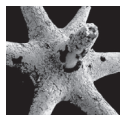


Middle Cambrian (Wuliuan Stage) Small Shelly Fossils from North Greenland (Laurentia)

JOHN S. PEEL



Acid residues from the Henson Gletscher Formation of North Greenland have yielded the most diverse assemblage of Small Shelly Fossils (SSF) known from the middle Cambrian (Miaolingian Series) of Laurentia. The fossils derive from the Wuliuan Stage (*Ptychagnostus gibbus* Biozone; Topazan Regional Stage of North America) and compare with faunas from the Ordian–Templetonian regional stages of Australia and the Kuonamka Formation of Northern Siberia, making a valuable contribution to world-wide early Miaolingian correlation. The assemblage is dominated by 21 species of helcionelloid molluscs, a third of which are referred to *Dorispira* Parkhaev, 2010. *Mellopegma* Runnegar & Jell, 1976 and *Erugoconus* Peel & Kouchinsky, 2022, are also conspicuous. Hyoliths include the operculate *Protowenella* Runnegar & Jell, 1976, *Crestjahitus* Sysoev, 1968 and *Yuku?* Kruse, 2002. Diverse form taxa of sponge spicules are also well represented in Siberia and Australia. The phosphatocopid *Dabashanella* Huo, Shu, & Fu, 1983, well known from China, is abundant. Diagenetic phosphatization of soft parts is common in bivalved arthropods, but rare cases include *Dietericambria* Peel, 2022a, the oldest known pentastomid, and a priapulid larva. Preservation as phosphatic internal moulds is otherwise characteristic. Multiaxial organisms include cnidarians and epiphytiform taxa of uncertain position. The stem group octocoral *Cambroctoconus* Park, Woo, Lee, Lee, Lee, Han, Chough & Choi, 2011, described from China and Kyrgyzstan, is common. Bromalites and casts of euendolith galleries are abundant and diverse in form. New taxa: *Crestjahitus groenlandicus* sp. nov., *Dabashanella? lunaiformis* sp. nov., *Hensonidendra tavsénica* gen. et sp. nov., *Hensonidendra hensoniensis* gen. et sp. nov., *Laugephakos groenlandicus* gen. et sp. nov., *Liangshanella? qassutit* sp. nov., *Tavsénicoralla avannaa* gen. et sp. nov. • Key words: Small Shelly Fossils, Cambrian, Miaolingian, Wuliuan, North Greenland, Laurentia.

PEEL, J. 2025. Middle Cambrian (Wuliuan Stage) Small Shelly Fossils from North Greenland (Laurentia). *Bulletin of Geosciences* 100(1), 1–56 (23 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received August 20, 2024; accepted in revised form December 4, 2024; published online March 9, 2025; issued April 13, 2025.

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Fossiliferous Cambrian strata crop out across northern Greenland from Inglefield Land in the west to Peary Land in the east within the shelf succession that formed along the southern margin of the transarctic Franklinian Basin (Higgins *et al.* 1991; Trettin 1991; Dewing & Nowlan 2012a, b; Fig. 1F). This north coast of Laurentia, extending almost to 83° 40' N, has yielded the northernmost Cambrian fossils known at the present day, including most notably the lower Cambrian Sirius Passet Lagerstätte of north-western Peary Land (82° 47.6' N, 42° 13.7' W; Conway Morris *et al.* 1987; Ineson & Peel 2011; Peel & Ineson 2011a, b; Harper *et al.* 2019). In the Cambrian, however, northern Greenland lay on the eastern side of the palaeocontinent and just south of the equator (Torsvik & Cocks 2016).

Middle Cambrian strata in northern Greenland currently assigned to the Wuliuan Stage (Miaolingian Series) accumulated in two general settings within the Cambrian shelf; they have not been recognised in the deep-water trough to the north. Sediments comprising outcrops close

to the Greenland Ice cap ('Inland Ice') in western and central areas (Inglefield Land – Wulff Land; Fig. 1F) were deposited in inner shelf environments and are dominated by pale, often stromatolitic carbonates, with subordinate siliciclastics. Sediments from outcrops extending from the northern coast of Nyeboe Land into western Peary Land were deposited in outer shelf environments and are dominated by thin-bedded, dark carbonates and siliciclastics interbedded with carbonate turbidites. All currently described fossils are derived from this outcrop belt.

