septum with structure of shell wall visible in B_2. **C**. MGUH 27116. From GGU sample 314809. Lateral view showing apical septum. **D**. MGUH 27117; D_1, lateral view showing apical septum; note oblique angle of constriction; D_2, enlarged view of apical septum and constriction. **E**. MGUH 27118, lateral view showing apical septum. All specimens except C from GGU sample 314807. Scale bars 0.2 mm except B_2 which is 0.1 mm.

Stratigraphic range and distribution.—Lower Cambrian, Australia, Antarctica, and North-East Greenland.

Family Coleolidae Fisher, 1962

Genus *Coleolus* Hall, 1879

Type species: *Coleolus tenuicinctum* Hall, 1879, Lower Devonian, New York.

Diagnosis.—Conch elongate and tubular with small apical angle; surface covered with rings that are oblique to the longitudinal axis of the shell; cross-section circular or nearly so.

Remarks.—This genus was founded upon tubular calcareous fossils of the kind so characteristic of the Lower Cambrian of the Siberian Platform and South China. It was illustrated under the name *Coleoprion tenuicinctum* by Hall (1876) but not described, thus that taxon is a *nomen nudum.* Later, Hall (1879) described it as *Coleolus tenuicinctum*. This genus is distinguished from similar calcareous tubes by its transverse lines that are oblique to the longitudinal axis of the tube. In contrast, *Coleoloides* Walcott, 1890 has longitudinal ornament on the conch, and *Coleoprion* Sandberger, 1847 possesses transverse elements of sculpture but they converge in a longitudinal groove on the shell. Specimens from North-East Greenland possess lines that best fit the description of *Coleolus*, and are assigned to that genus. The affinity of *Coleolus* is unknown, although Fisher (1962) suggested that it may be molluscan. The specimens from Greenland shed no light on the affinity of this taxon, and indeed cannot even be identified to species with certainty due to their fragmentary nature.

Stratigraphic range and distribution.—Lower Cambrian–Devonian; USA (New York), Siberia, and North-East Greenland.

Coleolus sp.

Figs. ?10G, 13.

Hyolithus (*Orthotheca*) *fistula* (Holl, 1865); Poulsen 1932: 21, pl. 3: 5.

Material.—MGUH 3527 (Fig. 13C = Poulsen 1932: pl. 3: 5), MGUH 27119–27120 and 142 additional specimens from GGU samples 314807, 314809, 314835, 314906, 314918, 314919, and 314933.

Description.—Tubular conch with very slight helical coil; apical angle small such that the sides of tube appear to be parallel in more mature regions of conch; surface of shell covered with transverse elements of sculpture that appear to consist of widely spaced ribs with interspaces that range from shallow to deep; ribs have inclination of approximately 110° from long axis; cross-section circular. Both apical and apertural terminations unknown.

Remarks.—*Coleolus* sp. is represented in the collections from North-East Greenland by 145 very fragmentary speci-

