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In-place operculum demonstrates that the Middle Cambrian *Protowenella* is a hyolith and not a mollusc

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ABSTRACT

Protowenella is an early–middle Cambrian, isostrophically coiled, calcareous microfossil originally described from the middle Cambrian (Miaolingian) of Australia; it has been referred previously to the molluscan classes Monoplacophora, Helcionelloida or Gastropoda. A unique specimen from the Henson Gletscher Formation (Miaolingian Series, Wuliuan Stage) of North Greenland has a bilaterally symmetrical operculum preserved in place within the shell aperture. Paired cardinal processes and clavicles on the inner side of the operculum indicate that *Protowenella* was a hyolith morphologically close to the orthothecid *Conotheca*. *Protowenella* is transferred from Mollusca to Hyolitha, Order Orthothecida, Family Protowenellidae nov., representing a novel morphological departure from the generally slender cones of other hyoliths.

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HELCIONELLOIDS and hyoliths are among the most prominent groups of Cambrian Small Shelly Fossils, the mainly phosphatic or phosphatized microfossils extracted from carbonate sediments by dissolution in weak acids. Their remains are most commonly preserved as phosphatic encrustations or as internal moulds of the calcareous shells (Bengtson *et al.* 1990, Creveling *et al.* 2014). While members of both groups are usually bilaterally symmetrical, hyoliths are characterized by a straight to slightly curved narrow conch, the aperture of which is closed by a robust calcareous operculum (Marek & Yochelson 1976, Berg-Madsen & Malinsky 1999, Martí Mus & Bergström 2005, Malinky & Yochelson 2007, Martí Mus *et al.* 2014). Two orders of hyoliths are recognized in the Cambrian. Hyolithids are distinguished by a shelf-like extension of the apertural margin, the ligula (Fig. 1A), which is not present in orthothecids (Fig. 1B). Furthermore, the outer surface of the operculum is divided into clearly demarcated cardinal and conical shields in most hyolithids, while orthothecid opercula are usually flat.

Helcionelloids are cap-shaped, often laterally compressed, and coiled through a quarter to slightly more than a full whorl (Peel 1991a, b, Jacquet & Brock 2016). There are no records of an operculum in helcionelloids. As in modern limpetoid gastropods, the presence of an operculum would be incompatible with their clamping or semi-infaunal mode of life (Vermeij 2016).

The general morphology of the shell of *Protowenella* Runnegar & Jell, 1976 supports its placement as a member of the helcionelloid group of molluscs (Berg-Madsen & Peel

1978, Missarzhevsky 1989, Peel 1991a, b), albeit with a distinctive, tightly coiled, form (Fig. 1E). The type species, *Protowenella flemingi* Runnegar & Jell, 1976 from the Miaolingian of Australia (Runnegar & Jell 1976), is known principally from internal moulds characterized by a tightly coiled, rather globose, isostrophic, shell without a median sinus in the apertural margin, but with a circumbilical channel impressed into the mould surface on each umbilico-lateral surface. The bilaterally symmetrical morphology may be described as ‘bellerophontiform’ by comparison to the coiling in the late Cambrian–Triassic mollusc group resembling *Bellerophon* Montfort, 1808. This similarity prompted Runnegar & Jell (1976) to interpret *Protowenella* as the oldest genus within a widely drawn Order Bellerophontida Ulrich in Ulrich & Scofield, 1897, which they transferred from its traditional place within the gastropods (Knight *et al.* 1960) to an expanded Class Monoplacophora Knight, 1952 (Fig. 1D). In describing *Protowenella* from the Miaolingian of Bornholm, Denmark, Berg-Madsen & Peel (1978) rejected this wholesale interpretation of bellerophontids as untorted monoplacophorans, returning most to the gastropods, but they considered *Protowenella* to be an untorted mollusc. Their opinion was based on a functional morphological analysis of the channels in the umbilico-lateral areas of *Protowenella flemingi*, a character not discussed by Runnegar & Jell (1976) although visible in their illustrations (Runnegar & Jell 1976, fig. 6G, H). Peel (1991a, b) placed *Protowenella* within Class Helcionelloida Peel, 1991a (Fig. 1E), an opinion followed by Gubanov *et al.* (2004), Wotte (2021) and Claybourn *et al.* (2019). MacKinnon (1985) followed Runnegar & Jell (1976) in assigning *Protowenella* to the Order Bellerophontida, while Brock (1998) considered *Protowenella* to be a bellerophontid, and tentatively a gastropod (Fig. 1F). Parkhaev (2008, 2017) placed *Protowenella* as a heterobranch of the Family Khairkhaniidae Missarzhevsky, 1989, but within the Order