Strata currently referred to the Wuliuan Stage were first documented by Poulsen (1927) who described assemblages with *Glossopleura* Poulsen, 1927 and other trilobites from Inglefield Land (Fig. 1F) from inner shelf carbonate successions; additional material was presented by Poulsen (1964). Peel (2020a, b; 2021a) reviewed regional stratigraphy in describing fossil assemblages from Dagaard-Jensen Land (Fig. 1F) and noted that the outcrops of Wuliuan strata extended eastward across southern Wulff Land, but without known fossils (Ineson &

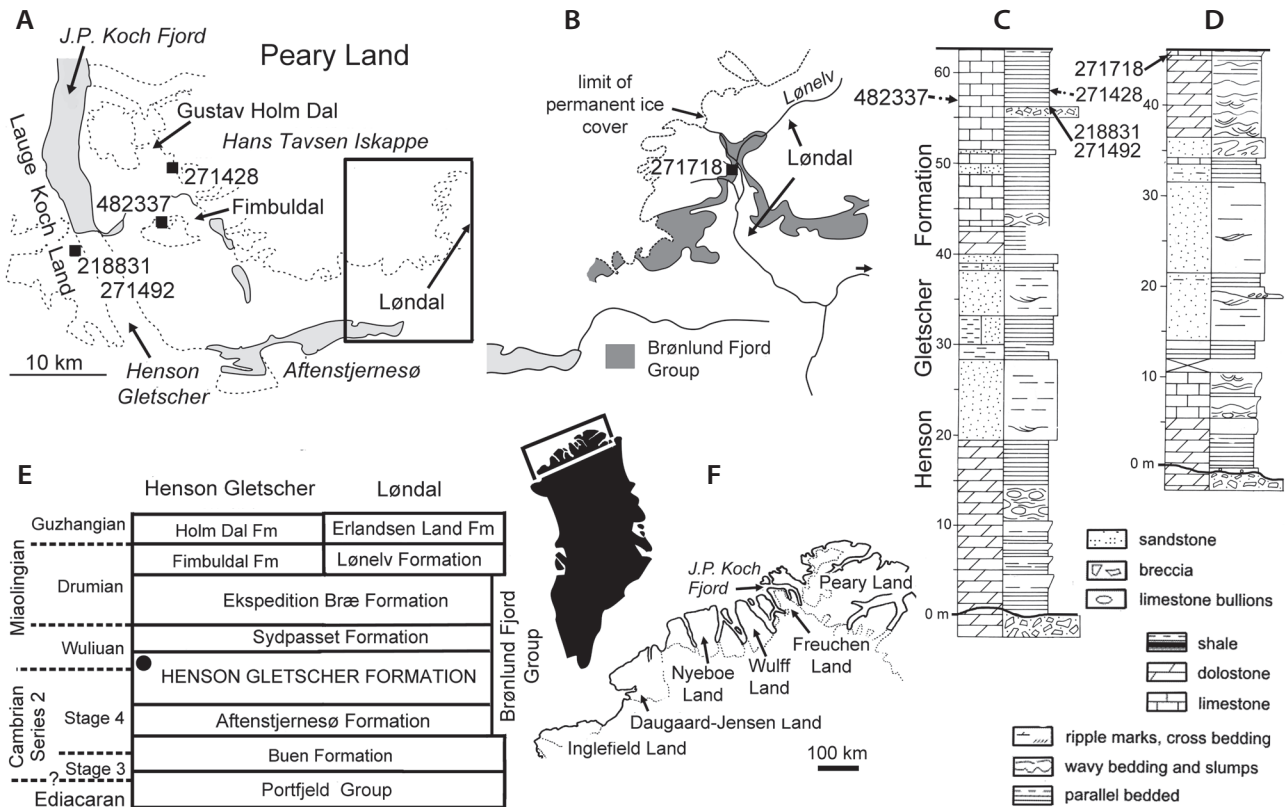


Figure 1. Geological and geographical information. • A – localities for GGU samples from the upper Henson Gletscher Formation (Wuliuan Stage) in the area around Henson Gletscher, with inset showing location of the Løndal area (B). • B – collection locality for GGU sample 271718 in Løndal. • C – geological section showing derivation of GGU samples 218831 and 271492 at the type locality of the Henson Gletscher Formation in southern Lauge Koch Land. The relative stratigraphic position of GGU samples 271428 and 482337 from western Peary Land are indicated by dotted arrows. • D – geological section showing derivation of GGU sample 271718 from the Henson Gletscher Formation in Løndal. • E – Ediacaran–middle Cambrian (Miaolingian Series) lithostratigraphic nomenclature in the Henson Gletscher–Løndal region of North Greenland. • F – land areas in North Greenland, located in inset map.

Peel 1997, Peel 2021b). In general, this Wuliuan material is almost completely dominated by trilobites. Carbonate samples from Daugaard-Jensen Land that have been processed using weak acids in search of Small Shelly Fossils (SSF) proved to be barren. In contrast, the outer shelf lower–middle Cambrian strata of northern Nyeboe Land – Peary Land often yield diverse faunas, with rich assemblages of SSF from acid residues.

This paper describes Small Shelly Fossils from the *Ptychagnostus gibbus* Biozone (Wuliuan Stage) of southern Lauge Koch Land and western Peary Land, North Greenland, the age of which is established from agnostoids (Figs 1, 2). The described microfossils (Figs 3–23) comprise the most diverse assemblage of middle Cambrian SSF reported from Laurentia, providing a reference point for intercontinental correlation of SSF within this widely recognised biozone. As a correlative of the Burgess Shale Lagerstätte (Gould 1990, Briggs *et al.* 1994, Conway Morris 1998), this Henson Gletscher SSF assemblage adds an extra dimension to the picture