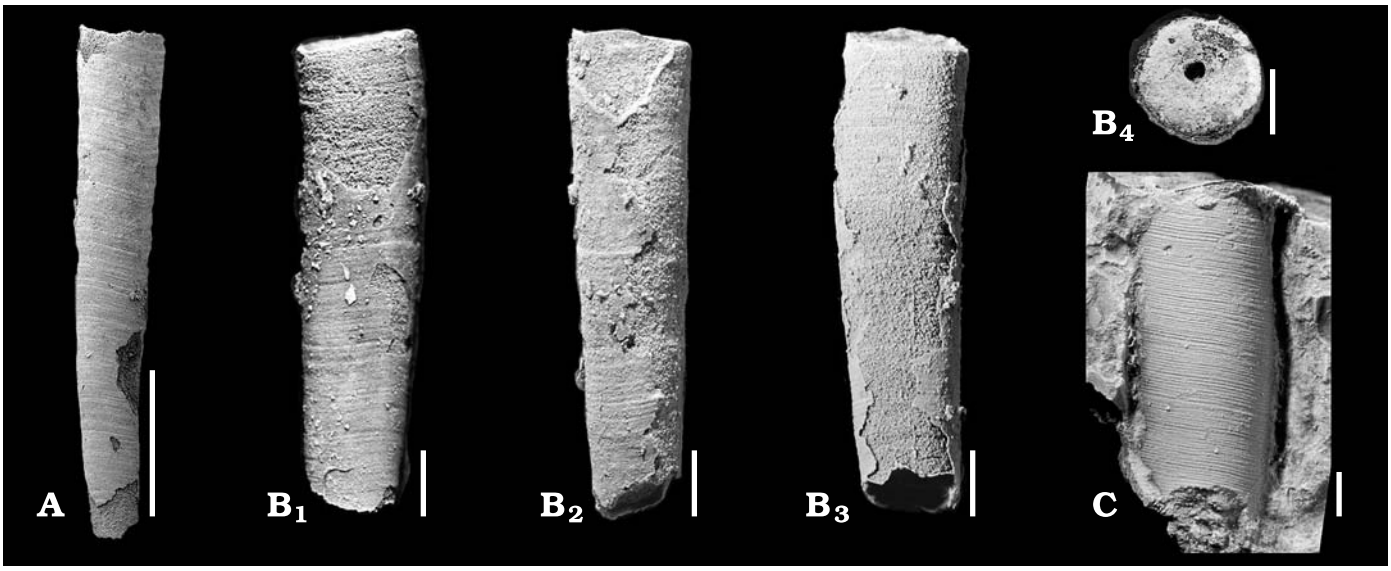


Fig. 13. *Coleolus* sp. **A**. MGUH 27119, from GGU sample 314933, lateral view. **B**. MGUH 27120, from GGU sample 314835; B_1–B_3, lateral views; B_4, cross-section. **C**. MGUH 3527 from the collections of C. Poulsen, lateral view. Scale bars 1 mm.

mens, widely differing in prominence of the obliquely inclined ribs on the shell. Shell on the acid-isolated but generally less well-preserved individuals (Fig. 13A, B) is exfoliated in some places, whereas preservation of shell is much better on the smaller though more fragmentary specimen from Poulsen's collections (Fig. 13C). Whether such variation between ornament falls within the range of normal variation of one species or warrants separate species status is unknown until more complete specimens become available for study. These specimens are referred to *Coleolus*, but referral to species is more difficult given that so few morphologic features are present on tubular fossils such as these. The oblique ribs somewhat resemble those of *C. tenuicinctum* Hall, 1879 from the Devonian of New York, but Hall's (1879) specimen is more complete than any Greenland specimen.

Coleolus trigonus Syssoiev, 1962 from Siberia, the only other species of *Coleolus* reported from the Lower Cambrian, has much coarser ribs on its shell. Poulsen (1932) referred a specimen of *Coleolus* to *Hyolithus* (*Orthotheca*) *fistula* (Holl, 1865) which was founded on phosphatic rather than calcareous tubes (Malinky, unpublished). In addition, a specimen referred to *Helenia bella* Walcott, 1890 by Poulsen (1932) may represent *Coleolus* as well (Fig. 10G). *Helenia* was the generic name used for the hyolithid skeletal pieces that subsequently were designated helens. The morphology of helens has been recently discussed by Marek et al. (1997), and the Greenland specimen bears only limited resemblance to any authentic helens. However, its tubular morphology and obliquely dipping ribs are not unlike *Coleolus*. If it indeed represents *Coleolus*, a separate species is probably required.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland.

Genus *Conotheca* Missarzhevsky, 1969

Type species: *Conotheca mammilata* Missarzhevsky, 1969, Tommotian Stage, Lower Cambrian, Siberian Platform.

Diagnosis.—Shell conical with circular cross-section and transverse elements of sculpture on the exterior; aperture planar and operculum with cardinal processes and circular ridges on interior.

Remarks.—This genus was erected for calcareous tubular fossils by Missarzhevsky (1969) from the Lower Cambrian of Siberia. He classified it as an orthothecid hyolith within the family Circothecidae Missarzhevsky, 1969, an assignment retained by Bengtson (1990b). However, Qian and Bengtson (1989) described *Conotheca subcurvata* (Yu, 1974) under the heading "other tubular shells", and pointed out that morphologic gradations between *Conotheca* and several other calcareous tubular forms could suggest that *Conotheca* might even be an anabaritid. If *Conotheca* indeed is a hyolith, it would be yet another example that seems to combine characteristics of both Hyolithida and Orthothecida. The tubular conch without distinct dorso-ventral differentiation and lack of a ligula, and operculum lacking the rooflets and furrows support affinity to Orthothecida. However, the rounded clavicle-like structures seen on the inner surface of the operculum of *C. australiensis* Bengtson, 1990b are a feature more closely associated with Hyolithida. Despite generally good overall preservation of *Conotheca* from North-East Greenland, the specimens shed no new light on the question of affinity, and we considered it a taxon of unknown affinity for the present. Specimens referred to *Conotheca* from Antarctica were recently described by Wrona (2003).

