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 Lendal, 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.

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 Konzervat-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

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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 Bønlund 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
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; 271718).
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 Hensel Gletscher Formation on the west side of Lendal (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 in fillings 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 linguliforme 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 Hensel 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
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

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**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 exfoliation 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. 5) 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 & Wolossek 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.

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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 paeoscolecidan 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 Wulian 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, Wulian 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, Wulian Stage (Peel 2022a).

Remarks. This unique flask-shaped specimen was compared by Peel (2022a) to the hatching larva 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 lorida in juvenile priapulids. While the larva of Inuitiphlaskus kouchinskyi has been affected by longitudinal wrinkling, evidence of a plated lorida is lacking. As in Priapulus caudatus and Halicryptus spinulosus, a plated lorida 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 vermiciform 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.
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.

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 Dabashellidae 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, Wulian 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, p. 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 Dabashanella from the Shujiangtuo 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,
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. 7KL), 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).

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.

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.

Discussion. 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.

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 Erkekot Formation (Cambrian Stage 4, Botoman Regional Stage) of Siberia.

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, Wulian Stage (Peel 2022c).

Problematica

Genus Cambrocoryne gen. nov.

Type species. Cambrocoryne lagenamorpha gen. et sp. nov. from the upper Henson Gletscher Formation of North Greenland, Cambrian, Wulian 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, Len-
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 structure (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 lagenamorpha 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 palea of an unusually heavily mineralised annelid.

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 & Karatjuu-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 CGU 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. 7J). 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 al. (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 Waptaia 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

Fieldwork was undertaken as part of the North Greenland Project (1978–80) organised by the Geological Survey of Greenland (GGU). The stratigraphic section log (Fig. 2) was kindly made available by Jon R. Ineson who is also thanked for sharing his insight into North Greenland Cambrian geology. Some SEM images were made during routine preliminary examination of collections by Artem Kouchinsky and Heda Agić. Michael Streng kindly provided the images of Lagena. Comments from Jean Vannier and an anonymous reviewer are greatly appreciated.

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