of Cambrian life in the Wuliuan Stage. The paper brings together earlier studies by Robison (1982, 1984), Stockfors & Peel (2005a), Clausen & Peel (2012), Peel (2015; 2017a, b; 2019; 2021c, d; 2022a, b; 2023a, b; 2024a, b) and Peel & Kouchinsky (2022, 2024) that collectively provide both full descriptions of many of the reviewed taxa and an expanded picture of diversity. However, diverse millimetre-sized agnostids (Fig. 2), trilobites and brachiopods, which occur frequently in hand specimens of the described North Greenland samples, are generally excluded from the present context, due to the focus on residues after treatment with weak acid.

Geological Setting

Overviews of the development and stratigraphy of the Cambrian of North Greenland were given by Higgins *et al.* (1991), Ineson *et al.* (1994), Ineson & Peel (1997), Dawes *et al.* (2000), Dawes (2004), Geyer & Peel (2011),

Hopper & Ineson (2021) and Peel (2021e). Carbonates of the Brønlund Fjord Group (Cambrian Series 2, Stage 4 to Drumian Stage; Fig. 1E) and the overlying Holm Dal Formation (Guzhangian Stage; Fig. 1E; see Peel 1988a) record the establishment of a prograding carbonate platform that extended across North Greenland during the early Palaeozoic following deposition of the siliciclastic lower Cambrian Buen Formation (Ineson & Peel 1997, Peel & Willman 2018, Wallet *et al.* 2021). The Brønlund Fjord Group is dominated by platform margin, carbonate slope apron and deep shelf carbonates and siliciclastic sediments (Ineson & Peel 1997). The lithostratigraphic subdivision of the group reflects the alternation of sea level highstand and lowstand deposition within the prograding sequence. Dark carbonates and shales representative of periods of relative lowstand are separated by units of carbonate turbidites and mass flows deposited under active progradation of the platform margin during periods of highstand (Ineson & Peel 1997). Recessive sediments of the Henson Gletscher Formation in Freuchen Land, southern Lauge Koch Land and western Peary Land (Løndal) represent a period of lowstand between the cliff-forming, prograding, highstand deposits of the Aftenstjernesø and Sydpasset formations (Fig. 1E).