Stratigraphic range and distribution.—Lower Cambrian in Siberia, Kazakhstan, India, South China, Australia, Antarctica, USA (New York), and North-East Greenland.

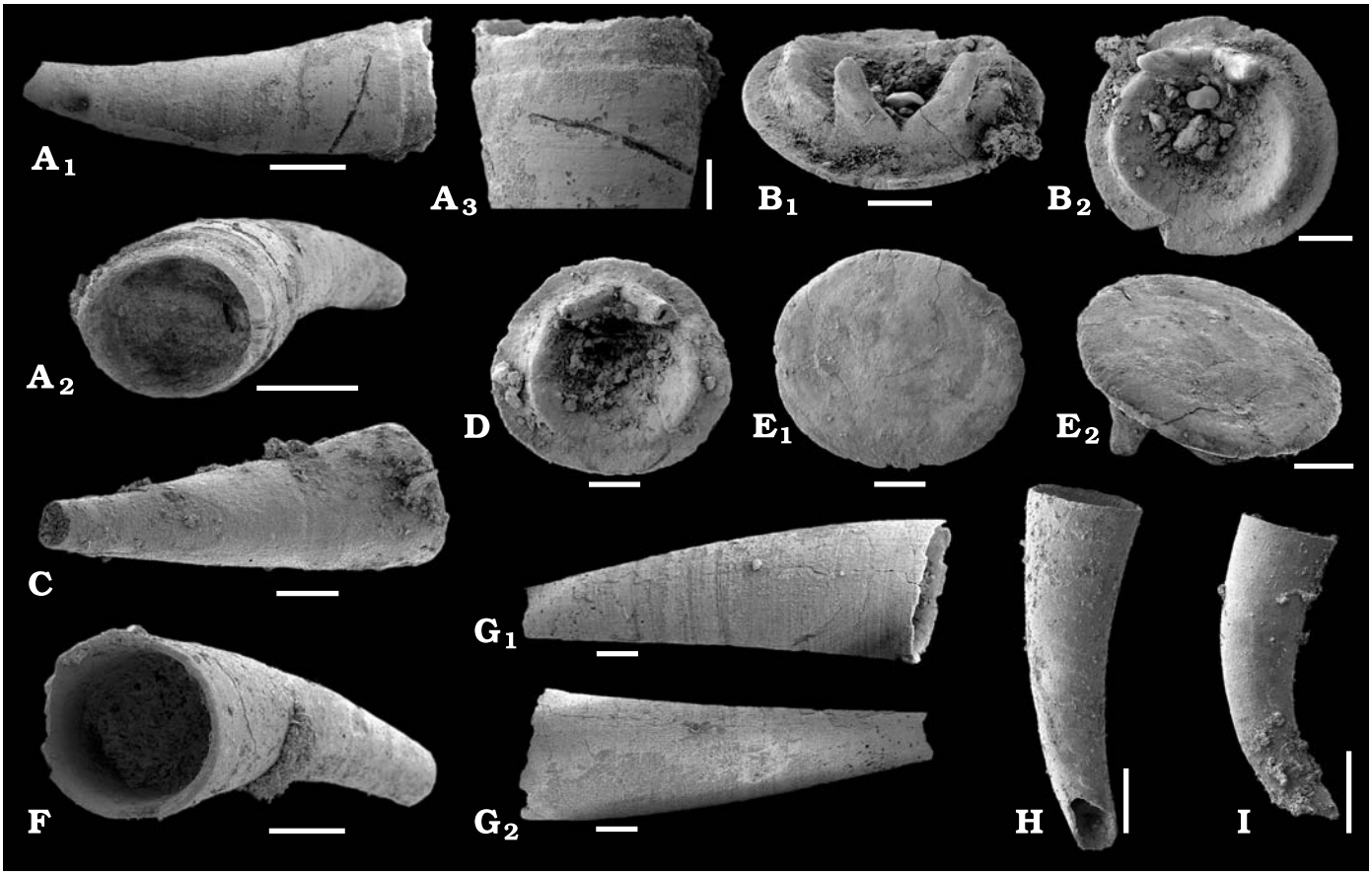


Fig. 14. *Conotheca australiensis* Bengtson, 1990b. **A**. MGUH 27121, from GGU sample 314933; A_1, conch in lateral view; A_2, cross-section of conch; A_3, enlarged view of ornamentation. **B**. MGUH 27122, from GGU sample 314835; B_1, B_2, interior views of operculum. **C**. MGUH 27123, from GGU sample 314933, lateral view. **D**. MGUH 27124, from GGU sample 314835, interior view of operculum. **E**. MGUH 27125, from GGU sample 314835; E_1, E_2, exterior views of operculum. **F**. MGUH 27126, from GGU sample 314906, cross-section. **G**. MGUH 27127, from GGU sample 314804; G_1, G_2, lateral views. **H**. MGUH 27128, from GGU sample 314906, lateral view. **I**. MGUH 27129, from GGU sample 314809, lateral view. All scale bars 0.2 mm, except A_1 and A_2 which are 0.5 mm.

