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A phosphatised fossil Lagerstätte from the middle Cambrian (Wuliuan Stage) of North Greenland (Laurentia)

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The upper Henson Gletscher Formation (Cambrian, Miaolingian Series, Wuliuan Stage) of southern Lauge Koch Land and Løndal, south-western Peary Land, North Greenland (Laurentia) yields diverse assemblages of phosphatised Small Shelly Fossils after treatment with weak acetic acid. The occurrence merits description as a fossil Lagerstätte on account of the exceptional preservation of soft parts in some specimens, although the phosphatisation itself is generally rather coarse. Bradoriid and phosphatocopid arthropods are common and display substantial variation in their preservational history. Some specimens retain traces of internal morphology, although details are generally obscured by indifferent preservation. Rare specimens extend the range of stem-group pentastomid arthropods back by more than 10 million years. A unique hatching larva demonstrates the same early developmental stage of a stem-group priapulan worm to that described in some present-day priapulans. The preservation of an in place operculum has demonstrated that the widespread, supposed mollusc *Protowenella* is actually an unusual, strongly coiled hyolith. Abundant coprolites and cololites provide additional evidence of early phosphatisation. In terms of morphology, *Cambrocoryne lagenamorpha* gen. et sp. nov. superficially resembles wiwaxiid and some annelid sclerites, thelodont scales and the foraminiferan *Lagena*, but its true identity is obscure.

Keywords: Lagerstätte, Henson Gletscher Formation, Cambrian, Miaolingian Series (Wuliuan Stage), North Greenland, Laurentia.

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Diagenetic phosphatisation is widespread in lower–middle Cambrian lowstand carbonates in central North Greenland and residues of fossiliferous samples treated with acetic acid (10%) are frequently dominated by phosphatised Small Shelly Fossils (SSF), some of which display exceptional preservation. Such deposits may provide unusual amounts of palaeontological information and are frequently described as fossil Lagerstätten, following Seilacher (1970; see also Itano 2019). Seilacher (1970) recognised two kinds of Lagerstätten: Konzentrat-Lagerstätten are accumulations of disarticulated fossils, often not particularly well-preserved, while Konservat-Lagerstätten are characterised by exceptional preservation of the fossils, frequently with details of original soft parts or with articulated skeletons.

To some extent, both terms may be applied to the middle Cambrian (Miaolingian Series, Wuliuan Stage) fossil assemblages described in this paper from the upper Henson Gletscher Formation of southern Lauge Koch Land and south-western Peary Land (Figs 1, 2). However, the preservational state of many of the constituent individual fossils is not exceptional so the term Lagerstätte is used in a wide sense. During deposition, the fossils and other clasts were concentrated in bioclastic limestones to produce rich and diverse assemblages of mainly disarticulated skeletal elements, a common depositional form in the geological record. However, early diagenetic phosphatisation has often enhanced morphological information concerning these remains (Peel 2021a,b; Peel & Kouchinsky 2022) and, in rare cases, resulted in the preservation of non-skeletonised faunal elements or soft parts associated with robust skeletal remains (Peel 2022a,b). As with other Cambrian Lagerstätten, such as the Chengjiang assemblages of China (Hou *et al*. 2017), the Burgess Shale of Canada (Gould 1990; Briggs *et al*. 1994; Conway Morris 1998), the Orsten Lagerstätte of Sweden (Maas *et al*. 2003, 2006) and the Sirius Passet Lagerstätte of North Greenland (Ineson & Peel 2011; Peel & Ineson 2011; Harper *et al*. 2019), the upper Henson Gletscher Formation Lagerstätte makes a significant contribution to our understanding of the early evolution of life through the preservation of exceptional fossils.

The Miaolingian (Wuliuan Stage) fauna of the upper member of the Henson Gletscher Formation in southern Lauge Koch Land and south-western Peary Land is diverse but only taxa with unusual preservation are included in the present study. Agnostids reported by Robison (1984) provide a firm biostratigraphic base, while Clausen & Peel (2012) described the abundant disarticulated echinoderm plates. Rich faunas of stenothecoids and molluscs were described by Peel (2021a) and Peel & Kouchinsky (2022), while rare, unusual, specimens were fully described by Peel (2021b; 2022a,b).

Geological background

The Henson Gletscher Formation in the Peary Land–Lauge Koch Land region of North Greenland (Fig. 1) is a highly fossiliferous unit that accumulated during a lowstand of sea level within a prograding complex of shelf carbonates and siliciclastic sediments referred to the Brønlund Fjord Group (Higgins *et al*. 1991; Ineson & Peel 1997; Geyer & Peel 2011; Peel *et al*. 2016). The formation is composed mainly of dark, recessive, bituminous and cherty limestones, dolostones and mudstones, with a conspicuous middle member of pale fine-grained sandstones (Fig. 2). Thin carbonate debris flows occur sporadically, with one flow forming a prominent bench in the type section in Lauge Koch Land (Figs 1A, 2A) immediately below fossil samples described herein (GGU samples 218831 and 271492). At this locality, the Henson Gletscher Formation is 62

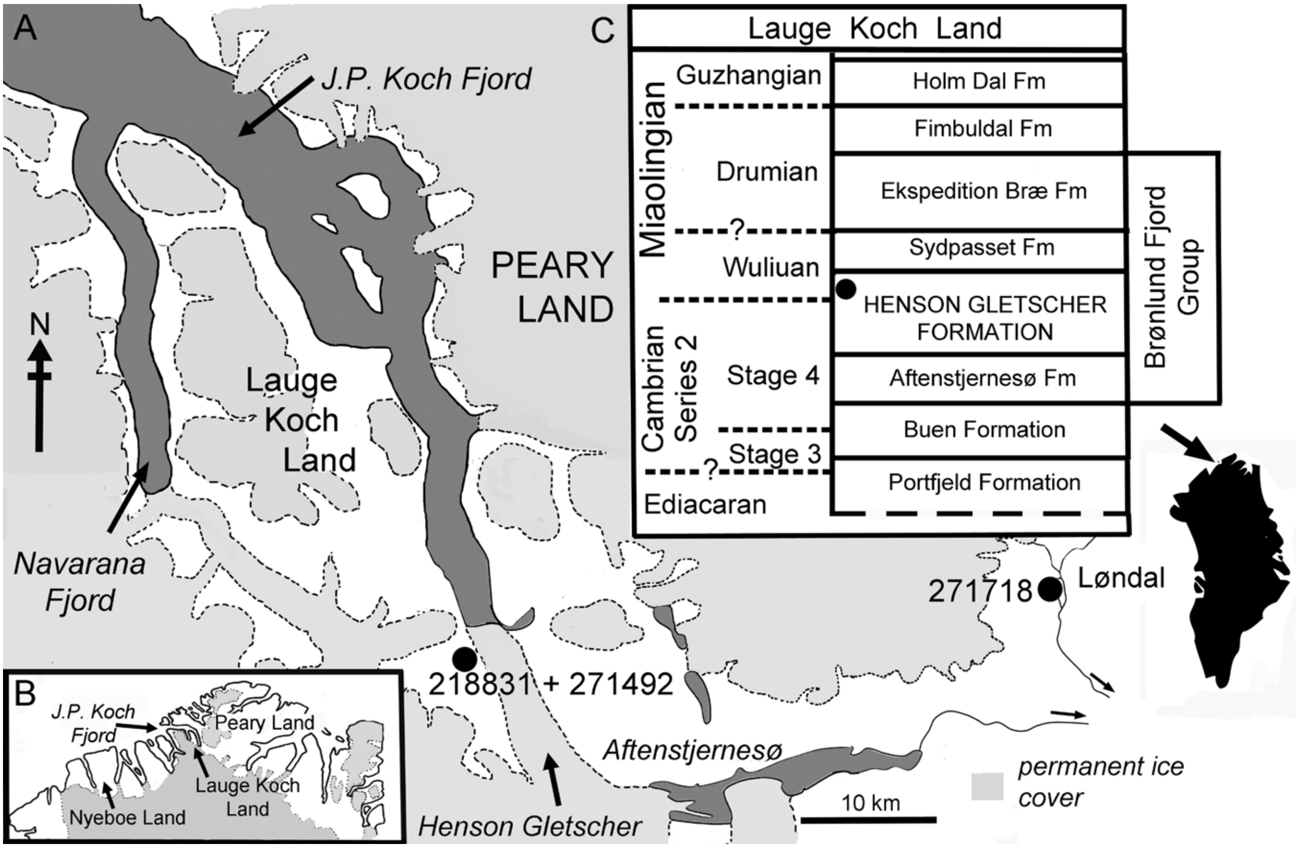


Fig. 1. Geographical and geological information. **A**, collection localities for GGU samples in Lauge Koch Land and Løndal. J.P. Koch Fjord is located by arrow in inset map of Greenland. **B**, North Greenland, with permanent ice cover shaded. **C**, Cambrian stratigraphy in southern Lauge Koch Land and south-western Peary Land. Black dot indicates stratigraphic location of described samples within the upper Henson Gletscher Formation.

m thick (Figs 1.1, 2.1), but it thins to 47 m in Løndal, to the east (Figs 1A, 2B).

Fossil assemblages from the Henson Gletscher Formation in southern Lauge Koch Land and Løndal in south-western Peary Land range from Cambrian Series 2 (Stage 4) to the Miaolingian Series (Wuliuan Stage). However, Drumian strata occur in Nyeboe Land along the northern coast of North Greenland (Robison 1984, 1994; Higgins *et al.* 1991; Babcock 1994; Blaker & Peel 1997; Ineson & Peel 1997; Geyer & Peel 2011; Fig. 1B). All material described here is derived from the *Ptychagnostus gibbus* Biozone. Trilobite faunas from the Henson Gletscher Formation are a mixture of mainly Laurentian polymeroids and agnostoids of value for global correlation (Babcock 1994; Robison 1984, 1994; Blaker & Peel 1997; Geyer & Peel 2011; Peel *et al.* 2016). Amongst polymeroid trilobites that are important for international correlation with Siberia, the Altai Sayan fold belt and South China, an *Ovatoryctocara granulata* assemblage (uppermost Cambrian Stage 4) is of particular note. It occurs in strata just below the presently described Wuliuan material, and establishes strong correlations between Laurentia, Russia and China (Geyer & Peel 2011; Sundberg *et al.* 2016, 2022; Geyer 2019).

Derivation of samples. Samples (Figs 1, 2) were collected during the North Greenland Project (1978–1980), a regional mapping programme of Grønlands Geologiske Undersøgelse (GGU, Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark.