The Henson Gletscher Formation is 62 m thick at its type locality in southern Lauge Koch Land (Ineson & Peel 1997, Geyer & Peel 2011; Fig. 1A, C) and consists of dark, recessive, bituminous and cherty limestones,

dolostones, mudstones and sooty-weathering shales, with a prominent middle member of pale weathering, cream, fine-grained sandstones. The lower part of the formation in Løndal (Fig. 1A, B, D) includes beds of coarse skeletal packstones and grainstones, and the middle sandstone member forms about half of the total 45 m thickness.

In examined sections in the Lauge Koch Land – Løndal area, strata with lower Cambrian (Stage 4) fossils occur 5–10 m below those yielding the Wuliuan faunas described herein (Blaker & Peel 1997, Geyer & Peel 2011). Earliest Wuliuan (pre-*Ptychagnostus gibbus*) faunas have not been recognised. To a large extent, this unsampled interval probably results from the hurried nature of collecting inherent in the regional mapping project. However, the potential influence of the widely recognised eustatic event associated with the *Ptychagnostus gibbus* Biozone (Babcock *et al.* 2007) should not be ignored, even if unnoticed in the field.

Dark limestones and shales (thickness 1 m) occurring just below the top of the middle sandstone member in Løndal (Fig. 1D, section height 33–34 m) yield a fauna referred to as the *Bonnina–Pagetides elegans* Biozone by Sundberg *et al.* (2016, 2022). This assemblage includes *Ovatoryctocara granulata* Chernysheva, 1962 and *Ovatoryctocara yaxiensis* Yuan, Zhao, Peng, Zhu & Lin, 2009 (uppermost Cambrian Stage 4; Geyer & Peel 2011, Peel *et al.* 2016, Sundberg *et al.* 2022) and was referred