Conotheca australiensis Bengtson, 1990b

Fig. 14.

Conotheca australiensis Bengtson, 1990b: 216, figs. 143, 144.

Conotheca laurentiensis Landing and Bartowski, 1996: 756, figs. 7.1–7.8, 7.20.

Conotheca australiensis Bengtson, 1990b; Demidenko 2001: 98, pl. 10: 1, 2.

?*Conotheca cf. australiensis Bengtson, 1990b*; Wrona 2003: 191, fig. 5A–E.

Holotype: South Australian Museum, Adelaide SAMP30877.

Material.—MGUH 27121–27129, 69 additional conchs and 314 opercula from GGU samples 314802, 314804, 314806, 314807, 314809, 314835, 314836, 314901, 314904, 314906, 314908, 314909, 314910, 314918 and 314933.

Description.—Gently tapering conch with small apical angle of about 15°; conch may have slight helical coil; aperture is planar and lying in a plane perpendicular to long axis of conch. Shell covered with closely though irregularly spaced transverse lines of varying intensity in different places on conch; apical termination unknown.

Operculum circular in outline; exterior with rounded summit that may be lower than surrounding surface; exterior may have coarse concentric lines; interior with two cardinal processes that diverge at angle of about 50°; cardinal processes broad at base but taper to eventually terminate in blunt rounded surface; emanating from the cardinal processes is a circular ridge set inward from edge of operculum. Interior otherwise smooth.

Remarks.—Specimens of *Conotheca* from North-East Greenland are assigned to *C. australiensis* based chiefly on features of the operculum. The interior matches quite well with specimens from Australia in terms of cardinal processes and the ridge that develops in places into tubular clavicles. Without the operculum, assignment to species is far more difficult because diagnostic morphologic features of a tubular conch are relatively few; they are limited mostly to the nature of ornament, apical angle and cross-section. The extensive synonymy under *C. subcurvata* (Yu, 1974) given by Qian and Bengtson (1989) well illustrates the problems surrounding recognition of different species among tubular fos-