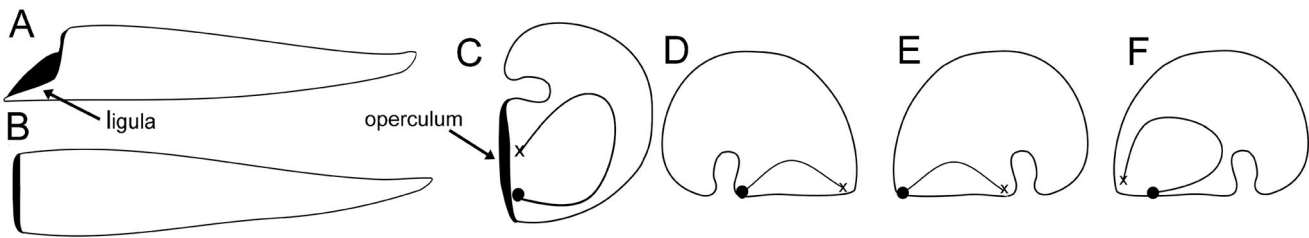


Figure 1. A, Hyolithid in lateral view. B, Orthothecid in lateral view. C, *Protowenella* with operculum in place reconstructed as an orthothecid hyolith. D–F, Alternative reconstructions of *Protowenella*; D, as an exogastric monoplacophoran (Runnegar & Jell 1976); E, as an endogastric helcionelloid (Peel 1991a, b); F, as a gastropod. Inferred digestive tract shown schematically with mouth (black dot) and anus (×).

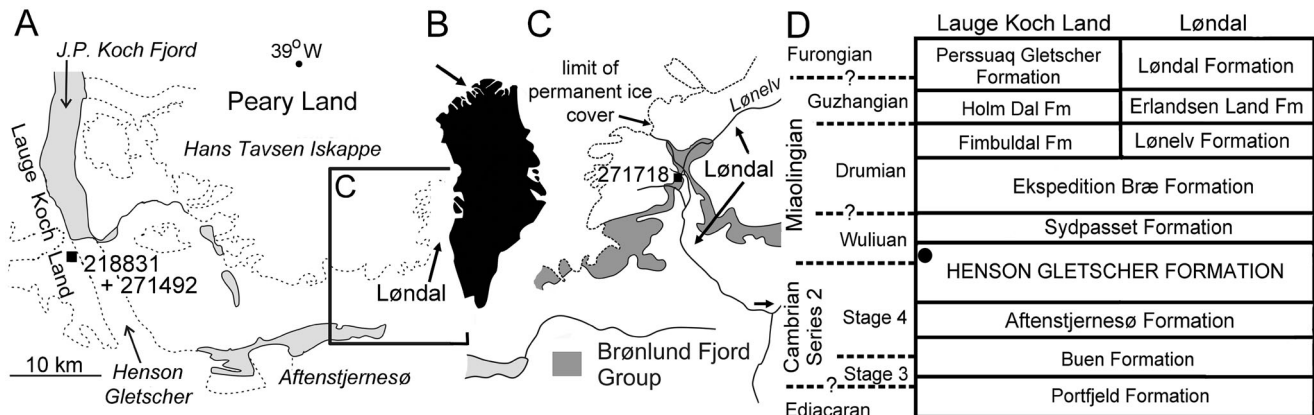


Figure 2. Locality and geological information. A, Lauge Koch Land – Løndal region of North Greenland showing collection site of GGU samples 218831 and 271492. B, Greenland, with arrow indicating location of A. C, Løndal region of Western Peary Land (see inset in A) showing collection locality for GGU sample 271718. D, Cambrian stratigraphic nomenclature of the Lauge Koch Land – Løndal region showing derivation of GGU samples from the Henson Gletscher Formation (black dot).

Khairkhaniformes Parkhaev, 2001 of the gastropod Subclass Divisabranchia Minichev & Starobogatov, 1979. In contrast, Parkhaev in Bouchet *et al.* (2017, p. 330) classified Khairkhaniiidae as Palaeozoic molluscs (gastropods or monoplacophorans) of uncertain position, unassigned to superfamily.

The interpretation of bellerophontiform molluscs as untorted molluscs, stem group gastropods, gastropods, or a conglomeration of all three, remains contentious (Missarzhevsky 1989, Peel 1991a, b, Wahlman 1992, Geyer 1994, Harper & Rollins 2000, Bouchet & Rocroi 2005, Frýda *et al.* 2008, Frýda 2012, Bouchet *et al.* 2017, Ponder *et al.* 2020). Peel (2016) considered the morphological group to be polyphyletic and that opinion is maintained here. However, the controversy in the literature concerning the phylogenetic position of *Protowenella* within molluscs loses relevance in the present context, with the description of an in-place operculum in a unique specimen of *Protowenella* from the Miaolingian of North Greenland (Fig. 2). The discovery would represent the first occurrence of an operculum in a bellerophontiform mollusc, be it torted or untorted. Remarkably, however, the morphology of the bilaterally symmetrical operculum clearly invites comparison with hyolith opercula. *Protowenella* is not a mollusc, but an orthothecid hyolith (Fig. 1C).

Hyolitha was proposed as a separate class within Mollusca by Marek & Yochelson (1976) and Malinky & Yochelson (2007) but regarded as a separate phylum by others (Runnegar *et al.* 1975, Runnegar 1980, Sysoev 1984,

Missarzhevsky 1989, Val'kov 1990). Sun *et al.* (2016) envisaged a relationship to sipunculids. Moysiuk *et al.* (2017) suggested they were lophophorates, although Liu *et al.* (2020a) considered that hyoliths were probably basal lophotrochozoans rather than lophophorates linked with brachiopods. Li *et al.* (2020) stressed similarities in shell structure in concluding that hyoliths might be part of the total group Mollusca, but left their phylogenetic position unresolved.