GGU samples 218831 and 271492 were collected from the upper Henson Gletscher Formation at 56.5 m above the base of the formation (thickness 62 m) at its type locality in southern Lauge Koch Land. They derive from bioclastic limestone filling scours in the top of a 1 m thick mass flow deposit (82°10′N, 40°24′W;

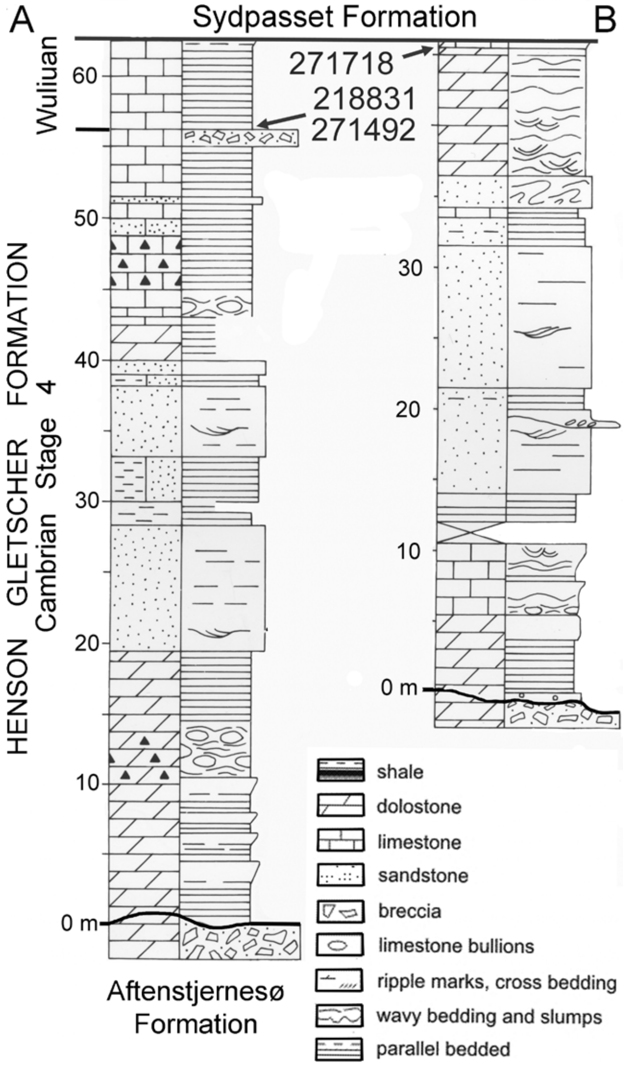


Fig. 2. Stratigraphic sections through the Henson Gletscher Formation showing the derivation of GGU samples. **A,** type section in southern Lauge Koch Land. **B**, Løndal in western Peary Land (modified after Peel & Kouchinsky 2022, based on original section logs by J.R. Ineson).

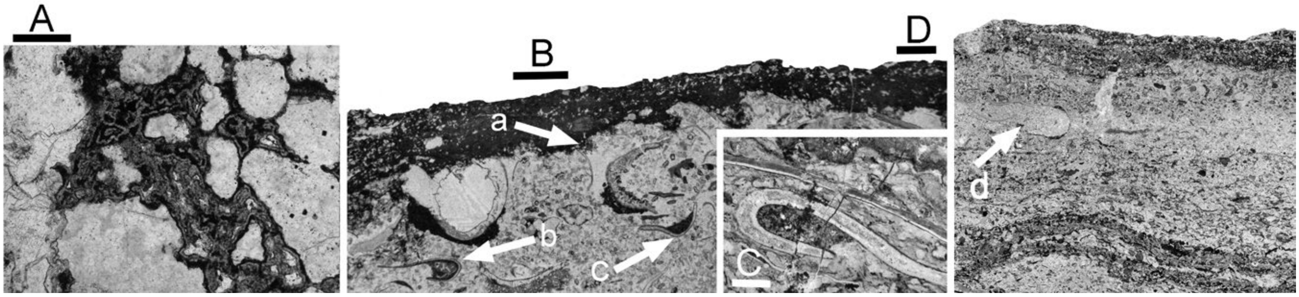


Fig. 3. Thin sections (plane polarised light) of limestone from GGU sample 271718, upper Henson Gletscher Formation, Løndal (Cambrian, Wuliuan Stage). **A**, intergranular phosphatisation of tangled microbial threads. **B**, dark phosphatised limestone forming hard ground overlying eroded limestone surface with truncated bioclasts and microborings (arrow a). Dark phosphatisation within re-deposited trilobite doublure fragment (arrow b) and inverted mollusc clast (arrow c). **C**, detail of fragment of trilobite doublure with dark phosphatisation. **D**, vertical thin section of phosphatised bioclastic limestone showing dark, phosphate-rich horizons and transverse section of helcionelloid (arrow d). Scale bars: 100 μm (A); 200 μm (C); 2 mm (B, D).

Ineson & Peel 1997, fig. 31; Geyer & Peel 2011, fig. 3; Figs 1A, 2A). Peter Frykman collected GGU sample 218831 on 24th June 1979. I collected GGU sample 271492 on 25th June 1978. I collected GGU sample 271718 on 15th July 1978 from a thinbedded, phosphatised, bioclastic, dolomitic limestone occurring about 1 m below the top of the Henson Gletscher Formation on the west side of Løndal (82°18′N, 37°00′W; Clausen & Peel, 2012, fig. 1; Figs 1A, 2B). This limestone contains numerous thin zones of dark phosphatisation (Fig. 3D), some of which formed hard grounds (Fig. 3B). The clastic component is clearly multi-sourced (Fig. 3), with re-deposited calcareous, phosphatised and silicified (Fig. 4B) shells associated with ooliths that were frequently bored and phosphate-covered prior to their final accumulation (Fig. 4K,L). Clots of phosphatised algal filaments may be present both as re-deposited clasts and infillings between grains (Fig. 3A).

Methods. The carbonate rock samples were dissolved in weak acetic acid (10%) and wet sieved into fractions (125 μm and coarser) prior to examination under a binocular microscope. Selected specimens were gold coated prior to scanning electron microscopy. Images were assembled in Adobe Photoshop CS4.

Preservation

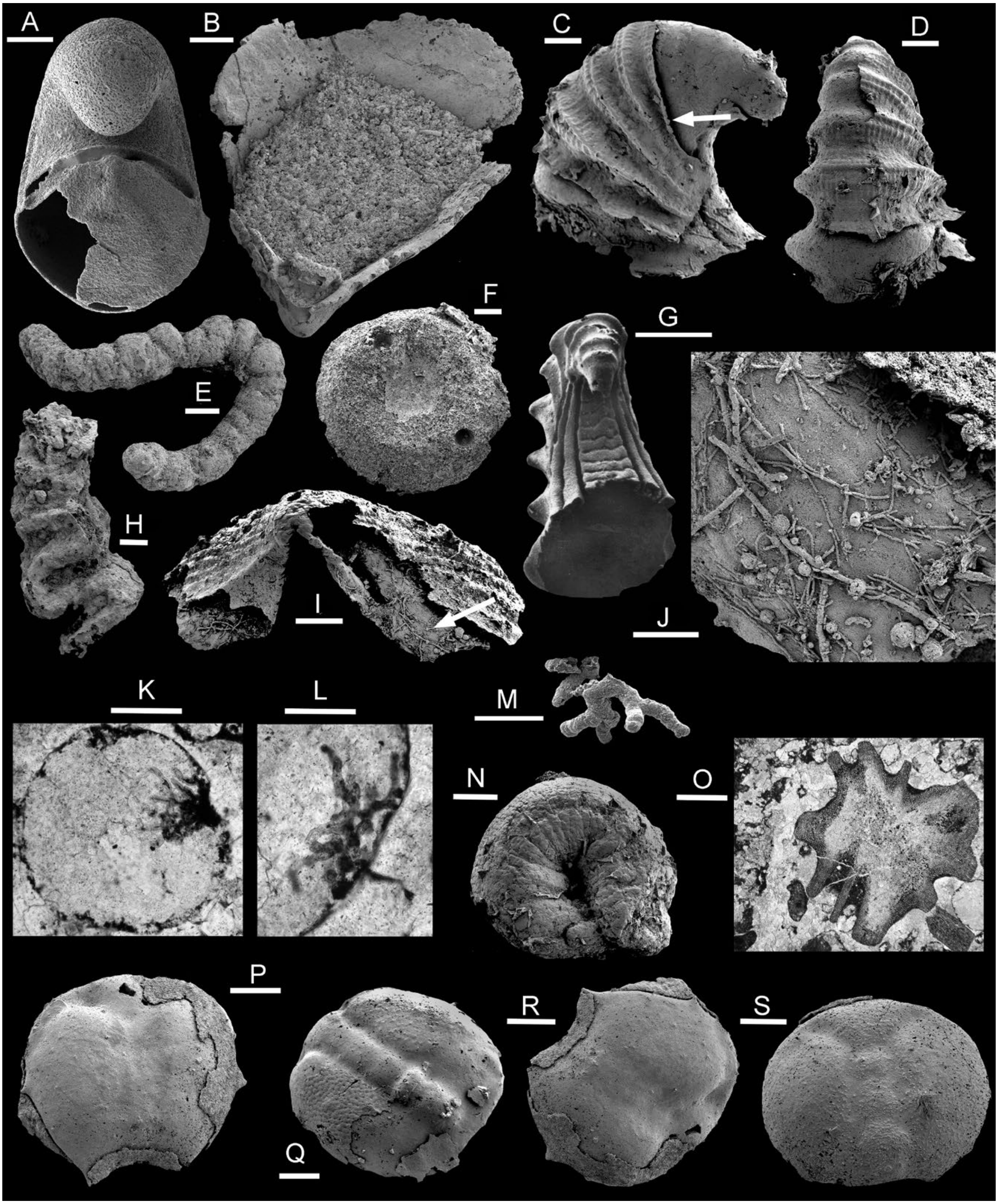
Bedding surfaces in GGU samples 218831 and 271492 are often covered with closely packed, disarticulated, head and tail shields of agnostoids that are associated with less common polymeroid trilobites. Trilobites are much less conspicuous on the phosphatised bedding surfaces of GGU sample 271718, where disarticulated valves of stenothecoids are noticeable. Articulated specimens of any taxa are very rare and, apart from juveniles (Fig. 4P–S), identifiable remains of the originally calcareous trilobite exoskeletons are seldom found in acid residues.