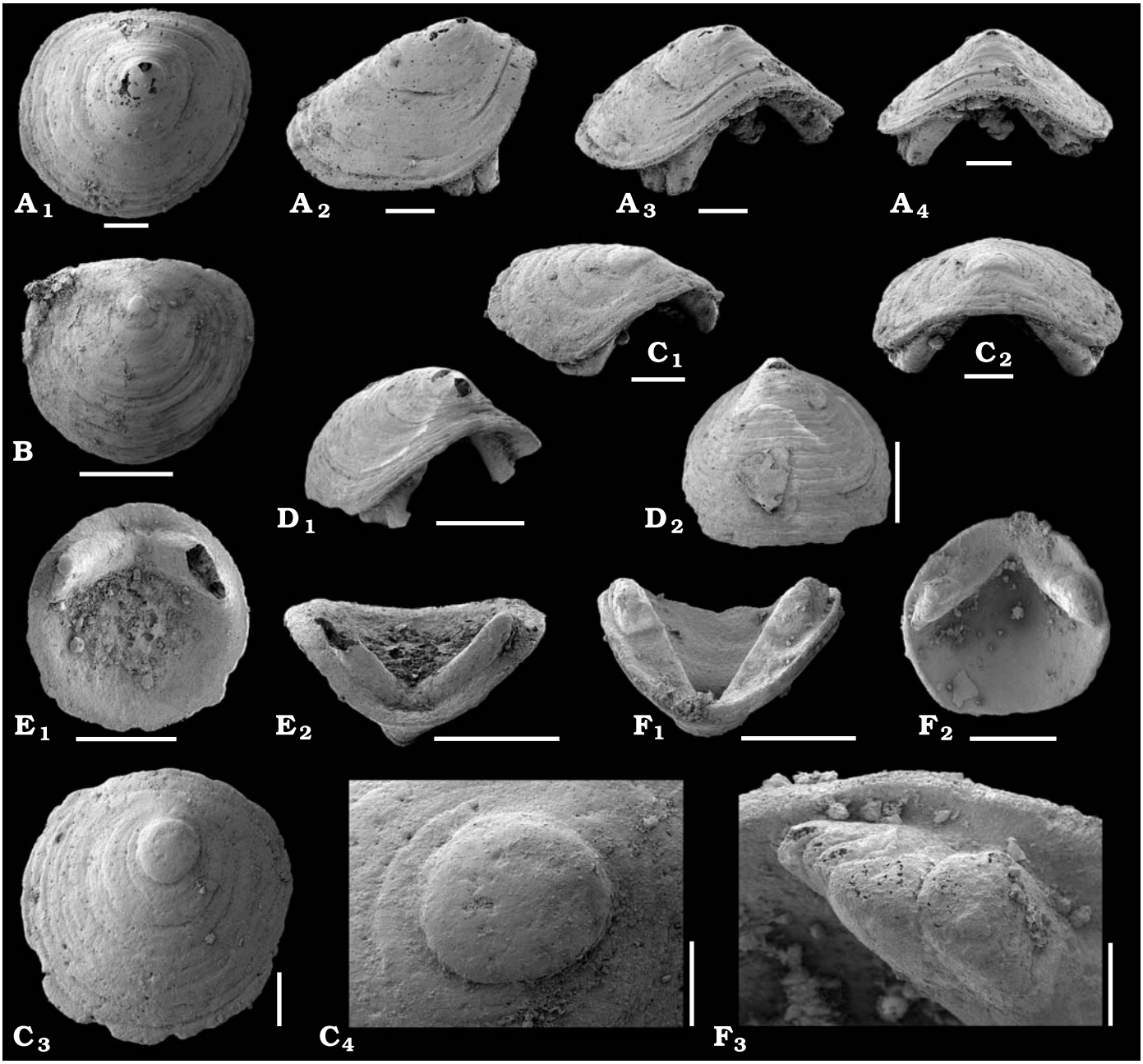


Fig. 15. *Cassitella baculata* sp. nov. **A**. MGUH 27130, holotype; scale bars 0.2 mm; A_1, view from above; A_2, lateral view; A_3, oblique lateral view showing ridges; A_4, view showing fold and ridges. **B**. MGUH 27131, exterior view from above; scale bar 0.5 mm. **C**. MGUH 27132; scale bars 0.2 mm except C_4 which is 0.1 mm; C_1, oblique lateral view showing ridges; C_2, view showing fold and ridges; C_3, view from above; C_4, enlarged view of "protoconch". **D**. MGUH 27133, from GGU sample 314807; scale bars 1 mm; D_1, oblique lateral view; D_2, oblique view of exterior. **E**. MGUH 27134; scale bars 0.5 mm; E_1, lateral view of interior showing diverging ridges; E_2, view from above of interior showing diverging ridges. **F**. MGUH 27135, from GGU sample 314807; scale bars 1 mm except F_3 which is 0.2 mm; F_1, lateral view of interior showing diverging ridges; F_2, view from above of interior showing diverging ridges; F_3, enlarged view of termination of ridge. All specimens, except D and F, from GGU sample 314835.

sils of generally limited morphologic variability. The conchs and opercula are referred to the same species as they co-occur at the same level and localities, and match each other in cross-section. Had only the conchs of the Greenland specimens been discovered, those individuals may just as easily have been accommodated under *C. mammilata* Missarzhevsky, 1969. *Conotheca circumflexa* Missarzhevsky, 1969 and *C. subcurvata* (Yu, 1974) both possess pronounced apical curvature, but several Greenland specimens under *C. australiensis* curve apically as well (Fig. 14F–I).

Landing and Bartowski (1996) described *Conotheca laurentiensis* from the Browns Pond Formation from the Taconic Allochthon of New York State, and distinguished the species from *C. australiensis* by the longer cardinal processes of the operculum. As this feature appear to be variable in the Greenland material, *C. laurentiensis* is here regarded as a ju-

nior synonym of *C. australiensis*. Internal moulds from King George Island, Antarctica of more questionable affinity to *C. australiensis* has recently been described by Wrona (2003).

Stratigraphic range and distribution.—Lower Cambrian; Australia, USA (New York), North-East Greenland and possibly Antarctica.

Genus *Cassitella* nov.

Type species: *Cassitella baculata* sp. nov. Monotypic.

Etymology: From Latin *cassis*, helmet and Latin *Tellus*, god of the Earth, for the resemblance of the shell in lateral view to a helmet.

Diagnosis.—Subtriangular to almost circular convex shells with rounded apex displaced towards the higher (proximal) side. Exterior with fine concentric ribs and depressions. Interior with two prominent, widely diverging ridges emanating from proximal edge of shell. Distal termination of ridges free from the shell margin and divided into distinct lobes.