Geological background and material

All described material is derived from the Henson Gletscher Formation of North Greenland (Fig. 2D). The Henson Gletscher Formation is a component of a prograding complex of shelf sediments that accumulated in North Greenland on the present day southern margin of the transarctic Franklinian Basin (Higgins *et al.* 1991, Ineson & Peel 1997, Geyer & Peel 2011, Peel *et al.* 2016). The formation is mainly composed of dark, recessive, shaly-weathering, bituminous and cherty limestones, dolostones and mudstones, with a middle member of pale fine-grained sandstones. The Henson Gletscher Formation is 62 m thick at its type locality in Lauge Koch Land (Fig. 2A, 82°10'N, 40°24'W, Ineson & Peel 1997, fig. 31, Geyer & Peel 2011, fig. 3, Fig. 2A), from which GGU samples 218831 and 271492 were collected at 56.5 m above the base. GGU sample 271718 was collected 1 m below the top of the formation in Løndal, to the east (Fig. 2A, B, 82°18'N, 37°03'W, Clausen & Peel 2012, fig. 1), where the formation has thinned to 47 m.

GGU sample 218831 was collected by Peter Frykman on 24 June 1979 from the same locality and horizon as GGU sample 271492 (J. S. Peel 25 June 1978). GGU sample 271718 was collected by J. S. Peel on 15 July 1978.

The Henson Gletscher Formation in southern Lauge Koch Land and southwestern Peary Land ranges in age from Cambrian Series 2 (Stage 4) to the Miaolingian Series (Wuliuan Stage, *Ptychagnostus gibbus* Biozone), although Drumian strata occur along the north coast of North Greenland (Higgins *et al.* 1991, Robison 1994, Blaker & Peel 1997, Ineson & Peel 1997, Geyer & Peel 2011, Fig. 2).

Carbonate rock samples were digested in weak acetic acid and the dried, sieved residues were handpicked under a binocular microscope. Selected specimens were gold-coated prior to scanning electron microscopy, using a Zeiss Supra 35VP scanning electron microscope, and images were assembled using Adobe Photoshop CS4.

Repositories and institutional abbreviations. GGU, a sample collected during field work by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark. PMU, palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden.

Operculum of *Protowenella*

Almost all of the more than 100 specimens from GGU samples 218831, 271492 and 271718 are assigned to *Protowenella flemingi* Runnegar & Jell, 1976. They are preserved as compact apatite internal moulds of the type documented by Creveling *et al.* (2014) in the Thornton Limestone (Cambrian, Miaolingian Series) of Australia, and widespread in Cambrian samples from North Greenland (Fig. 3C, E, F, H) and elsewhere. Rare specimens additionally preserve patches of a thin phosphatized encrustation that was formed on the outside of the shell (Fig. 4). The void between the encrustation and the internal mould thus corresponds to the dissolved calcareous shell. In contrast, the unique operculate specimen from GGU sample 218831 is preserved as a thin encrusting layer deposited on the inner surface of the shell (Fig. 3A, B, D, G, I). Dissolution of the carbonate infilling in this specimen during sample preparation has left a hollow interior. The internal mould of the shell preserves no trace of the shallow comarginal corrugation sometimes visible on solid internal moulds (Fig. 3C, E) or the fine growth lines present on the external shell surface (Fig. 3C, arrow). In all the available specimens of *Protowenella*, the circumbilical channels on the umbilico-lateral walls are clearly delimited (Figs 3A–I, 4A arrow).

Description

Although partly broken, the preserved inner surface of the unique operculum is clearly bilaterally symmetrical about the same plane as the coiled shell (Fig. 3A, B) and fits

closely to the shell aperture. Both the margins of the operculum and the shell aperture are coplanar, lacking invaginations. The shallowly convex surface of the internal mould, corresponding to the concave inner surface of the operculum itself, is marked by a triangular raised area, narrowing towards the umbilical area of the shell from points located about half way between the lateral extremities of the shell aperture (and the operculum) and the median dorsal line of the supra-apical surface of the shell (Fig. 3B, G). The apex of this triangle continues as a short ridge to the margin of the operculum, below the shell apex (Fig. 3D).

The adumbilical margin of the operculum is a deep channel that in its width extends between the circumbilical channels of the shell internal mould (Fig. 3B). It represents a prominent comarginal ridge on the interior of the operculum that fits within the apertural margin of the shell (Fig. 3D). The channel is U-shaped in cross-section, with two deep holes penetrating to the interior on each side of the median line (Fig. 3D). These holes equate with prongs on the interior surface of the operculum.

Discussion

The role of opercula as a primary defensive element in tube-dwelling or cone-dwelling organisms is documented already in the early Cambrian where heavily calcified, bilaterally symmetrical, opercula are present in hyolithid and orthothecid Hyolitha (Marek & Yochelson 1976, Berg-Madsen & Malinsky 1999, Martí Mus & Bergström 2005, Peel 2010, 2021, Martí Mus *et al.* 2014, Peel & Willman 2018). While the identity of the associated tube is uncertain, phosphatic mobergellan opercula may be locally abundant in lower Cambrian strata (Bengtson 1968, Streng & Skovsted 2006, Skovsted & Topper 2018), but even rare Cambrian corallomorphs developed an operculum to cover the calice (Jell & Jell 1976, Peel 2011).