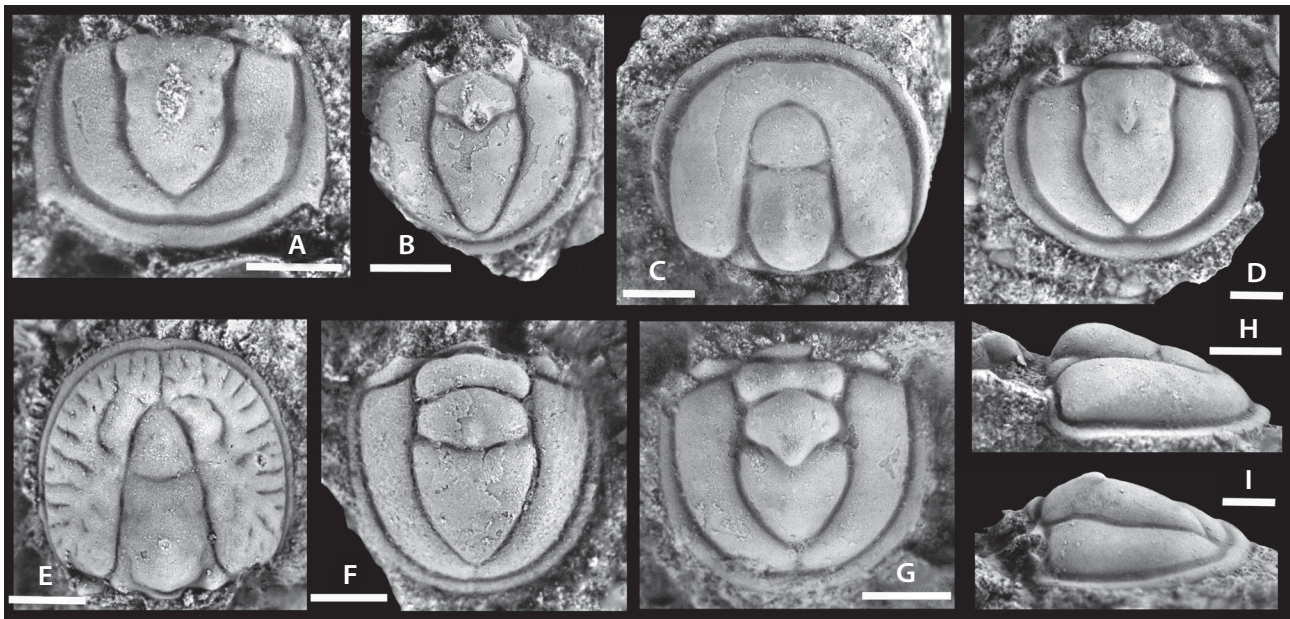


Figure 2. Agnostids from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage). All from GGU sample 271492. • A – *Peronopsis fallax* (Linnarsson, 1869), MGUH 34825, pygidium. • B – *Onymagnostus seminula* (Whitehouse, 1939), MGUH 34826, pygidium. • C, D, H, I – *Peronopsis interstricta* (White, 1874). C, H – MGUH 34827, cephalon in dorsal (C) and lateral (H) views. D, I – MGUH 34828, pygidium in dorsal (D) and lateral (I) views. • E, F – *Ptychagnostus sinicus* Lu, 1957. E – cephalon, MGUH 34829. F – pygidium, MGUH 34830. • G – *Ptychagnostus gibbus* (Linnarsson, 1869), pygidium, MGUH 34831. Scale bars: 1 mm.

to as the *Ovatoryctocara granulata* by Peel *et al.* (2016). Fossils referred to the *Ptychagnostus gibbus* Biozone (Cambrian, Miaolingian Series, Wuliuan Stage; GGU sample 271718) were collected about 10 m higher, 1 m below the top of the Henson Gletscher Formation (Fig. 1D). The first recorded Wuliuan fossils in Lauge Koch Land (GGU samples 218831 and 271492; Fig. 1C) occur about 10 m above strata that yield trilobites of the *Bonnia–Pagetides elegans* Biozone (Geyer & Peel 2011, fig. 10; see also Blaker & Peel 1997, fig. 9). This gap is reduced to about 5 m in Fimbuldal (Fig. 1A, GGU sample 482337; Geyer & Peel 2011, fig. 5).

Trilobite faunas from the Henson Gletscher Formation are mainly polymeroids of Laurentian aspect that occur together with agnostids of value for global correlation (Babcock 1994a, b; Robison 1982, 1984, 1994; Blaker & Peel 1997; Geyer & Peel 2011; Peel *et al.* 2016). Geyer & Peel (2011, fig. 10) displayed the observed succession of trilobite faunas in Cambrian Stage 4 of the upper Henson Gletscher Formation, placing the *Bonnia–Pagetides elegans* faunule above the *Ovatoryctocara granulata* faunule, and an underlying *Eoagnostus roddyi–Arthricocephalus chauveaui* faunule. However, it is doubtful if a distinction between the *Bonnia–Pagetides elegans* faunule and the *Ovatoryctocara granulata* faunule is merited.

Sundberg *et al.* (2016, fig. 1) listed three biozones in the early Cambrian (Cambrian Stage 4) succession of the Aftenstjernesø and lower Henson Gletscher formations, but admitted the limitations of this scheme (Sundberg *et al.* 2016, p. 88). The *Ovatoryctocara granulata* faunule was absorbed into the *Bonnia–Pagetides elegans* faunule, the youngest Stage 4 faunule, and the *Eoagnostus roddyi–Arthricocephalus chauveaui* faunule of Geyer & Peel (2011) was replaced by the *Eoagnostus roddyi–Oryctocarella duyunensis* faunule. A revised version concerning the interval immediately below the lower–middle Cambrian (Cambrian Stage 4–Wuliuan Stage) boundary in the upper Henson Gletscher Formation was presented by Sundberg *et al.* (2022, fig. 4), with focus on the distribution of trilobites within an *Eoagnostus roddyi–Oryctocarella duyunensis* Biozone and the overlying *Bonnia–Pagetides elegans* Biozone of Stage 4, the latter considered to extend almost to the base of the Wuliuan Stage. The boundary between the two coincides with the appearance of *Ovatoryctocara granulata* and *Ovatoryctocara yaxiensis*. However, it is difficult to reconcile the displayed ranges of taxa in the graphical representation presented by Sundberg *et al.* (2022, fig. 4) with the primary range chart data in Geyer & Peel (2011). Furthermore, due to an unfortunate draughting error, *Oryctocarella duyunensis* is displayed as occurring within the *Bonnia–Pagetides elegans* Biozone rather than in the underlying biozone that bears its name. Thus, in Sundberg *et al.* (2022, fig. 4), *Pagetides elegans* and *Oryctocarella*