Remarks.—Although at this time poorly understood, the unusual morphology of *Cassitella* makes this genus distinguishable from all other cap-shaped problematica described from the Early Cambrian. *Cassitella* resembles a hyolithid operculum and the ridge-like structures on the interior are suggestive of the clavicles ordinarily seen among hyolithids (but see *Hyptiotheca*), although there are no cardinal processes associated with them. The lobate distal ends of the "clavicles" are also unusual and have not been documented in any unequivocal hyolithid. Some individuals of *Cassitella baculata* display a saddle-shaped profile with the shell curving upward between apex and proximal edge. The hyolithid *Patholites* Marek et al., 1997 (for which the operculum is unknown) from the Middle Cambrian of Morocco possesses an unusual aperture which could have been closed by a saddle-shaped operculum.

There is some resemblance in terms of external morphology between *Cassitella* and the problematical *Ocruranus* Liu, 1979 and *Eohalobia* Jiang in Luo et al., 1982 from the Meishucunian of South China. Shells referable to *Ocruranus* occur together with *Cassitella* in the Bastion Formation (Skovsted, unpublished). However, like the Chinese fossils, these shells lack clavicle-like structures on the interior. *Ocruranus* and *Eohalobia* appear to be most closely comparable to helcionelloid molluscs, although as Qian and Bengtson (1989) pointed out, they have previously been interpreted variously as brachiopods, bivalves, polyplacophorans or tommotids. At this time, the most likely affinity of *Cassitella* appear to be to hyoliths, although the presumed conch remain to be discovered.

Cassitella baculata sp. nov.

Fig. 15.

Holotype: Phosphatised shell MGUH 27130 (Fig. 15A) from GGU sample 314835, Albert Heim Bjerge, North-East Greenland.

Type horizon: Bastion Formation, Lower Cambrian.

Type locality: North-East Greenland.

Etymology: From Latin, *baculum*, stick, rod, for the sturdy ridges on the interior surface.

Diagnosis.—As for genus.

Material.—Holotype, paratypes MGUH 27131–27135 and 173 additional specimens from GGU samples 314807, 314808, 314809, 314835, 314904, 314906, 314908, 314919, and 314931.

Description.—Generally cap-shaped shell of near circular to subtriangular outline, with rounded knob-like apex displaced to about one third the distance toward the proximal side of the shell. Angle of dip between apex and both distal and proximal areas equal in some individuals, but other individuals with shell curving upward between apex and proximal edge resulting in a saddle-shaped profile. Surface with fine, widely and generally equally spaced concentric ribs and narrow depressions between ribs. Two rod-like and widely diverging ridges on the internal surface emanating from proximal edge of shell. Ridges are attached to one side of shell but free on the opposite side where they terminate in a straight, rounded edge. Termination of ridges rounded, usually divided into lobes. The shell is relatively thick (up to 0.35 mm) and the interior surface often has a finely pitted ornamentation.

Remarks.—As discussed above, no previously described fossil closely resemble *Cassitella baculata* from North-East Greenland and no conch or other type of shell from the same suite of samples can be matched with the fossil. Although the function and taxonomic affinity of *C. baculata* is uncertain, the species is apparently widely distributed in the late Early Cambrian of eastern Laurentia. Undescribed specimens attributable to *C. baculata* are found in acid-digested limestone samples from the Aftenstjernesø Formation of North Greenland as well as the Forteau Formation of western Newfoundland (Skovsted, unpublished), making this species potentially interesting for regional biostratigraphical correlation.

Stratigraphic range and distribution.—Lower Cambrian, North-East Greenland and possibly North Greenland and western Newfoundland (unpublished).

Conclusions

The fauna documented herein provides a basis for statements regarding its potential for correlation, its paleobiogeographic significance, and permits speculation concerning the evolution of hyoliths in the Early Cambrian. The salient points are summarized below.