The most familiar association of opercula is with gastropods. Most gastropod groups develop an operculum at some stage in their ontogeny and fossil gastropod opercula are known from the early Ordovician to the present day (Yochelson 1979). While isolated heavily calcified opercula may be common at certain horizons in the Lower Palaeozoic (Lindström 1884, Yochelson 1979, Boucot & Poinar 2010), the general lack of calcification in most gastropod opercula precludes their preservation as fossils (Checa & Jiménez-Jiménez 1998, Ponder *et al.* 2020). Records of Palaeozoic gastropods with the operculum preserved in place are rare, and therefore well documented (Lindström 1884, Perner 1903, Yochelson & Linsley 1972, Horný & Peel 1995, Peel & Horný 1996, Rohr & Frýda 2001, Rohr 2004, Peel 2015). The opercula do not display bilateral symmetry, reflecting their association with anisotrophically coiled gastropod groups (Checa & Jiménez-Jiménez 1998). Opercula are not present in limpets or in bellerophonoid gastropods, and have not been described from supposed Cambrian gastropods. Northrop (1939) reported two possible opercula within the aperture of the holotype of the bellerophonoid *Salpingostoma inornatum*

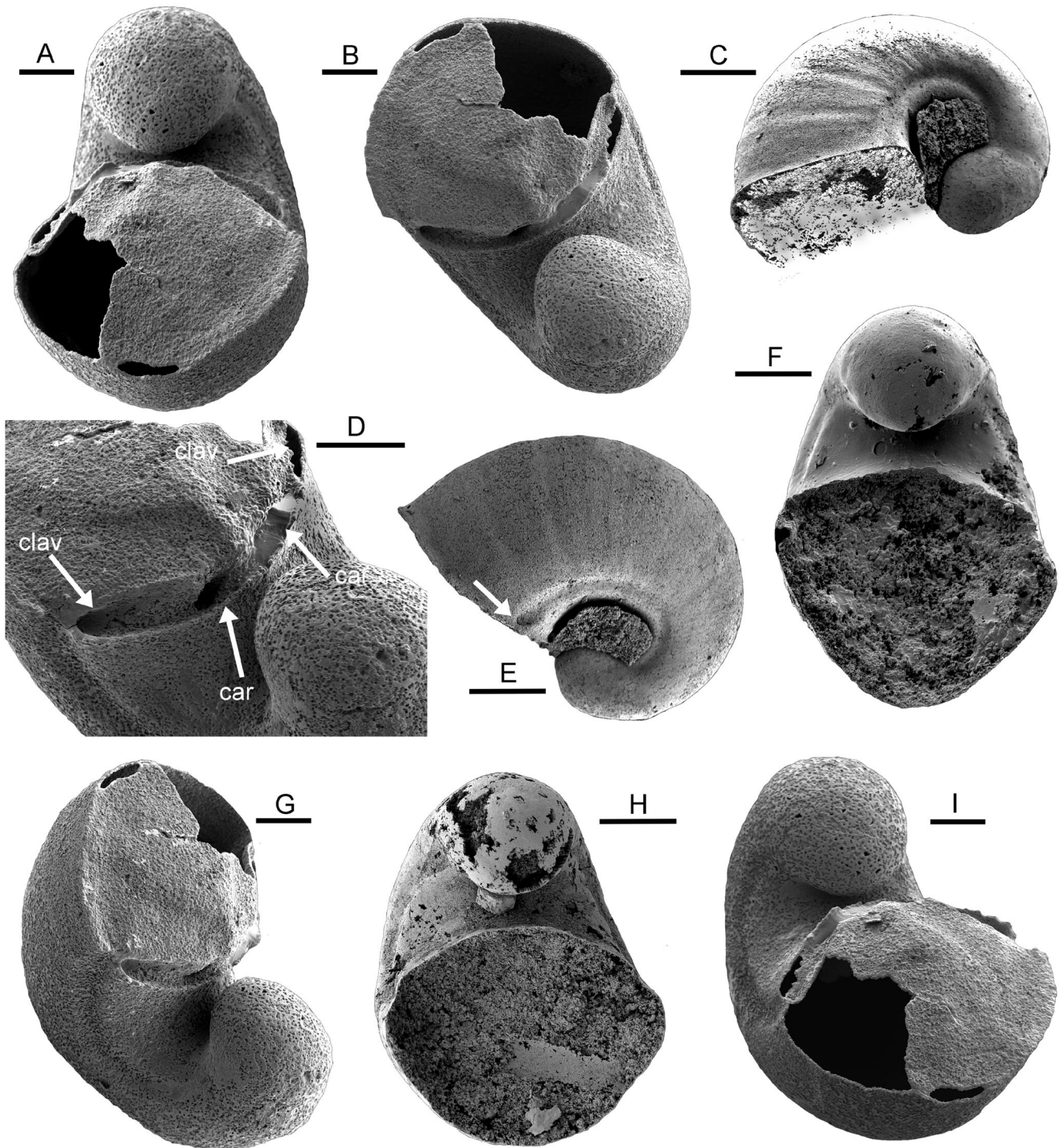


Figure 3. *Protowenella flemingi* Runnegar & Jell, 1976, internal moulds from the Henson Gletscher Formation, North Greenland, Cambrian, Miaolingian Series, Wuliuan Stage, *Ptychagnostus gibbus* Biozone. A, B, D, G, I, PMU 38329 from GGU sample 218831, Lauge Koch Land. A, B, apertural views showing isostrophic form and bilaterally symmetrical operculum. D, detail of umbilical area showing pits representing the cardinal processes (car) and clavicles (clav). G, I, oblique apertural views. C, E, PMU 38330 from GGU