With the exception of linguliformean brachiopods and tubes of *Hyolithellus* Billings, 1871, almost all specimens within the acid residues are diagenetically phosphatised internal moulds of calcareous or organic fossils, encrustations of the shell exterior or a combination of both. The calcareous shells themselves do not survive the treatment with acid but are clearly visible in thin sections of the untreated samples (Fig. 3B–D). A gap (Fig. 4C, arrow) between the internal mould and external phosphatic encrustation reflects the presence of the now dissolved calcareous shell. A few stenothecoids have silicified shells (Fig. 4B), but most are preserved as phosphatised internal moulds (Peel 2021a). Phosphatisation in many internal moulds, such as chancelloriids, hyoliths or the ubiquitous helcionelloid molluscs, is usually confined to the inner parts of the shell cone (Fig. 4G). The shell itself and phosphatised details of its internal structure of the type described by Kouchinsky (1999, 2000a,b) and Vendrasco *et al*. (2010, 2011) are usually not known. Rugae or deep grooves (Fig. 4C,G) on internal moulds of helcionelloid molluscs are not always expressed on the shell exterior, as noted by Runnegar (1985), Skovsted (2004) and Peel & Kouchinsky (2022). While describing molluscs from the upper Henson Gletscher Formation Lagerstätte, Peel & Kouchinsky (2022) noted earlier work (e.g., Runnegar 1985; Vendrasco *et al*. 2010, 2011) describing the replication with great fidelity during phosphatisation of shell structure from the inner surface of the original shell; this may be abundant in helcionelloid and other molluscs from other horizons in the Cambrian of Greenland and elsewhere, although it is infrequent in the present material. Other

▼ **Fig. 4.** Phosphatic preservation within the upper Henson Gletscher Formation (Cambrian, Wuliuan Stage). **A**, *Protowenella flemingi* Runnegar & Jell, 1976, PMU 38329 from GGU sample 218831, phosphatised encrustation of inner shell surface forming an internal mould with operculum in place within aperture. **B**, *Stenothecoides terraglaciei* Peel, 2021a, holotype, PMU 38322 from GGU sample 271718, internal view of silicified ventral valve partly filled by sediment. **C,D**, *Dorispira septentrionalis* Peel & Kouchinsky, 2022, holotype, PMU 39173 from GGU sample 271718, with phosphatised outer surface with ornamentation separated from internal mould by narrow cavity (arrow) in oblique lateral (C) and supra-apical (D) views. **E**, coprolite, MGUH 31218 from GGU sample 271492. **F**, echinoderm holdfast with borings, PMU 39664 from GGU sample 271718. **G**, *Dorispira tippik* Peel & Kouchinsky, 2022, MGUH 19561 from GGU sample 271718, internal mould with channels on the subapical surface equivalent to ridges on the shell interior. The ridges are not expressed on the outer surface of the shell. **H**, cololite, MGUH 31220 from GGU sample 271492. **I,J**, rhynchonelliformean brachiopod, PMU 39665 from GGU sample 271718, with infilled euendoliths (J**,** arrow in I), located on phosphatic encrustation of inner surface of the brachiopod shell. **K**, *Eohyella* sp. penetrating oolith, MGUH 27656 from GGU sample 271718. **L**, *Eohyella* sp. penetrating oolith, GGU sample 271718. **M**, phosphatised mould of *Eohyella* boring, MGUH 27654 from GGU sample 271718. **N**, possible larva, PMU 39666 from GGU sample 271718. **O**, echinoderm plate showing penetration of phosphatisation into the stereome, GGU sample 271718. **P,R,** trilobite protaspid, PMU 39669 from GGU 271492. **Q**, partially exfoliated trilobite protaspid, PMU 39668 from GGU sample 271718. **S**, trilobite protaspid, internal mould, PMU 39670 from GGU sample 271492. Scale bars: 50 μm (A,J); 100 μm (C–E,M,Q–S); 200 μm (F,H,L,N–P), 300 μm (I), 400 μm (K); 500 μm (B,G).

replicated internal structures include muscle attachment scars, various tubercles reflecting pores in the original shell and a widespread pitting of the surface of internal moulds (Vendrasco *et al*. 2010, 2011).

A unique specimen of the widespread *Protowenella* Runnegar & Jell, 1976 is preserved as a thin coating of phosphate on the shell interior, including the in-place operculum (Fig. 4A). Significantly, the morphology of the operculum demonstrates that *Protowenella* is a hyolith rather than a mollusc (Peel 2021b).



When viewed in thin section, the abundant and diverse, disarticulated, echinoderm plates described from GGU sample 271718 by Clausen & Peel (2012) show progressive phosphatisation penetrating into the stereome (Fig. 4O).

Bivalved or pseudo-bivalved arthropods are a conspicuous element of the upper Henson Gletscher Formation Lagerstätte, and display a variety of preservational states of the phosphatised carapaces (Fig. 5). Specimens usually preserve both the left and right shields but are frequently deformed (Fig. 5F,G), possibly following passage of their flexible carapaces through the gut of predators or even moulting (Müller *et al*. 1995). However, it seems unlikely that moulted carapaces would retain conjoined, closed shields. Other specimens more clearly indicate their bromaltic origin due to significant crushing (Fig. 5C) or the forming of fragments into spherical coprolites (Fig. 5E). Wrinkled surfaces often suggest phosphatisation on the inner surface of the carapace integument (Fig. 5H) or inner lamellae. Most forms appear to have been smooth but outer surface ornamentation may be recognisable (Fig. 5A,K). Recognisable details of the carapace interior are rare (see description below), although the presence of forms with acute distal margins (Fig. 5A), interpreted as bradoriids, or the doublure that is generally found in phosphatocopids (Fig. 5B) is noted. Threads of cavity-dwelling organisms (cryptoendoliths) preserved by encrustation with spherulitic phosphate may be conspicuous (Peel & Willman 2022; Fig. 5D).

Many fragments are indeterminable due to heavy coating with phosphate, but rare specimens preserve

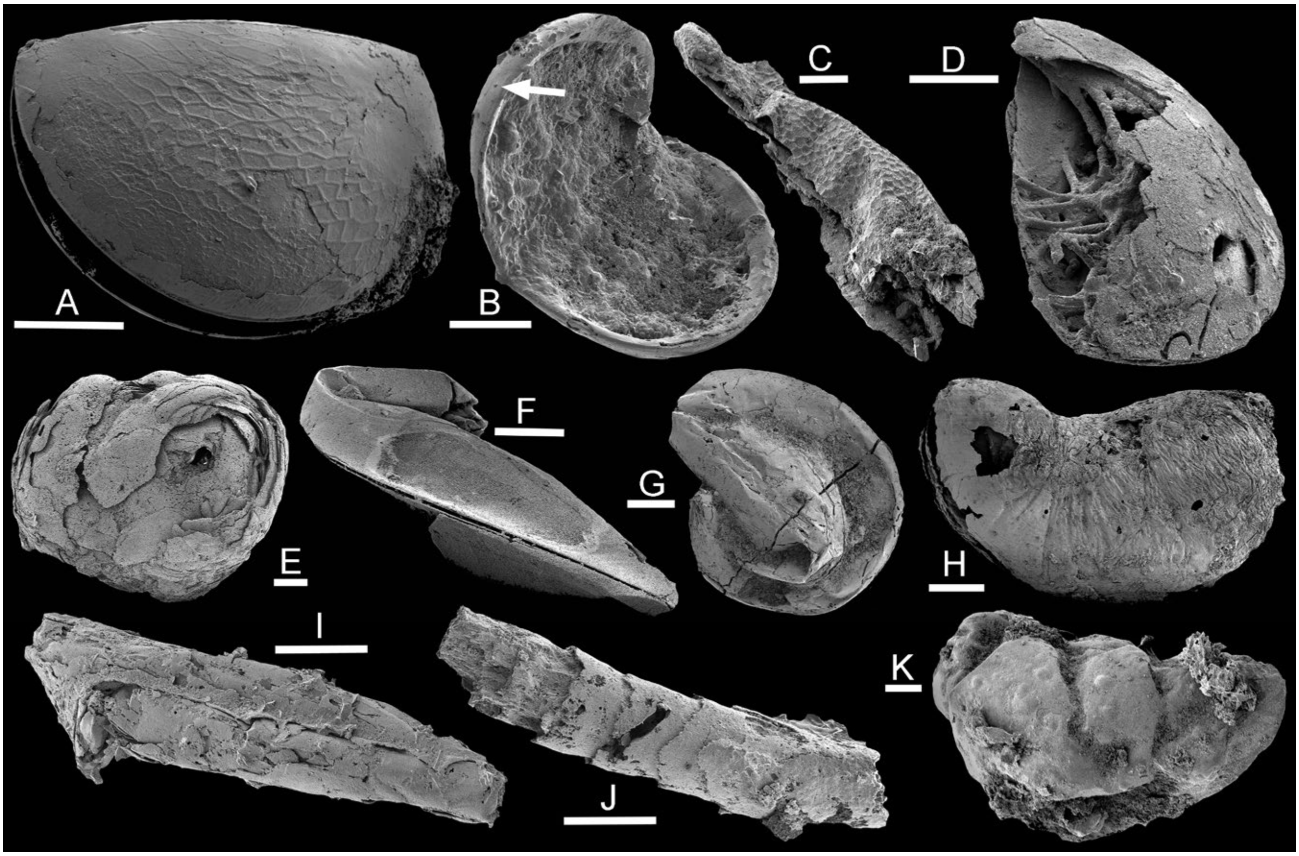


Fig. 5. Preservation of arthropods from the upper Henson Gletscher Formation (Cambrian, Wuliuan Stage). **A**, bradoriid in lateral view, PMU 39671 from GGU sample 218831, showing narrow brim without doublure and partial exfoliatiion of ornamented outer surface. **B**, phosphatocopid, PMU 39672 from GGU sample 271718, with opened valves showing doublure (arrow). **C**, bradoriid, PMU 39673 from GGU sample 271492, crushed by ingestion. **D**, phosphatocopid, PMU 38170 from GGU sample 271492, with thin phosphatic encrustation on outer and inner surfaces and cavity-dwelling endoliths covered by phosphate spherulites. **E**, coprolite composed of phosphatocopid and/or bradoriid fragments, MGUH 31217 from GGU sample 271718. **F,G**, phosphatocopids deformed following ingestion; **F**, PMU 39674 from GGU sample 271492; **G**, PMU 39675 from GGU sample 271492. **H**, bradoriid?, PMU 39676 from GGU sample 271492, lateral view with phosphatic encrustation of wrinkled inner surface of carapace. **I**, fragment of euarthropod abdomen, PMU 39677 from GGU sample 271718. **J**, fragment of euarthropod abdomen with telescopic segments, PMU 39678 from GGU sample 271718. **K**, deformed bradoriid with tuberculate ornamentation, PMU 39679 from GGU sample 271492. Scale bars: 100 μm (A–F, I–K); 200 μm (G,H).

portions of the segmented abdomen of euarthropods. (Fig. 5I,J). One seems to preserve about seven telescopic, slightly conical segments (Fig. 5J) that are similar in shape to those in the abdomen of *Skara annulata* Müller, 1983 from the Cambrian (latest Miaolingian–Furongian) Orsten Lagerstätte of southern Sweden (Müller & Walossek 1985).