duyunensis are both missing from the biozones that bear their names

The *Bonnia–Pagetides elegans* Biozone established by Geyer & Peel (2011) and Sundberg *et al.* (2016, 2022) within strata of the uppermost part of Cambrian Series 2 (Stage 4), and preserved in strata just below the presently described Wuliuan material, is of particular importance for international correlation. It establishes strong correlations between Laurentia (Nevada and North Greenland), Siberia and South China, and further into Avalonia (Newfoundland) and eventually West Gondwana (Geyer & Peel 2011; Geyer 2019; Sundberg *et al.* 2016, 2022).

The formal base of the Miaolingian Series and the Wuliuan Stage is based on the first occurrence of *Oryctocephalus indicus* (Zhao *et al.* 2019), which is tentatively recognised in the upper Henson Gletscher Formation of Fimbuldal (Fig. 1A) about 1–2 m below Wuliuan Stage fossils described here from GGU sample 482337 (Geyer & Peel 2011, fig. 5). This horizon is assigned to the *Ptychagnostus gibbus* Biozone, which has a cosmopolitan distribution (Babcock *et al.* 2007, fig. 2). Characteristic agnostids from the *Ptychagnostus gibbus* Biozone of the Henson Gletscher Formation are illustrated in Figure 2. Note that *Ptychagnostus intermedius* (Tullberg, 1880) of Robison (1984) was reassigned to *Ptychagnostus sinicus* Lu, 1957 by Ahlberg *et al.* (2007).

Material

GGU samples 218831 and 271492 were collected at 56.5 m above the base of the Henson Gletscher Formation (thickness 62 m) at its type locality in southern Lauge Koch Land (Fig. 1A, C) from bioclastic limestone that fills scours in the top of a 1 m thick mass flow deposit (82° 10' N, 40° 24' W; Ineson & Peel 1997, fig. 31; Geyer & Peel 2011, fig. 3; Figs 1A, C). GGU sample 218831 was collected by Peter Frykman on 24th June 1979. GGU sample 271492 was collected by J.S.P. on 25th June 1978.

GGU sample 271428 was collected by J.S.P. on 20th June 1978 from about 4 m below the top of the Henson Gletscher Formation (thickness 32 m), on the east side of Gustav Holm Dal at its junction with Fimbuldal, western Peary Land (82° 19.5' N, 39° 37' W; Fig. 1A, C).

GGU sample 271718 was collected by J.S.P. on 15th July 1978 from thin-bedded, phosphatized, bioclastic, dolomitic limestone, about 1 m below the top of the Henson Gletscher Formation on the west side of Løndal (82° 18' N, 37° 00' W; Figs 1B, D). The dolomitic limestone contains numerous thin layers of dark phosphate that sometimes form hard grounds (Peel 2023a, fig. 3). Redeposited calcareous, phosphatized and silicified shells are associated with oolites that were frequently