sample 271718 in oblique lateral and lateral views, with arrow in E showing termination of circumbilical channel prior to the broken aperture. F, PMU 38331 from GGU sample 271718, apertural view. H, PMU 38332, apertural view. Scale bars: 50 μm (A, B, D, G, I), 100 μm (C, E, F, H).

Northrop, 1939 from the Silurian of Gaspé, but the two bodies were identified as a bivalve and a trilobite cephalon by Peel (1972).

The morphology of the operculum in *Protowenella* demonstrates its hyolith character. Key features are the bilateral symmetry and the paired cardinal processes and clavicles represented by the deep holes into the interior (Fig. 3D, arrowed as car and clav). While clavicles and cardinal

processes are present in both hyolithids (Fig. 5A, G) and orthothecids (Fig. 5C), the operculum outer surface in most hyolithids is divided into clearly demarcated cardinal and conical shields (Fig. 5B, E) that are not seen in *Protowenella*. Furthermore, a shelf-like ligula that is associated with the development on the operculum of cardinal and conical shields is not developed in *Protowenella*, although diagnostic of hyolithids. Additionally, a pronounced clavicular ridge

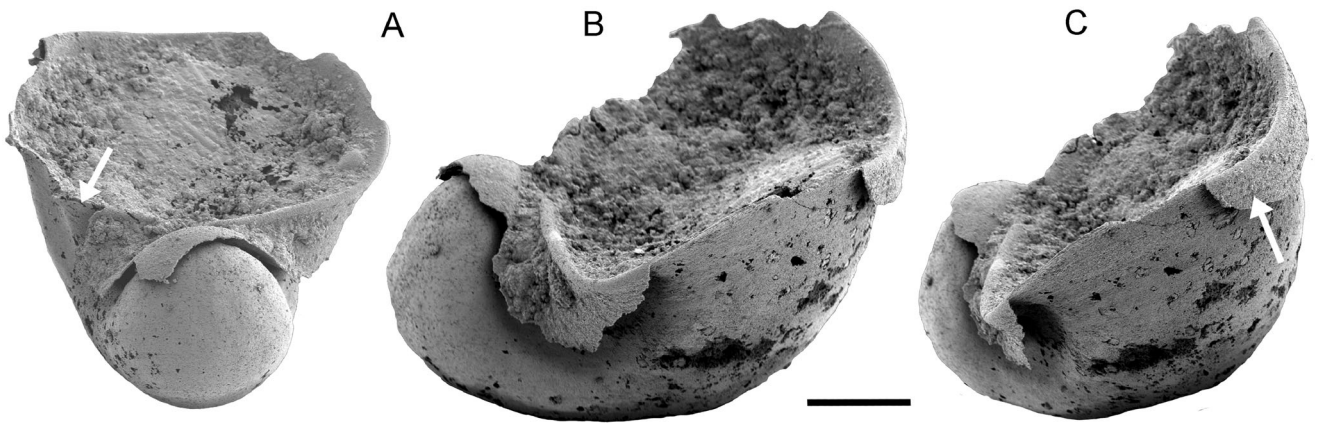


Figure 4. *Protowenella flemingi* Runnegar & Jell, 1976, PMU 38333 from GGU sample 271492, largely exfoliated internal mould, Henson Gletscher Formation, North Greenland, Cambrian, Miaolingian Series, Wuliuan Stage, *Ptychagnpustus gibbus* Biozone. A, oblique apertural view with channel on internal mould (arrow). B, oblique lateral view showing apertural margin lacking emargination corresponding to the circumbilical channel on the internal mould. C, oblique lateral view showing growth lines (arrow) near apertural margin. Scale bar 100 µm.