Borings by euendolithic organisms are common in GGU sample 271718 from Løndal (Fig. 4F, I–M). They were first observed in the course of routine examination of the present samples in my laboratory in Copenhagen (Larsen 1989) and described subsequently by Stockfors & Peel (2005). In thin section, the bioclasts and ooliths often display a dark coating representing a phosphatised biofilm, which also fills microbial borings penetrating the grains (Fig. 4K,L). In biological nomenclature, forms with branching linear cell series (Fig. 4K,L) and their internal moulds (Fig. 4M) have been referred to *Eohyella* Zhang & Golubic, 1987 (Green *et al*. 1988; Larsen 1989; Stockfors & Peel 2005), but the internal moulds are perhaps better referred to the ichnogenus *Fascichnus* Radtke & Golubic, 2005. Diverse assemblages of euendoliths are preserved as phosphatised internal moulds in some calcareous skeletal elements from GGU sample 271718, such as chancelloriid sclerites and rhynchonelliformean brachiopods (Fig. 4I,J), where phosphate-filled spherical cavities resemble *Planobola macrogota* Schmidt, 1992, as illustrated by Wisshak *et al*. (2008).

Early phosphatisation of soft material is most clearly demonstrated by a varied assemblage of bromalites (Peel 2015, fig. 5), which includes both expelled faecal remains (coprolites; Fig. 4E) and internal fillings of the gut (cololites; Fig. 4H). The zigzag folding of the latter prompted Peel (2015) to suggest derivation from orthothecid hyoliths. Some forms appear to be phosphatised larvae (Fig. 4N) but their interpretation is equivocal. Of greater significance, however, are rare examples of phosphatic replacement of original non-skeletonised tissues, although the quality of replacement does not approach the superlative preservation of many Orsten fossils (Maas *et al*. 2006). These include specimens interpreted by Peel (2022a,b) as the larva of a priapulan cycloneuralian (Fig. 6A,D,E) and a stem-group pentastomid arthropod (Fig. 6B,C?,F). Both discoveries represent the oldest known representatives of animal groups well-known at the present day.

Systematic paleontology

Repositories and institutional abbreviations. The prefix GGU indicates a sample collected by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. MGUH indicates a specimen deposited in the palaeontological type collection of the Natural History Museum of Denmark, Copenhagen. PMU indicates a specimen deposited in the palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden.

This published work and the nomenclatural acts it contains have been registered in ZooBank: http://zoobank.org:pub:24B89910-9F5D-484C-A33E-BFF9153E36C6

Stem-group priapulan (Cycloneuralia)

Remarks. Stem-group priapulan worms have a more diverse record in the Cambrian than the 22 species reported from the present day (Schmidt-Rhaesa 2013; Schmidt-Rhaesa & Freese 2019; Yang *et al.* 2016). A single species was described by Peel (2017) from the Sirius Passet Lagerstätte (Cambrian Series 2, Stage 3) of North Greenland, although other scalidophoran cycloneuralians are well represented in the same assemblage (Conway Morris & Peel 2010; Peel 2010a,b; Peel *et al.* 2013). Isolated phosphatic sclerites of palaeoscolecidan cycloneuralians (*Hadimopanella* Gedik, 1977) may be locally abundant in carbonates of Cambrian Stage 4 in Greenland (Peel & Larsen 1984; Bendix-Almgren & Peel 1988; Peel & Skovsted 2021) but have also been documented in Wuliuan Stage strata from other areas (Streng *et al.*, 2017).

Genus *Inuitiphlaskus* Peel, 2022a

Type species. *Inuitiphlaskus kouchinskyi* Peel, 2022a from the upper Henson Gletscher Formation of Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Inuitiphlaskus kouchinskyi Peel, 2022a

Fig. 6A,D,E

2022a *Inuitiphlaskus kouchinskyi* Peel, p. 448, fig. 3I–J.

Holotype. PMU 28893 from GGU sample 271492, Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage (Peel 2022a).

Remarks. This unique flask-shaped specimen was compared by Peel (2022a) to the hatching larvae of the extant crown-group priapulans *Priapulus caudatus* Lamarck, 1816 and *Halicryptus spinulosus* Siebold, 1849, as described by Wennberg *et al*. (2009) and Janssen *et al*. (2009), respectively, from seas around Sweden. With a preserved length of about 1250 μm and a width of about 400 μm, it is about five times wider than the larvae of the living forms (Peel 2022a). The hatching larva precedes the development of a plated lorica in juvenile priapulids. While the larva of *Inuitiphlaskus kouchinskyi* has been affected by longitudinal wrinkling, evidence of a plated lorica is lacking. As in *Priapulus caudatus* and *Halicryptus spinulosus*, a plated lorica likely was developed in a later growth stage. An anterior introvert with scalids is not observed in the Greenland specimen and was considered to have been withdrawn.

Smooth, rather featureless phosphatised spheres with a diameter of about 400 μm occur together with *Inuitiphlaskus kouchinskyi* and may represent its eggs. Such spheres are generally referred to *Olivooides* Qian, 1977, usually interpreted as a cnidarian (Dong *et al.* 2016), or *Markuelia* Val'kov, 1983, which is considered to be a scalidophoran (Dong *et al.* 2010, 2022; Duan *et al*. 2012). The early ontogenetic development of *Markuelia* is well known (Dong *et al.* 2010) and the numerous transverse annulations of the vermiform trunk, directly developed from the egg but without an intermediate flask-shaped larval stage, readily distinguish it from *Inuitiphlaskus kouchinskyi*.

While the limited morphological information currently available concerning *Inuitiphlaskus kouchinskyi* contributes little to elucidating the overall phylogeny

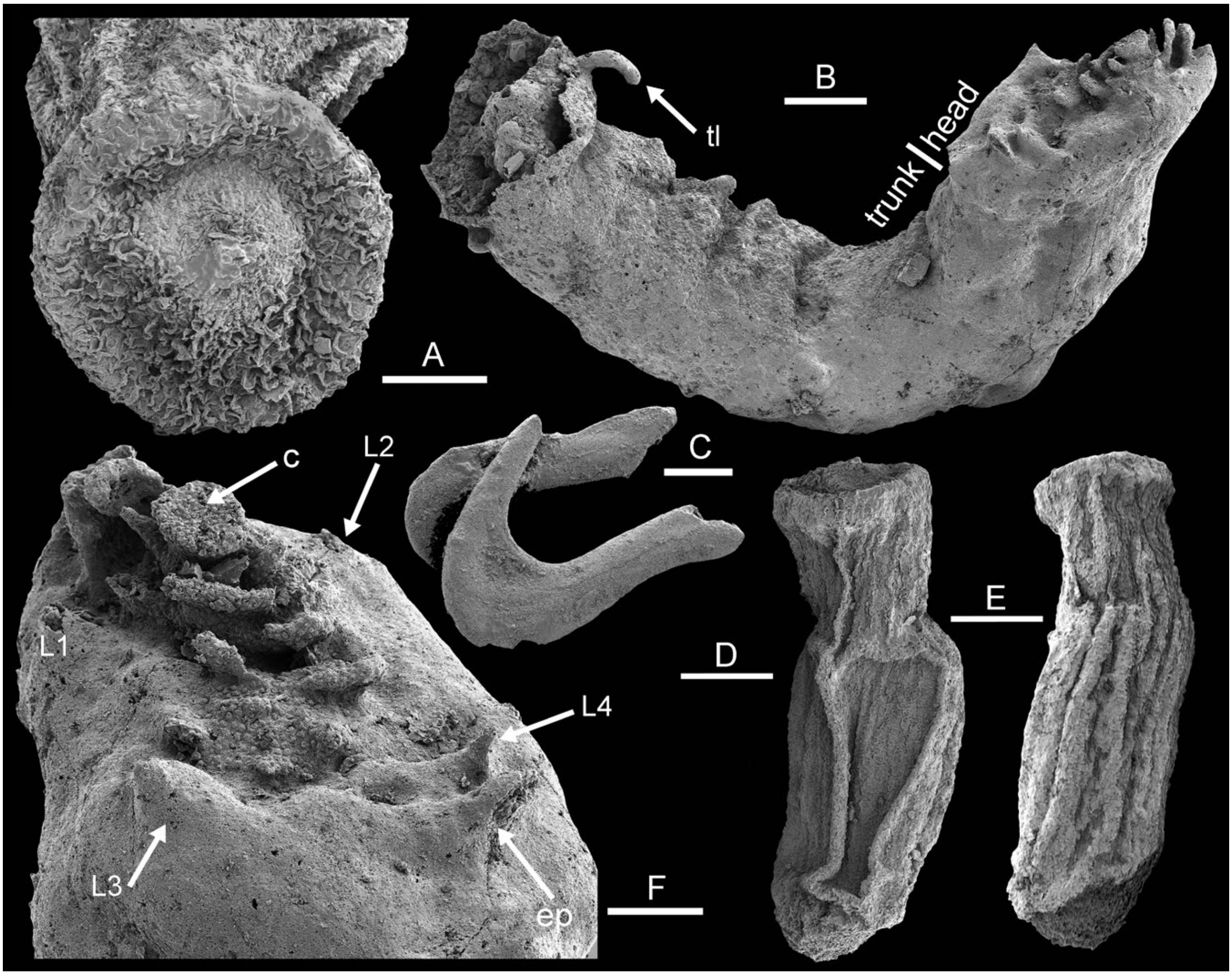


Fig. 6. Phosphatised, non-skeletonised fossils from the upper Henson Gletscher Formation (Cambrian, Wuliuan Stage). **A,D,E,** *Inuitiphlaskus kouchinskyi* Peel, 2022a, PMU 28893 from GGU sample 271492, holotype, southern Lauge Koch Land, anterior (A) and lateral (D,E) views. **B,F,C?,** *Dietericambria hensonensis* Peel, 2022b. **B**,**F**, PMU 39167 from GGU sample 271492, holotype, southern Lauge Koch Land, in lateral view (B) and detail of the undersurface of the head (F); cd, central disc; ep, posterior flangelike extension; L1–L4, cephalic limbs ; tl, trunk limb. **C**, PMU 36170 from GGU 218831, southern Lauge Koch Land, conjoined pair of opposing hooks resembling eupentastomid cephalic hooks. Scale bars: 50 μm (F); 100 μm (A–C); 200 μm (D,E).

of priapulans and cycloneuralians in general, the hatching larva of *Inuitiphlaskus kouchinskyi* indicates a developmental stage in priapulan evolution that has persisted for more than 500 Ma from the middle Cambrian until the present day.