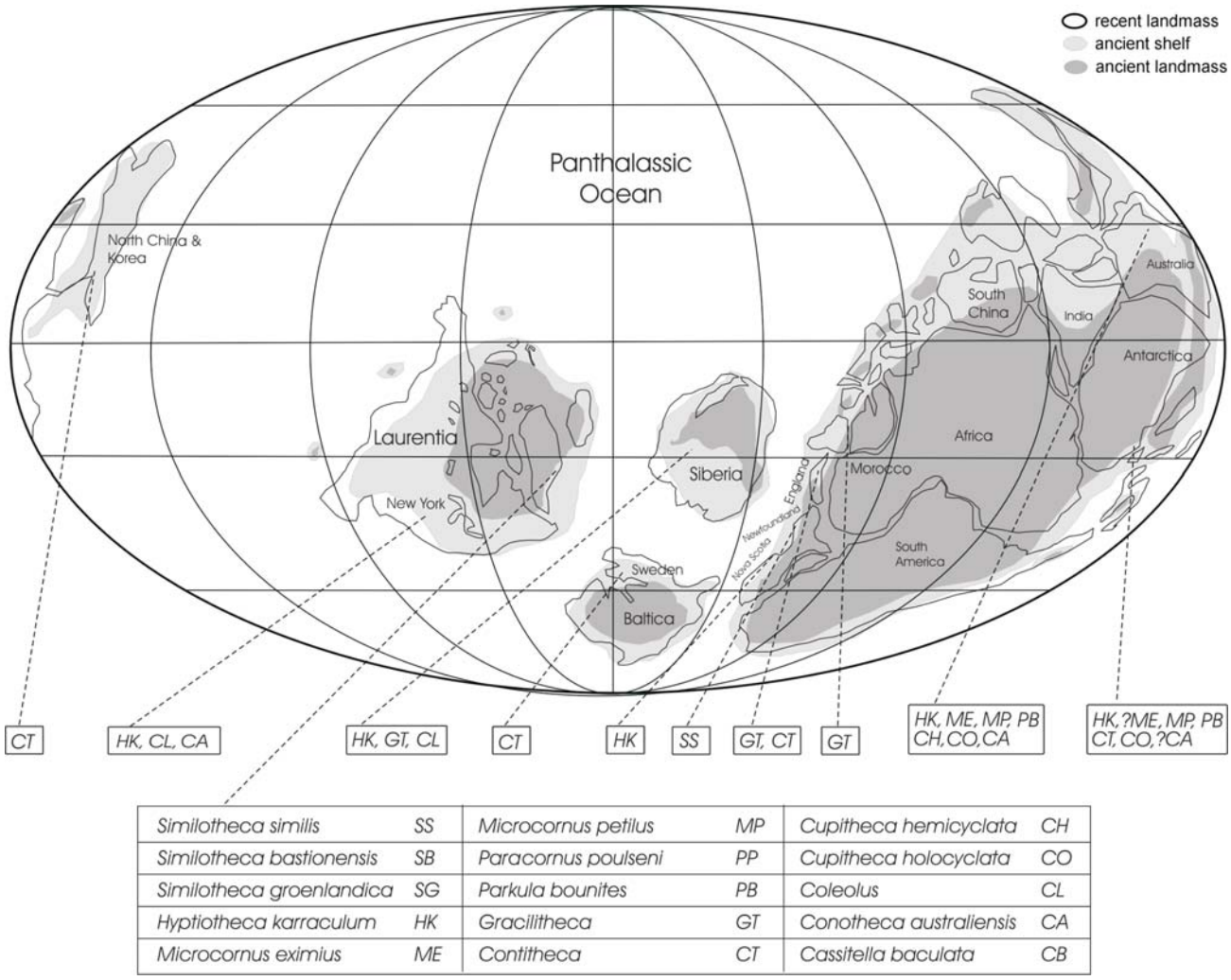
- The hyoliths documented herein are among the best preserved from strata of this age and can be unequivocally identified as such, in contrast to many of the Early Cambrian tubular fossils from the Siberian Platform and South China assigned to the Hyolitha (see Missarzhevsky 1989 and Qian and Bengtson 1989, and references in each) which lack definitive evidence for hyolith affinity.
- The occurrence of the hyolith species *Hyptiotheca karraculum* Bengtson, 1990a, *Parkula bounties* Bengtson,

	Taxon \ Locality	Antarctica	Australia	England	Korea	Morocco	New York	Newfoundland	Nova Scotia	Siberia	South China	Sweden
Order Hyolithida Syssoiev, 1957	*Similotheca similis* (Walcott, 1890)							X				
	Similotheca bastionensis sp. nov.											
	Similotheca groenlandica sp. nov.											
	Hyptiotheca karraculum Bengtson, 1990a	X	X				X		X	X	X	
	Microcornus eximius Duan, 1984	X?	X								X	
	Microcornus petilus Bengtson, 1990a	X	X									
	Paracornus poulseni gen. et sp. nov.											
	Parkula bounites Bengtson, 1990a	X	X									
Order Orthothecida Marek, 1966	*Gracilitheca* Syssoiev, 1968			X		X				X		
	Contitheca Syssoiev, 1972	X		X	X							X
	Cupitheca hemicyclata (Bengtson, 1990a)		X									
Affinity uncertain	*Cupitheca holocyclata* (Bengtson, 1990a)	X	X									
	Coleolus Hall, 1879						X			X		
	Conotheca australiensis Bengtson, 1990a	X?	X				X					
	Cassitella baculata gen. et sp. nov.											