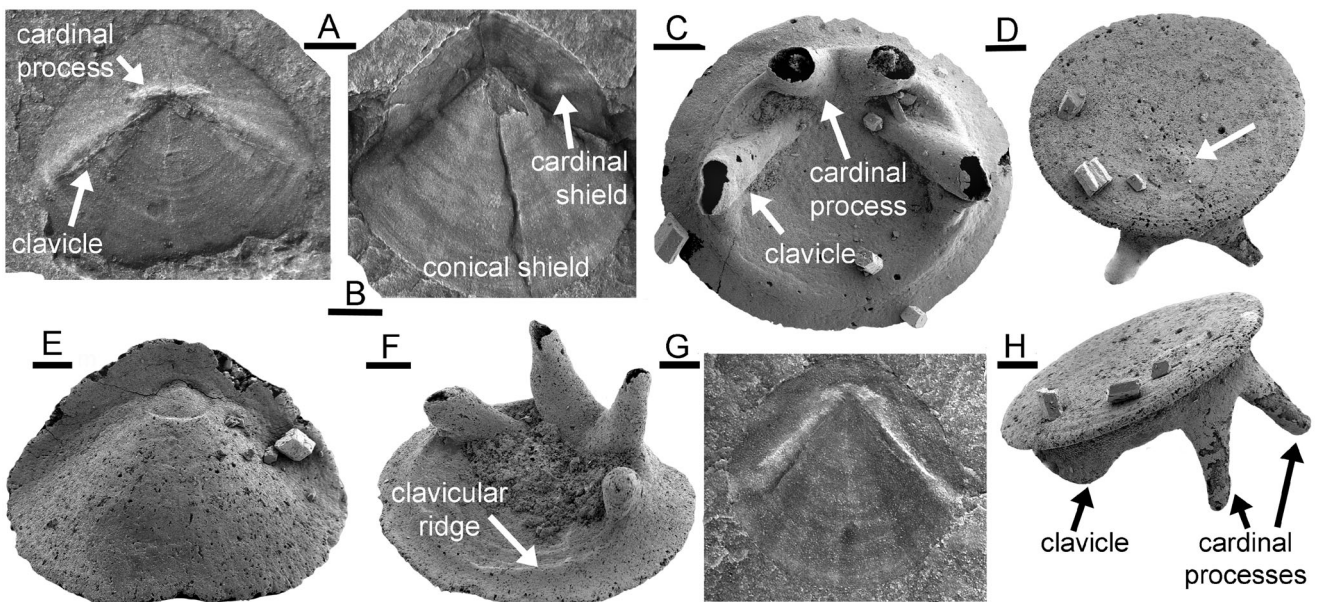


Figure 5. Hyolith opercula, Cambrian Series 2 (Stage 4), North Greenland. A, PMU 22963, Buen Formation, internal surface of hyolithid operculum showing cardinal processes and clavicles. B, PMU 22969, Buen Formation, external surface of hyolithid *Kalaallitia myliuserichseni* Peel & Willman, 2018 showing cardinal and conical shields. C, *Conotheca?* sp., PMU 36944, Aftenstjernesø Formation, showing internal surface with cardinal processes and clavicles set in clavicular ridge. D, H, *Conotheca laurentiensis* Landing & Bartowski, 1996, PMU 36952, Aftenstjernesø Formation, oblique views showing flat external surface with protoconch (arrow in D), and clavicle and cardinal processes (H). E, *Parkula bounites* Bengtson in Bengtson *et al.*, 1990, PMU 36931, Aftenstjernesø Formation, external surface. F, *Conotheca?* sp., PMU 36947, Aftenstjernesø Formation, showing internal surface with cardinal processes and clavicles set in clavicular ridge. G, PMU 22968, Buen Formation, internal surface of hyolithid *Kalaallitia myliuserichseni*. Scale bars: 100 µm (C–F, H), 1 mm (A, B, G).

(Fig. 5F), locking the operculum into the shell aperture, is a characteristic feature of *Conotheca* Missarzhevsky, 1969 (Fig. 5C, F) and other orthothecid hyoliths. In *Protowenella*, the clavicular ridge is represented by the U-shaped channel at the adumbilical margin of the internal mould of the operculum (Fig. 3B, D, G). The flattened marginal area peripheral to the clavicular ridge in *Conotheca* (Fig. 5C) is equivalent therefore to the thickness of the orthothecid conch wall and is not seen in the preserved internal mould of *Protowenella*.

The clavicles in *Conotheca* may vary in degree of expression from narrow prongs (Fig. 5C, F) to lower, more blade-like ridges (Fig. 5H), with the former comparing best to the holes present in the internal mould of

Protowenella (Fig. 3D). In *Neogloborilus* Qian & Zhang, 1983, as illustrated by Pan *et al.* (2019) and Peel (2021), the clavicles are raised, but differ from *Protowenella* in being directed almost horizontally towards the ventral margin of the operculum.

The outer surface of the operculum of *Protowenella* is not known but it was likely flat or shallowly convex as in *Conotheca* (Fig. 5D, H), with the protoconch placed just above the cardinal processes (arrow in Fig. 5D).

Circumbilical channels on the internal mould are a diagnostic character of *Protowenella* and were interpreted as internal thickenings of the shell wall or possible shallow emarginations in the aperture by Berg-Madsen & Peel (1978). The latter interpretation promoted the suggestion

that these emarginations in *Protowenella* represented the loci of inhalant currents into the mantle cavity (Berg-Madsen & Peel 1978, Peel 1991a, b). However, almost all described specimens of *Protowenella* are internal moulds and precise details of the apertural margin generally are not preserved. Poorly preserved silicified material from the Kuonamka Formation (Miaolingian) described by Gubanov *et al.* (2004) lacked any indication of the circumbilical channels on the shell exterior. The notion that the channels may form emarginations in the aperture of some specimens is not discounted, but the channel in one illustrated specimen terminates prior to the margin (Fig. 3E, arrow), suggesting that the channel was a ridge on the shell interior rather than a fold in the shell wall. Ridges on the shell interior would form a support for the margin of the operculum, as also would simple folds in the margin that do not form emarginations.