Phylum Arthropoda Siebold, 1848

Stem-group pentastomid

Present day pentastomids (tongue worms) are parasitic arthropods generally regarded as crustaceans or as early offshoots of arthropods (Castellani *et al*. 2011; Haug *et al*. 2021).

Genus *Dietericambria* Peel, 2022b

Type species. *Dietericambria hensonensis* Peel, 2022b from the upper Henson Gletscher Formation of North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage (Peel 2022b).

Remarks. *Dietericambria* was described by Peel (2022b) from the Henson Gletscher Formation Lagerstätte (Wuliuan Stage) and interpreted as the oldest known stem-group pentastomid. It is some 15 my older than specimens from the Orsten Lagerstätten (Furongian) of southern Sweden (Waloszek & Müller 1994; Waloszek *et al*. 2006; Castellani *et al*. 2011) and Newfoundland (Waloszek *et al*. 1994). *Dietericambria* is readily distinguished from described Cambrian stem-group pentastomids by its narrow oval head (Fig. 6F) with a complex of steeply inclined flanges in the median axial region, minute cephalic limbs (L1–L4 in Fig. 6F), greater number of trunk segments and extended posterior section.

Present day pentastomids are vermiform arthropods that live mainly as parasites within tetrapods, but also some fishes and insects, and attach to their hosts with two pairs of hooked grasping limbs. There is no direct evidence that Cambrian stem-group pentastomids were parasites, although such a mode of life was supported by De Baets *et al*. (2021).

Dietericambria hensonensis Peel, 2022b

Fig. 6B,F,?C

2022b *Dietericambria hensonensis* Peel, p. 100–102, figs 3, 4A–C,E,G,H.

Holotype. PMU 39167 from GGU sample 271492, Henson Gletscher Formation, Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage (Peel 2022b).

Remarks. In addition to the holotype (Fig. 6B,F) and fragments of two additional specimens from GGU sample 271718 (Peel, 2022b), a pair of conjoined hooks interpreted as possible cephalic grasping hooks (Fig. 6C) was figured by Peel (2022b, fig. 4D,F) from GGU sample 218831. Two pairs of sclerotised grasping hooks are known from present day pentastomids but have not been recorded from the fossil record. However, Waloszek & Müller (1994) and Castellani *et al*. (2011) considered the distal part of the segmented cephalic limbs in described Cambrian stem-group pentastomids to be a finger-like claw with a similar function. Morphologically similar hooks to the Greenland fossil occurrence were described in the extant *Raillietiella* Sambon, 1910 by Kelehear *et al*. (2011), see also Peel (2022b, fig. 5). In addition to the hooks, males of *Raillietiella* develop a pair of copulatory spicules (Kelehear *et al*. 2011, fig. 4c; Peel 2022b, fig. 5C). Peel (2022b, fig. 4I–K) speculated that rare, morphologically similar spicules from GGU sample 271492 may have had the same function, but firm evidence of association is lacking.

Bivalved arthropods

Order Bradoriida Raymond, 1935

?Bradoriida sp. indet.

Fig. 7N–P

Figured material. PMU 39690 from GGU sample 218831, southern Lauge Koch Land. Upper Henson Gletscher Formation, Cambrian, Wuliuan Stage.

Discussion. This elongate internal mould has a subcircular cross-section, the diameter of which is about 45% of the length. The dorsal surface is shallowly concave between bluntly rounded terminations and appears to lack any longitudinal hinge or fold. The ventral surface carries a longitudinal shallow median groove (Fig. 7O) that extends around both terminations. The surface of the lateral areas is covered by slightly irregular fine transverse (radial) wrinkles that terminate at a narrow zone of longitudinal (comarginal) wrinkles of similar magnitude at the base of the median groove (Fig. 7P).

The outer surface of the specimen is formed by a thin phosphatic layer interpreted as an internal mould of the integument. The median ventral groove thus represents a ridge on the inner surface of this integument interpreted as the line of junction between opposing lateral shields; there is no indication of an inner doublure. The lack of a longitudinal median ridge or groove on the dorsal surface indicates that the carapace was univalve, an interpretation supported by a thin phosphatic encrustation (Fig. 7N, arrow) that appears to cross the median line without disruption.

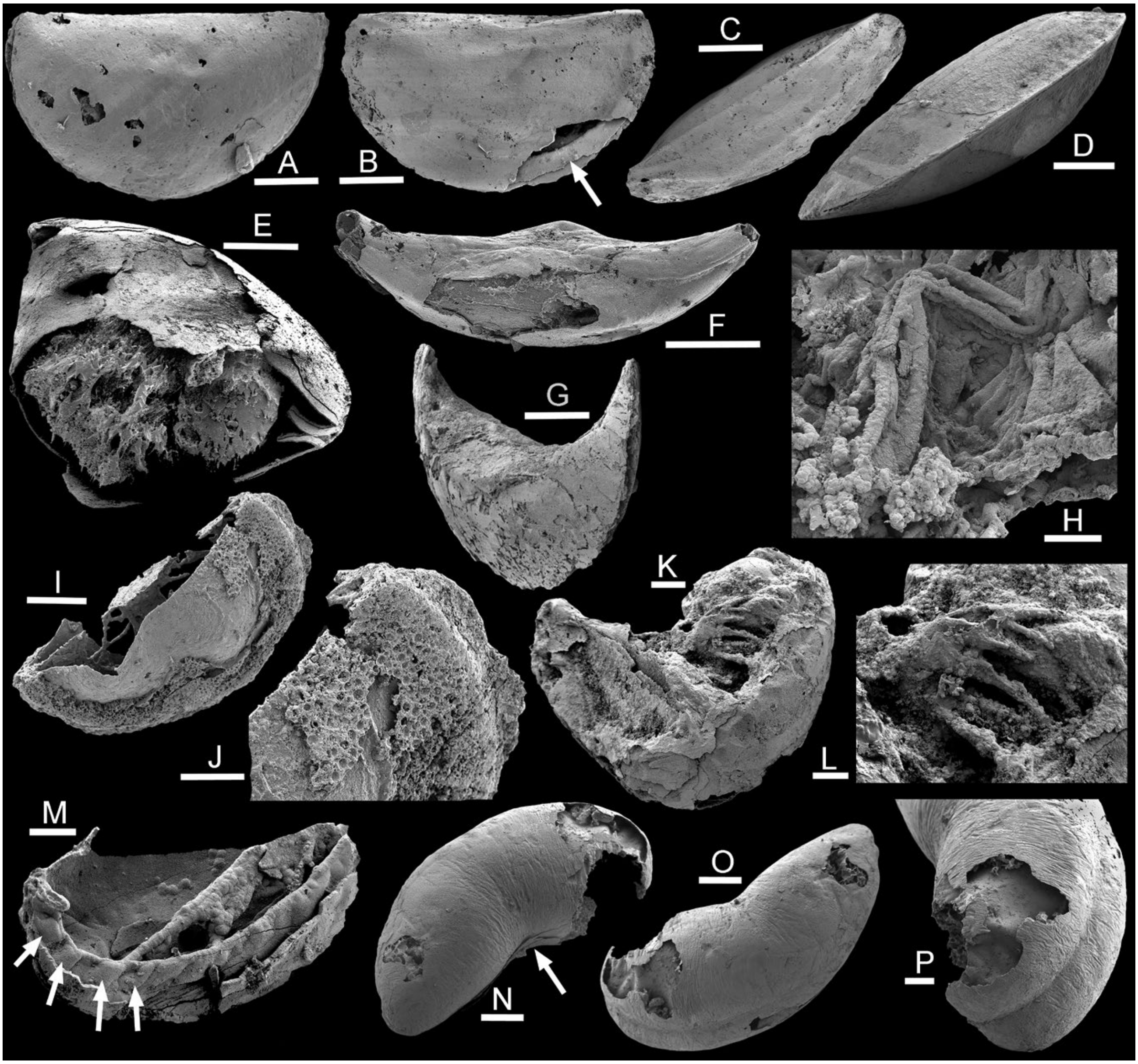


Fig. 7. Arthropods from the upper Henson Gletscher Formation (Cambrian, Wuliuan Stage). **A–E**, *Dabashanella* cf. *retroswinga* Huo, Shu & Fu, 1983 *in* Huo *et al*., 1983 from GGU sample 271492, southern Lauge Koch Land. **A**, PMU 39680, lateral view. **B,C**, PMU 39681, lateral view showing doublure (arrow in B) and oblique dorsal view showing median ridge (C). **D**, PMU 39682, ventral margin. **E**, PMU 39683, broken specimen showing blunt terminal spine, doublure and indeterminate internal phosphatised mass. **F,G**, Phosphatocopida spp. indet. **F**, PMU 39684 from GGU sample 271718, oblique dorso-lateral view. **G**, PMU 39685 from GGU sample 271492, oblique dorso-lateral view. **H,K–M**, internal structures, GGU sample 271492. **H**, phosphatised limb? PMU 39686. **K,L**, PMU 39687, phosphate encrustation of setae? **M**, PMU 39688 from GGU sample 271492, attachment of limbs on carapace interior. **I,J**, acritarch cluster within a phosphatised mass on the surface of *Dubashanella*, PMU 39689 from GGU sample 271492. **N–P**, ?Bradoriida sp. indet., PMU 39690 from GGU sample 218831, phosphate encrustation on the interior surface of the carapace. Arrow in N indicates phosphatic lamellae on the exterior of the integument that cross the mid-dorsal line without interuption. Scale bars: 50 *μ*m (H,J,L); 100 *μ*m (D–G,I,K,M.P); 200 *μ*m (A–C,N,O).