Fig. 16. Table showing distribution outside North-East Greenland of taxa documented herein. Forms endemic to Greenland are included for completeness.

1990a, *Microcornus eximius* Duan, 1984, and *M. petilus* Bengtson, 1990a, and the hyolith genera *Contitheca*, *Gracilitheca*, and *Similotheca* and possibly *Burithes*, as well as the problematic *Coleolus*, *Conotheca*, and *Cupitheca* further attests to their widespread distribution in the Early Cambrian (Figs. 16, 17), and except for *Coleolus*, enhances the value of these fossils for correlation. In contrast, many hyolith taxa previously used for correlation, such as *Allatheca degeeri* (Holm, 1893) are poorly founded upon incomplete specimens, and consequently not recognizable beyond their type material (see Malinky and Berg-Madsen 1999: 54). Furthermore, the occurrences of *Contitheca*, *Similotheca*, and *Coleolus* in the Bastion Formation extend the ranges of these genera into the Lower Cambrian, making these the oldest known occurrence for at least *Contitheca* and *Similotheca*, and possibly for *Coleolus*, depending upon whether the Lower Cambrian *C. trigona* Syssoiev, 1962 from Siberia actually represents this genus.

- Occurrence of these fossils in North-East Greenland provides further evidence of their global distribution in the Early Cambrian, with occurrences elsewhere in strata of that same age in Europe, North America, the Siberian Platform, Kazakhstan, South China, and Antarctica (Fig. 16). Only *Similotheca bastionensis* sp. nov. and *S. groenlandica* sp. nov., *Paracornus poulseni* gen. et sp. nov. and *Cassitella baculata* gen. et sp. nov. appear to be endemic to Greenland. The distribution of these fossils supports the notion that paleobiogeographic provinces can not be recognized in the Early Cambrian utilizing hyoliths and certain other problematica, as can otherwise be done with trilobites and certain other organisms (Fig. 17).
- Morphology of the operculum of *Hyptiotheca* is unusual in that there is no distinct boundary, seen as rooflets and furrows on other hyolithid taxa, between the cardinal and conical shields on the operculum, and clavicles are lacking on the interior. These missing features have long been considered to be defining traits of the order Hyolithida. Perhaps these structures were not mineralized in this taxon, or the functional morphology and mode of life was sufficiently different for *Hyptiotheca* such that clavicles were not a necessary component of its skeletal structure. Members of the Orthothecida possess cardinal processes but no clavicles on their opercula. In contrast, opercula A and B possess cardinal processes and clavicles, but lack the dorso-ventral differentiation normally associated with the opercula of hyolithids. Furthermore, each has an outline that approaches a circular or subcircular shape. The apparent lack of differences between dorsal and ventral edges and the subcircular outline are traits normally associated with the order Orthothecida. Perhaps *Hyptiotheca* and the two opercula combine traits of both Hyolithida and Orthothecida, and could be similar in some respects to the ancestral form that ultimately gave rise to both hyolith orders. The problematic *Cassitella* possesses clavicle-like structures but no structures comparable to cardinal pro-



Similotheca similis	SS	*Microcornus petilus*	MP	*Cupitheca hemicyclata*	CH
Similotheca bastionensis	SB	*Paracornus poulseni*	PP	*Cupitheca holocyclata*	CO
Similotheca groenlandica	SG	*Parkula bounites*	PB	*Coleolus*	CL
Hyptiotheca karraculum	HK	*Gracilitheca*	GT	*Conotheca australiensis*	CA
Microcornus eximius	ME	*Contitheca*	CT	*Cassitella baculata*	CB

Fig. 17. Map of the Early Cambrian world showing distribution of taxa documented herein (modified after C.R. Scotese, University of California)

cesses, and although its affinity to hyoliths is uncertain, may represent a similar case. Alternatively, these organisms may represent short-lived, unsuccessful experiments with a new mode of life for the hyoliths.

- The relationship between the micro-sized hyoliths reported herein and the much larger individuals reported by Poulsen (1932) from the same level in Greenland remains unresolved. No individuals of intermediate sizes, representing intermediate stages of ontogeny, have as yet been recovered from this area. Thus, whether certain smaller and larger individuals belong to the same taxon cannot be determined at present.

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