A second specimen of *Protowenella* (Fig. 4) preserves the shell apertural margin due to a thin encrustation of the external surface, but no emargination is visible. A circumbilical channel is preserved on the internal mould (Fig. 4A, arrow) but does not produce an invagination in the apertural margin. Runnegar (1985, fig. 1A–C) noted that the interior surface of some helcionelloids (not morphologically close to *Protowenella*) developed comarginal thickenings that formed deep channels on the internal mould without any visible indication of their presence on the external surface.

Hyolithes Eichwald, 1840, a hyolithid and the eponymous genus of Hyolitha, develops lateral, longitudinal, furrows on the dorsal surface close to the lateral extremities of the conch in Ordovician specimens (Malinky 2002, pl. 3, figs 10, 14, 22), similar structures are present in *Rodentilites* Marek, Malinky & Geyer, 1997 and several other genera (Marek *et al.* 1997). The furrows are located in an analogous position to the circumbilical channels in *Protowenella*, although the latter is much more tightly coiled than the longitudinally shallowly concave *Hyolithes*.

The small size and unusually tight curvature may suggest that *Protowenella* is the protoconch of a larger orthothecid hyolith. The North Greenland samples contain internal moulds (and isolated protoconchs) of several hyoliths but coiled protoconchs similar to *Protowenella* that are attached to mature shells have not been observed. Such associations are not known in other samples from North Greenland nor reported in the literature.

A single phosphatized specimen from the early Cambrian Meishucunian Stage of Yunnan, China, described by Feng *et al.* (2007), was considered to combine a hyolith-type microstructure with a mollusc-like shell. The open-coiled, cyrtconic, shell (length about 1 mm) is coiled through more than half a whorl, although the apex and aperture are broken (Feng *et al.* 2007, fig. 2). The outer surface is ornamented by numerous, closely spaced, acute transverse ribs separated by concavities. The circular aperture is planar without median or circumbilical emarginations. Feng *et al.* (2007) described a shell structure consisting of two layers, which they considered indicative of hyolith affinity. The outer layer preserved longitudinal fibres, perpendicular to

the transverse ribs, whereas the inner layer consisted of transverse elements, similar to structures described in Siberian material by Kouchinsky (2000). Duan (1984) assigned similar shells to four new species assigned to *Paragloborilus* Qian, 1977 (see also Qian 1989), a genus of orthothecid hyoliths. Illustrated specimens may be curved through about one third of a whorl near the apex (Duan 1984). The degree of coiling and nature of the ornamentation bears little resemblance to described helcionelloid molluscs. As indicated by the shell structure, the Chinese material is interpreted as curved orthothecid hyoliths. *Protowenella* is readily distinguished by its tightly coiled shell and lack of the prominent transverse ribbing.

In summary, *Protowenella* is interpreted as an orthothecid hyolith with an operculum closely similar to *Conotheca* (Fig. 5C, D, F, H). However, the tightly coiled shell is unlike other described orthothecids or hyolithids, which have straight or shallowly curved shells, promoting its assignment to a new Family Protowenellidae (Order Orthothecida Marek, 1966).

Systematic palaeontology

Phylum uncertain

Class HYOLITHA Marek, 1963

Discussion. The phylogenetic placement of Hyolitha is controversial. Hyoliths have been regarded as molluscs (Marek & Yochelson 1976, Malinky & Yochelson 2007), a separate phylum (Runnegar *et al.* 1975, Runnegar 1980, Sysoev 1984, Missarzhevsky 1989, Val'kov 1990), lophophorates (Moysiuk *et al.* 2017), basal lophotrochozoans (Liu *et al.* 2020a) or possibly members of the stem lineage within total group Mollusca (Li *et al.* 2020). While increasing the known morphological diversity, the present transfer of *Protowenella* to Hyolitha does not contribute materially to this discussion.

Hyoliths are traditionally grouped within two orders (Hyolithida and Orthothecida), mainly based on the morphology of the apertural margin and operculum, although recent studies have described Cambrian hyoliths that are intermediate or possibly ancestral to the two groups (Malinky & Skovsted 2004, Li *et al.* 2020, Liu *et al.* 2020b, Skovsted *et al.* 2020). The authorship of Hyolithida is the subject of discussion (Fischer 1962, Malinky 1990, Malinky and Yochelson 2007, Geyer 2018) but Malinky & Yochelson (2007) argued for the maintenance of Sysoev (1957) as its author. Peel & Yochelson (1984) proposed a late Palaeozoic Order Toxeumorphida Shimansky, 1962, referred to as Toxeumorphida by Malinky & Yochelson (2007), but their proposal has generated little comment.

Order ORTHOTHECIDA Marek, 1966

Family PROTOWENELLIDAE fam. nov.

Diagnosis. Strongly coiled, globose, isostrophic (to anisostrophic?), with broad circumbilical channels on the umbilico-lateral walls of the internal mould. Operculum interior

with prong-like cardinal processes and clavicles rising from a prominent comarginal clavicular ridge.