A smooth, wrinkled, inner surface visible through a hole in the outer surface is interpreted as a phosphatised inner lamella.

The lack of a doublure promotes interpretation as a bradoriid rather than a phosphatocopid, but even this is speculative; it may represent an early developmental stage of another arthropodan group. Numerous other specimens in all samples appear (e.g. Fig. 5H) to be deformed specimens of the same taxon or similar taxa.

Order Phosphatocopida (=Phosphatocopa) Müller, 1982

Suborder Dabashanellina Shu, 1990a

Family Dabashanellidae Zhao, 1989

Discussion. Schram & Koenemann (2021) assigned authorship of Suborder Dabashanellina to Hinz-Schallreuter & Schallreuter (2009a) but these authors did not propose or define such taxa. However, Hinz-Schallreuter & Schallreuter (2009b, p. 47) referred to Suborder Dabashanellina Shu, 1990a,b. Order Dabashanellida was proposed by Melnikova *in* Melnikova & Mambetov, 1990 and recognised as a taxon equivalent in rank to the Order Bradoriida Raymond, 1935, within Superorder Bradoriamorphes Kozur, 1972. Thus, Phosphatocopida contains both univalved (Dabashanellina) and bivalved taxa, the latter described in detail by Maas *et al.* (2003), although the hinge area of dabashanellids was sufficiently flexible to permit closure of the carapace (Fig. 7D).

Genus *Dabashanella* Huo, Shu & Fu *in* Huo *et al.*, 1983

Type species. *Dabashanella hemicyclica* Huo, Shu, & Fu *in* Huo *et al.*, 1983, Cambrian Stage 3, China.

Discussion. Zhang (1987) distinguished *Phaseolella* Zhang, 1987 from *Dabashanella* Huo, Shu & Fu *in* Huo *et al.*, 1983 by its univalve carapace and prominent duplicature (=doublure). He commented that a hinge was present in *Dabashanella*, which was therefore bivalved, but that it also lacked a doublure. Melnikova & Mambetov (1990) considered *Phaseolella* to be a junior synonym of *Dabashanella*, but presented no evaluation of the supposed difference in doublure. The synonymy has been accepted by later authors who have described a well-developed doublure in *Dabashanella* (Hou *et al.* 2002; Zhang & Pratt 2012; Zhang 2022). Hou *et al.* (2002) provided a detailed review of other published material, often deformed, that can be referred to *Dabashanella*.

Dabashanella cf. *retroswinga* Huo, Shu & Fu, 1983 *in* Huo *et al.*, 1983

Fig. 7A–E

Figured specimens. PMU 39680–39683 from GGU sample 271492, upper Henson Gletscher Formation, southern Lauge Koch Land, Cambrian, Wuliuan Stage.

Description. The carapace is amplete, or nearly so, but with slight relative variation in the anterior and posterior angles; height almost two thirds of length. Terminal spines are absent or obscure, blunt and upturned (Fig. 7E). The hinge line is straight, with a median ridge that may become more strongly expressed towards the extremities (Fig. 7C). The doublure is well-developed on the interior (Fig. 7B,E) and its inner margin may be reflected by a broad groove, or flattened peripheral zone on the exterior. The outer surface is smooth and often glossy; it is sometimes textured with very fine, elongate wrinkles and comarginal striations.

Discussion. *Dabashanella* is common in all samples, but the majority of specimens are deformed. Deformation often produces irregular folds sub-parallel to the hinge in the dorsal area (Fig. 7C) or causes the formation of a concave dorsal surface. While a hinge delimiting two separate lateral shields is not present, the narrow dorsal ridge clearly acted as a flexible hinge, as readily indicated by the general preservation of the narrow carapace, with continuous contact of the left and right lateral shields around the margin (Fig. 7D). The doublure on each shield (Fig. 7E) is similar to that preserved in *Dabashanella retroswinga* Huo, Shu & Fu, 1983 *in* Huo *et al.*, 1983 (Huo *et al.* 1991, pl. 38, fig. 9). Proportions of the Greenland specimens are similar to material from the Heilinpu Formation (Cambrian Stage 3), Yongshan, Yunnan Province, China, illustrated by Zhang & Pratt (2012), although anterior and posterior spines in the latter are better preserved. The material was referred to the type species *Dabashanella hemicyclica* by Zhang (2022) who described five species of *Dubashanella* from the Shuijingtuo Formation (Cambrian Stage 3) of western Hubei Province, south China. However, specimens of the type species illustrated by Zhang (2022) and Huo *et al.* (1991) are proportionately taller, although studies by Zhang (1987) re-illustrated by Huo *et al.* (1991) indicate considerable morphological variation in the morphology of *Dabashanella* during ontogeny. Material from the early Cambrian of Antarctica, referred to ?*Dabashanella* sp. by Wrona (2009), has a narrow brim, but no doublure.

Peel *et al.* (2016) referred rare amplete specimens from the Henson Gletscher Formation (Cambrian Stage 4) in Løndal to *Pseudindiana* cf. *sipa* (Flemming, 1973), which Hou *et al*. (2002) had referred to *Dabashanella*. While the carapace has a similar amplete form, a doublure is absent in the Greenland specimen, as are the terminal spines usually characteristic of *Dabashanella*.

Phosphatocopida spp. indet.

Fig. 7F,G

Figured material. PMU 39684 from GGU sample 271718, Løndal. PMU 39685 from GGU sample 271492, southern Lauge Koch Land. Upper Henson Gletscher Formation, Cambrian, Wuliuan Stage.

Discussion. Development of concave curvature of the dorsal surface between the anterior and posterior extremities is a common deformational feature in phosphatocopids from the upper Henson Gletscher Formation (Fig. 5G) and elsewhere (Hou *et al.* 2002). However, rare, elongate specimens show strongly upturned terminations without apparent deformation (Fig. 7F,G). One specimen shows broad lobes developed high on each dorso-lateral surface, at the median line (Fig. 7F). In a second specimen, the pointed anterior and posterior terminations are curved almost perpendicular to the dorsal line (Fig. 7G). *Dabashanella curvata* (Zhang, 1987) from the early Cambrian Shuigoukou Formation of Xichuan, Henan Province, China, has an elongate, curved carapace but lacks the strong tapering of the terminations seen in both the illustrated Greenland specimens.

Bradoriid/phosphatocopid internal structures

Fig. 7H,K–M, 8A–F

Figured specimens. PMU 39686–39688, PMU 39691, all from GGU sample 271492, southern Lauge Koch Land; PMU 39667, PMU 39692 and PMU 39693 from GGU sample 271718, Løndal. Upper Henson Gletscher Formation, Cambrian, Wuliuan Stage.

Discussion. In many deformed specimens, the outer phosphatised coating is broken away or incomplete to reveal internal structures. Taxonomic determination, for example as bradoriid or phosphatocopid, is usually impossible. Internal phosphatised masses are heavily encrusted, generally lacking recognisable form (Fig. 7E), although in this case the doublure indicates phosphatocopid affinty. Other specimens appear to lack a doublure, suggesting that they may have been bradoriids (Fig. 8B). In this respect, the material contrasts markedly with the exceptionally preserved structures visible in many Orsten Lagerstätte arthropods (Müller 1979, 1982; Müller & Walossek 1985; Walossek 1993; Maas *et al*. 2003, 2006).

Rare structures appear to be fans of setae associated with limbs (Fig. 7K,L), while others can be interpreted as possible limbs (Fig. 7H). Short, broad ridges (arrows in Fig 7M) may be impressions of the basal portion of limbs moulded against the inner surface of the carapace. The outer surface layer in the lower part of this figure is encrusting phosphate, while the central cavity in the specimen is crossed by a bundle of endolithic threads covered in spheroidal phosphate.

Sheets of phosphatic mineralisation that appear to represent phosphatised inner lamellae are commonly present and often covered with bundles of rounded ridges (Fig. 8A–C). These ridges are tubular but are covered to varying degrees by thin layers of phosphate that obscure details of the surface, for example indications of segmentation, possibly as a result of the detached inner lamellae draping underlying (inner) setae. Some ridges seem to result just from wrinkling of the lamellae. Other specimens display a mass of thin fragments of phosphate sheets and spheroidal encrustations presumably deposited on the integument of inner elements and subsequently fractured (Fig. 8E, possible limb, arrow a; arrow b locates branching seta shown in Fig. 8F).

Bivalved arthropod sp. indet.

Fig. 8G–L

Figured material. PMU 39694 from GGU sample 271718, Løndal; PMU 39695 and PMU 39696 from GGU sample 271492, Lauge Koch Land. Upper Henson Gletscher Formation, Cambrian, Wuliuan Stage.

Description. A short, robust abdomen extends from between the postero-lateral margins of the carapace (Fig. 8G,H), which is truncated posteriorly (Fig. 8I). Wrinkling in the encrusting phosphate in one specimen may suggest the original segmentation in the abdomen that, as preserved, expands at its distal termination. Thin sheets of encrusting phosphate wrap around the ventral margins of the carapace (Fig. 8H, arrow), suggesting that a doublure was not present. The abdominal area is occupied by numerous irregular sheets of encrusting phosphate, some of which were deposited on the inside and outside of the integument, as is the case with the carapace (Fig. 8G, arrow a). Other deformed phosphate sheets are tenuously interpreted as possibly representing the intestinal tract (Fig. 8G, arrow b). A V-shaped structure may represent the basipod of a limb (Fig. 8G, arrow c).

A second specimen is interpreted as a phosphate impression of a wrinkled internal lamella (Fig. 8I,J). A fragment of the segmented abdomen extends beyond the truncated carapace margin, the postero-ventral margin of which is pointed (Fig. 8I, arrow). The anterior margin displays a gape between the lateral shields of the carapace but it is uncertain if a true hinge zone is present.

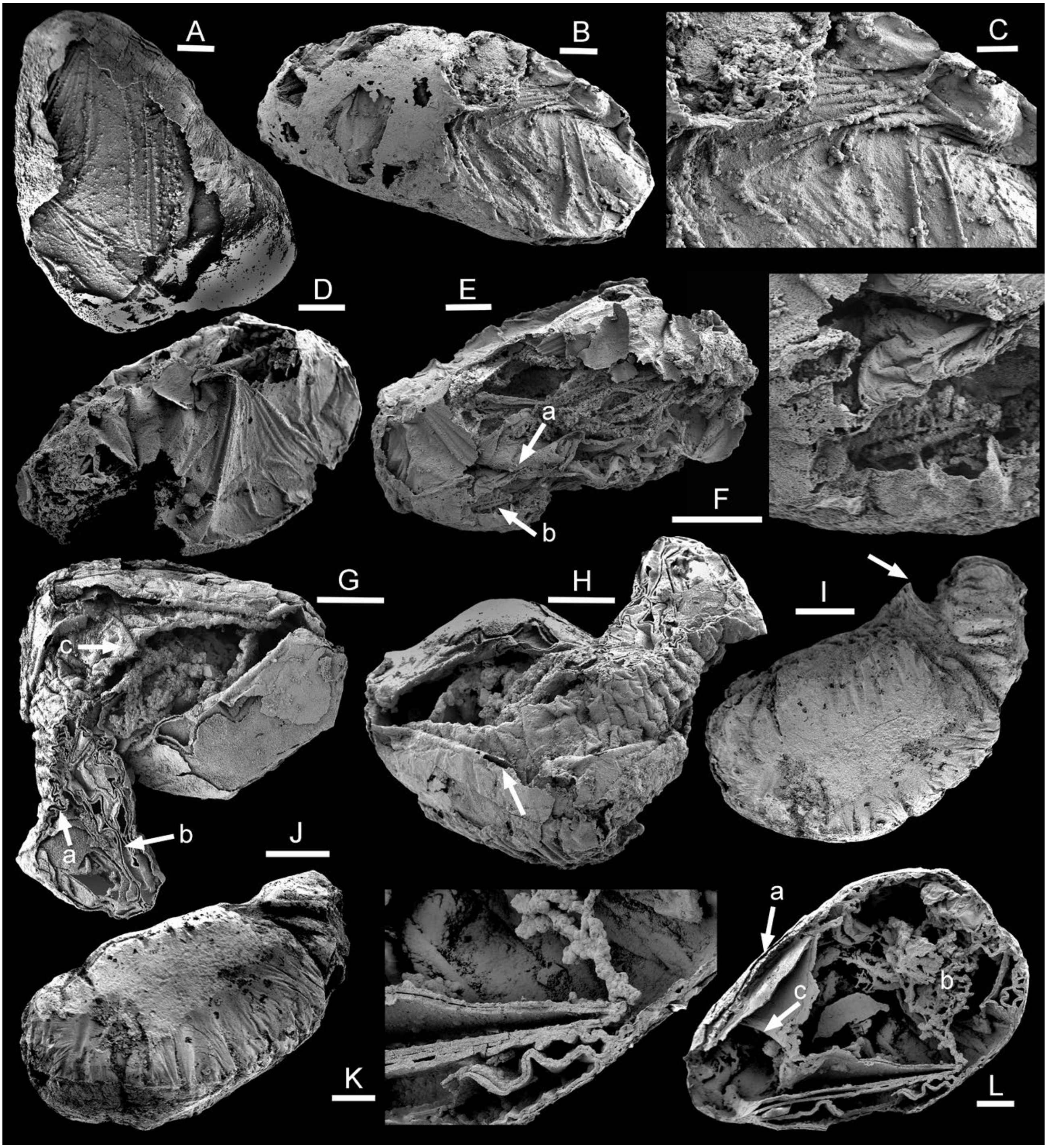


Fig. 8. Arthropods from the upper Henson Gletscher Formation (Cambrian, Wuliuan Stage). **A–F**, bradoriid/phosphatocopid internal structures. **A**, PMU 39691 from GGU sample 271492, southern Lauge Koch Land. **B,C**, PMU 39692 from GGU sample 271718, Løndal. **D,** PMU 39667 (271718-XX) from GGU sample 271718. **E,F**, PMU 39693 from GGU sample 271718, Løndal. **G–L,** bivalved arthropod sp. indet. **G–H**, PMU 39694 from GGU sample 271718, Løndal. **I,J**, PMU 39695 from GGU sample 271492, Lauge Koch Land. **K,L**, PMU 39696 from GGU sample 271492, Lauge Koch Land. Explanation of arrows is given in the text. Scale bars: 50 μm (C,F,K); 100 μm (A,B,D,E,G,H,L); 200 μm (I,J).

A third specimen is broken along a horizontal plane, perpendicular to the axial plane (Fig. 8L, the upper surface represents the right shield; the lower surface represents the left shield, both viewed ventrally). The integument is delimited by encrusting phosphatisation on its inner and outer surfaces (Fig. 8L, arrow a). The anterior part of the carapace is occupied by an irregular network of threads covered by spheroidal phosphate, probably representing postmortal endolithic threads (Fig. 8L, b). Posteriorly, phosphatisation has preserved an internal organic lamella that originates at the junction between the abdomen (which is missing in the specimen) and the carapace before extending anteriorly along the lateral areas of the latter. At about mid-length of the carapace, the lamella curves abruptly back towards the posterior, delimiting a funnel-shaped structure that terminates with a smooth margin (Fig. 8L, arrow c) just anterior to the abdomen.

Phylum uncertain
Class Hyolitha Marek, 1963

Order Orthothecida Marek, 1966

Family Protowenellidae Peel, 2021b

Genus *Protowenella* Runnegar & Jell, 1976

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

Protowenella flemingi Runnegar & Jell, 1976

Fig. 4A

1976	*Protowenella flemingi* Runnegar & Jell, p. 133, fig. 6B–K.
2021	*Protowenella flemingi*; Li *et al*., p. 556, fig. 25a–j.
2021b	*Protowenella flemingi*; Peel, figs 3,4.
2022	*Protowenella flemingi*; Peel & Kouchinsky, p. 76, fig. 5A–D.

Figured material. PMU 38329 from GGU sample 218831, Henson Gletscher Formation, Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage (Peel 2022c).

Remarks. Almost all of the more than 100 specimens of *Protowenella flemingi* from GGU samples 218831, 271492 and 271718 are preserved as robust phosphatic internal moulds, as is also the case with other records of the widespread genus (Runnegar & Jell, 1976; MacKinnon, 1985; Peel 1991a,b; Brock, 1998; Gubanov *et al*., 2004; Wotte, 2006; Parkhaev, 2008, 2017; Claybourn *et al*., 2019; Kouchinsky *et al*., 2022). In contrast, an exceptional specimen of *Protowenella flemingi* described by Peel (2021b; Fig. 4A) from GGU sample 218831 is preserved just as a very thin phosphatic layer deposited on the inner surface of the shell. The specimen is unique in preserving an impression of the inner surface of the operculum in place within the mouth of the coiled shell, demonstrating that *Protowenella* is an orthothecid hyolith and not a mollusc, as previously widely supposed (Peel, 2021b; Peel & Kouchinsky, 2022). As with other hyoliths, the operculum is bilaterally symmetrical. Clavicles and the cardinal processes are preserved as deep pits along the adumbilical margin, confirming the interpretation as an orthothecid hyolith (Peel 2021b; Fig. 4A). Subsequently, a similar operculate specimen was recorded by Kouchinsky *et al*. (2022) in *Michniakia minuta* Missarzhevsky *in* Rozanov & Missarzhevsky, 1966 from the Erkeket Formation (Cambrian Stage 4, Botoman Regional Stage) of Siberia.

Problematica

Genus *Cambrocoryne* gen. nov.

Type species. *Cambrocoryne lagenamorpha* gen. et sp. nov. from the upper Henson Gletscher Formation of North Greenland, Cambrian, Wuliuan Stage.

Derivation of name. A combination of Cambrian and the Greek *koryne*, meaning club or mace; feminine.

Diagnosis. Elongate, club-shaped with basal stalk, coarse longitudinal, bifurcating ridges and concave interspaces draped by a thick (now phosphatised) mineralised layer with finely striated, smooth outer surface.

Description. Mono-specific, as for the type species.

Cambrocoryne lagenamorpha gen. et sp. nov.

Fig. 9

Holotype. PMU 39697 from GGU sample 271718, Løndal; upper Henson Gletscher Formation, Cambrian, Wuliuan Stage.

Other figured material. PMU 39699, paratype, and PMU 39698 from GGU sample 271718, Løndal, upper Henson Gletscher Formation.

Derivation of name. From the fancied similarity in overall shape to the foraminiferan *Lagena* Walker & Jacob, 1798 *in* Kanmacher 1798.

Description. Club-shaped, elongate, with a maximum observed length of about 700 μm and maximum width about 40% of length. Increasing in width from the (presumed) basal shaft to attain maximum width at about mid-length, then narrowing towards the distal surface. Outer surface of holotype (Fig. 9A–D) and paratype (Fig. 9H) carrying prominent longitudinal ridges, which may branch distally and are separated by concave interspaces.

The three available specimens show two contrasting preservational states, which may cast some doubt on their proposed assignment to the same taxon. In the holotype, the core with acute longitudinal ridges and separating U-shaped channels is draped by a thick outer layer (Fig. 9C, arrow), which is finely textured with longitudinal strations (Fig. 9B,H,I). A second specimen displays acute, blade-like ridges and concave interspaces but lacks the thick outer covering (Fig. 9F,G). A flaky texture of thin phosphate layers and cross-partitions in this specimen indicates a complex diagenetic history, seemingly with phosphatisation penetrating between presumably calcareous grains that were dissolved during acid preparation. Comparable patterns of the prominent longitudinal ridges are present on the basal stalk of both preservational variants. A detail of the distal filling to one of the interspaces (Fig. 9E, located by arrow in B) displays a concentric structure. The narrow gap between the draping outer layer and the core indicates dissolution of a thin shell layer or integument (Fig. 9C, arrow).

The smooth, but fine texturing of the outer surface suggests that this is an original surface that has been replaced by phosphatisation, rather than the result of phosphatic encrustation of a pre-existing surface. The concentric stucture (Fig. 9E) suggests sequential accretion. The absence of this outer layer in the specimen with blade-like ridges (Fig. 9F,G) suggests that this specimen may be an internal mould.