Discussion. In addition to *Protowenella*, the anisostrophic *Xinjispira* Yu & Rong in Yu, 1987 originally described from Cambrian Series 2 in Henan, China (Zhou & Xiao 1984, Yu 1987, Li *et al.* 2021), is tentatively placed here on account of the development of circumbilical channels on the internal mould described from Antarctica by Claybourn *et al.* (2019). The channels leave no indication in the shell ornamentation (Claybourn *et al.* 2019). An operculum is not known in *Xinjispira*.

Yu & Rong (1991) considered *Xinjispira* to be a macluritiid gastropod. Parkhaev (2001, 2008, 2019) placed *Xinjispira* together with *Protowenella* within the molluscan Family *Khairkhaniidae* Missarzhevsky, 1989. Claybourn *et al.* (2019) tentatively placed *Xinjispira* in the Family *Pelagiellidae* Knight, 1956 within total group *Gastropoda* Cuvier, 1797, on account of its anisometry, while Li *et al.* (2021) regarded it as probably a stem group gastropod of uncertain ordinal position.

The status of other coiled Small Shelly Fossils, such as *Khairkhania* Missarzhevsky, 1980 and *Ardrossania* Runnegar in Bengtson *et al.* 1990 invites investigation, although their similarity to *Protowenella* is limited to their bilateral symmetry. While hyoliths are diverse and widely distributed through Lower Palaeozoic strata, no obvious descendants of *Protowenella* have been described from post-Miaolingian strata.

Protowenella Runnegar & Jell, 1976

Type species. *Protowenella flemingi* Runnegar & Jell, 1976 from the Currant Bush Limestone (Gowers Formation), Queensland, Australia, Cambrian, Miaolingian Series.

Emended diagnosis. Strongly coiled, globose, isostrophic, with broad circumbilical channels on the umbilico-lateral walls of the internal mould. Whorl profile elliptical to circular, aperture simple, its margins coplanar. Operculum bilaterally symmetrical, seemingly with flat external surface, with prong-like cardinal processes and clavicles rising from a prominent comarginal clavicular ridge on the interior at the adumbilical margin. Shell ornamentation of comarginal growth lines and shallow corrugations, the latter sometimes visible on the internal mould.

Discussion. Berg-Madsen & Peel (1978) emended the original diagnosis of Runnegar & Jell (1976) to include the circumbilical channels on the internal mould; this is further emended here to include characters of the operculum. Circumbilical channels are present in *Protowenella lancaraensis* Wotte, 2021 from the Miaolingian of Spain, which may prove to be a junior synonym of *Protowenella flemingi*. *Protowenella cobbensis* MacKinnon, 1985 from the Miaolingian of New Zealand lacks the circumbilical channels

on the internal mould and has a more pointed early growth stage in apertural view (MacKinnon 1985, fig. 9A–G); it is tentatively excluded from the genus. Specimens of *Protowenella plena* Missarzhevsky in Missarzhevsky & Mambetov, 1981 illustrated by Missarzhevsky & Mambetov (1981) and Missarzhevsky (1989) from the early Cambrian of Maly Karatau are too poorly preserved for confident assignment. Material from Cambrian Series 2 in China, assigned to *Protowenella primaria* Zhou & Xiao, 1984 and *Protowenella huainanensis* Zhou & Xiao, 1984, was placed in synonymy of *Protowenella flemingi* by Li *et al.* (2021).

Li *et al.* (2021, fig. 25) described the early ontogeny of the type species *Protowenella flemingi* based on internal moulds from the Xinji Formation (Cambrian Series 2, Stages 3–4) of North China. Vendrasco *et al.* (2010) described shell structure with bundles of fibres parallel to growth lines in Australian material of the type species. A fine transverse fibrous texture is present on the surface of some internal moulds from Greenland (Fig. 3F). The surface of the phosphate coating moulding the shell interior in the operculate specimen shows a fine pitting on the shell surface, but this merges into a pattern of low ridges on the preserved internal surface of the operculum (Fig. 3D).

Xinjispira possesses the globose form and broad circumbilical channels on the internal mould characteristic of *Protowenella* (Claybourn *et al.* 2019) but differs in its clear anisostrophic coiling, referred to as hyperstrophic in the comparison to *Maclurites* Lesueur, 1818 made by Yu & Rong (1991). Oriented in apertural view (as in Fig. 3F), the aperture is displaced to the right in specimens of *Xinjispira simplex* (Zhou & Xiao 1984), the type species of *Xinjispira* (Li *et al.* 2021) from the Xinji Formation China. However, in specimens from the Shackleton Limestone (Cambrian Series 2) of Antarctica, the aperture is displaced to the left (Claybourn *et al.* 2019).

Profound variation in coiling, including from sinistral to dextral morphologies, is well known in early Cambrian helcionelloid molluscs and often can be attributed to variation within species or genera (Landing 1988, Gubanov & Peel 2000, Jacquet *et al.* 2017). Parkhaev (2001, 2008, 2019) included several sinistral, isostrophic and dextral forms, including *Protowenella* and *Xinjispira*, within the molluscan Family *Khairkhaniidae* Missarzhevsky, 1989, although Claybourn *et al.* (2019) questioned the grouping together of the differently coiled genera. If *Xinjispira* (Cambrian Series 2) is a protowenellid hyolith, the variation in anisostrophic coiling may have stabilized into the isostrophic norm for *Protowenella* by the Miaolingian.

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