Discussion. The true identity of *Cambrocoryne lagenamorpha* is obscure. In lateral view, *Cambrocoryne lagenamorpha* superficially resembles a wiwaxiid sclerite illustrated by Porter (2004, fig. 11.7) from the

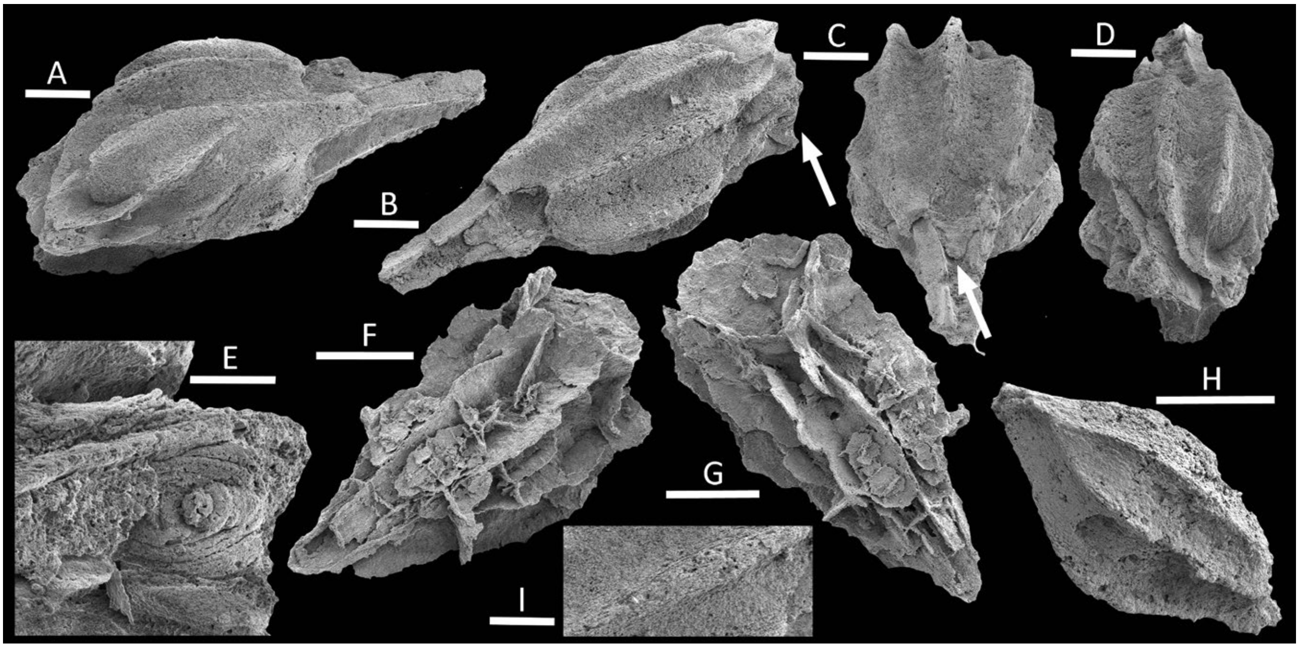


Fig. 9. *Cambrocoryne lagellamorpha* gen. et sp. nov., GGU sample 271718, Løndal, upper Henson Gletscher Formation (Cambrian, Wuliuan Stage). **A–E,I**, PMU 39697, holotype, in lateral (A,B, with detail of surface texture in I), basi-lateral (C) and apico-lateral (D) views. Note filling of channel between inner ridges (arrow in C) and concentric lamination in E (located by arrow in B). **F,G**, PMU 39698, lateral view of specimen lacking the outer massive layer. **H**, PMU 39699, lateral view of paratype showing the finely striated outer surface. Scale bars: 100 μm, except E (30 μm) and I (50 μm).

Monastery Creek Formation (Miaolingian Series, Wuliuan Stage, *Ptychagnosts gibbus* Biozone) in the Georgina Basin of Australia, although the latter specimen is flattened, has more rounded terminations and the longitudinal ridges are more sharply delimited. However, the Australian specimen lacks the massive thickening and circular cross-section of *Cambrocoryne lagenamorpha*.

Butterfield (1990), Smith (2014, fig. 5b), Zhang *et al*. (2015, fig. 5a) and Slater *et al.* (2017) noted that sclerites in *Wiwaxia* Walcott, 1911 consist of a hollow tubular root that opens out to form a flattened blade. The blade is ornamented by longitudinal ridges that are restricted to the upper surface. While the stalk of *Cambrocoryne lagenamorpha* can be compared in shape to the tubular root of *Wiwaxia*, its elliptical to round cross-section contrasts with the thin blades of *Wiwaxia*, although most material of the latter is compressed. Butterfield (1990) noted the similarity of *Wiwaxia* sclerites to the palea of chrysopeltid and aphroditid polychaetes and interpreted *Wiwaxia* as a jawed annelid. An illustrated palea of the present day *Bhawania goodei* Webster, 1884 shows a sclerite with an equidimensional cross-section (Butterfield 1990, fig. 4D) similar to that seen in *Cambrocoryne lagenamorpha*. Smith (2014) acknowledged that the dorsal sclerites of *Wiwaxia* were suggestive of polychaete worms but stated that the mouth parts, digestive tract and creeping foot established a solid relationship with molluscs, as proposed by Conway Morris (1976, 1985). All specimens of *Wiwaxia* illustrated by these authors lack the massive mineralisation seen in *Cambrocoryne lagenamorpha*, but the latter might represent the palae of an unusually heavily mineralised annelid.

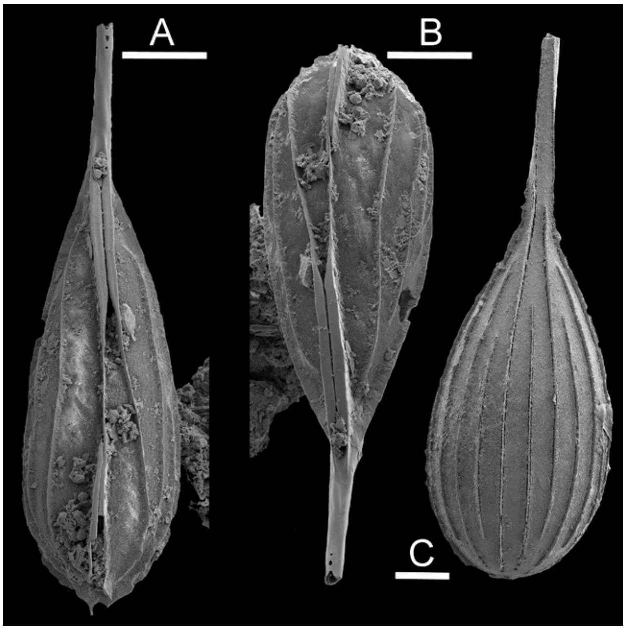


Fig. 10. Tests of the foraminiferan *Lagena*. **A,B**, PMU 39700 from a Pleistocene drill core (CRP-1) in the Ross Sea, Antarctica; 77.0088°S, 163.7558°E, 16 km offshore from Cape Roberts, McMurdo Sound, western Ross Sea. **C**, specimen mic03-06 of collective number PMU 29987, Holocene, Gulmar Fjord, Sweden (SEM Images Michael Streng). Scale bars. 20 μm (A,B); 50 μm (C).

The two massive specimens of *Cambrocoryne lagenamorpha* (Fig. 9A–E,H) are morphologically similar in their external form to thelodont trunk scales, such as specimens of *Loganellia* Turner, 1991 described by Turner & Peel (1986), Blom (1999) and Märss & Karatajūtē-Talimaa (2002). However, the internal structure of the *Cambrocoryne lagenamorpha* sclerites is quite unlike the dense histology of the Ordovician–Devonian thelodont vertebrates.

The ribbed, club-shaped external form of *Cambrocoryne lagenamorpha* is similar to many species of the Mesozoic–Recent foraminiferan *Lagena* Walker & Jacob, 1798 *in* Kanmacher, 1798, where a thin-walled, minute, inflated basal flask with prominent ribs passes into a narrow neck (Fig. 10). This neck is described as a basal stalk in the present description of *Cambrocoryne lagenamorpha*. However, the thin-walled, frequently unilocular test of *Lagena* and other nodosarinid foraminiferans is readily distinguished from the massively thickened outer layer of *Cambrocoryne lagenamorpha*. Interpretation of *Cambrocoryne lagenamorpha* as a foraminiferan comparable to *Lagena* would seem to imply that the narrow gap between the outer surface and the inner core (Fig. 9C, arrow) represents the test, which has been heavily encrusted both internally and externally. However, the fine surface texture of the outer layer (Fig. 9H,I) is not consistent with diagenetic encrustation.

Acritarch cluster

Fig. 7I,J

Figured material. PMU 39689 from GGU sample 271492, southern Lauge Koch Land, upper Henson Gletscher Formation, Cambrian, Wuliuan Stage.

Discussion. One poorly preserved specimen of the phosphatocopid *Dabashanella* preserves a phosphatic mass containing closely packed impressions of spheres on its external surface (Fig. 7I,J). The spheres range in diameter from 5–10 μm and display a compact, thin outer wall that probably reflects phosphatic encrustation. Moczydłowska (2011) illustrated clusters of *Asteridium tornatum* (Volkova 1968) from the Cambrian of Estonia that she considered to represent natural associations. Individual spheres are slightly larger than the Henson Gletscher Formation material (Fig. 7I,J). The spheres from Estonia are in contact with each other, whereas those described here from Greenland are preserved in a phosphatic ground mass. Slater *et al.* (2017) described clusters of smooth-walled vesicular acritarchs from the early Cambrian File Haidar Formation of Baltica, although individual spheres are about 25 μm in diameter. Wallet *et al*. (in press) described four morphotypes of acritarch clusters from the Buen Formation (Cambrian Series 2) of North Greenland with individual spheres up to 45 μm, although most were less than 20 μm.

Clusters of spheres described from the Kaili Formation (Maiolongian Series) of China by Lin *et a*l. (2006) were interpreted as eggs, but the spheres range in diameter from 508–945 μm (Lin *et al*. 2006), significantly larger than the present material. The widespread distribution of spheres of similar large size in the Cambrian was reviewed by Donoghue *et al*. (2006) and examples occur also in the current material, with a diameter of about 300 μm. Caron & Vannier (2016) described spherical structures interpreted as eggs within the carapace of specimens of *Waptia fieldensis* Walcott, 1912 from the Burgess Shale Lagerstätte (Miaolingian Series) of British Columbia, but these varied in size between 700 μm and 2.4 mm in specimens with a total length up to more than 50 mm. Numerous eggs attached to appendages of the bradoriid *Kunmingella douvillei* (Mansuy, 1912) from China (Cambrian Series 2) ranged in size between 150 and 180 μm (Duan *et al.* 2014; Caron & Vannier 2016).

Acknowledgements

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