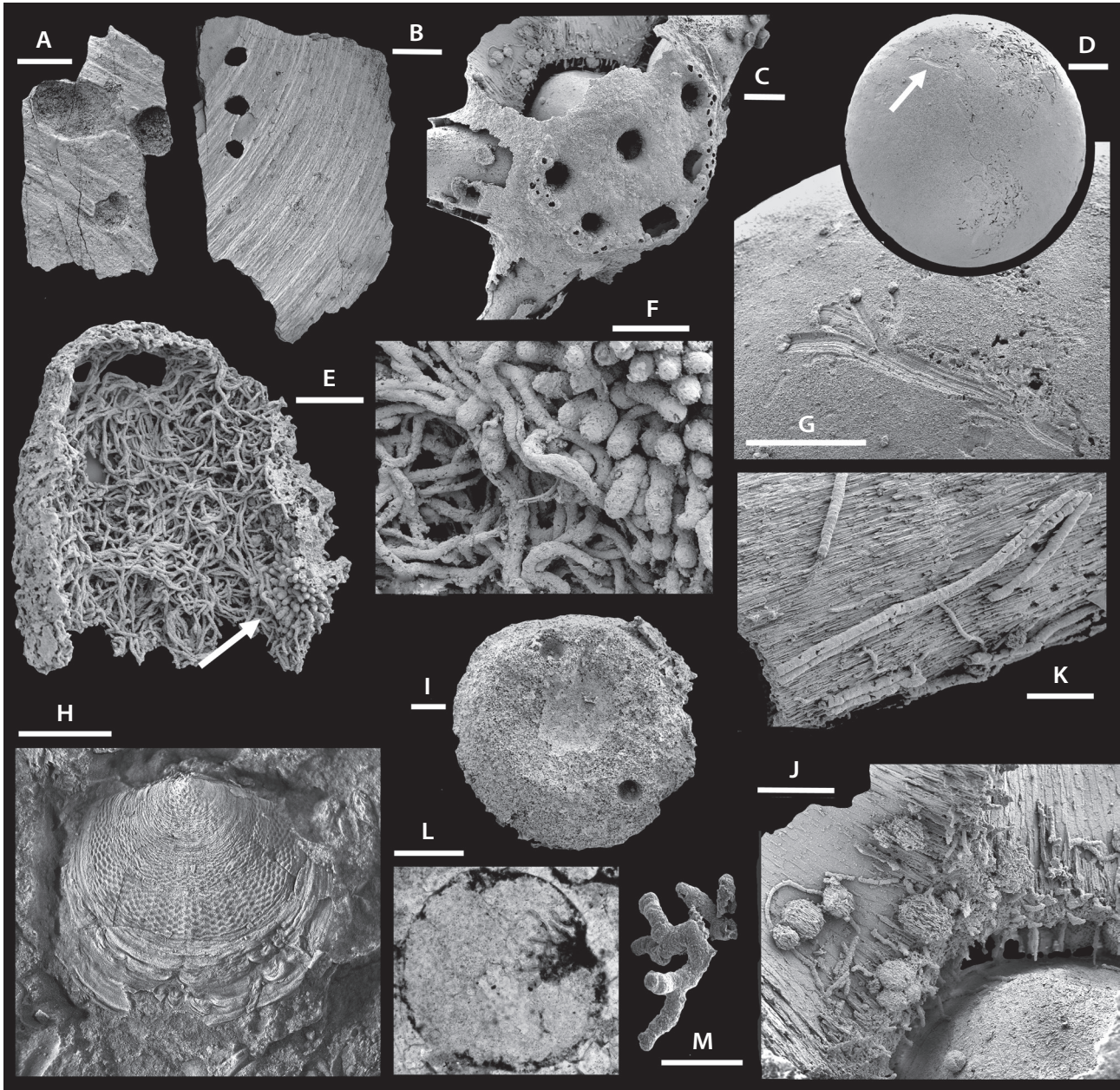


Figure 3. Trace fossils from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A – PMU 18252 from GGU sample 271492. • B – PMU 18253 from GGU sample 271492. • C, J – PMU 21440 from GGU sample 271718, internal mould of sclerite of *Chancelloria* sp. with casts of euendoliths on encrustation of outer surface. • D, G – PMU 18254 from GGU sample 271718, ambient inclusion trails on surface of phosphatized sphere with arrow in D locating G. • E, F – PMU 18255 from GGU sample 271492, phosphatic casts of euendoliths; detail (F, arrow in E) shows *Scolicia* isp. lower left and *Fascichnus* isp. upper right. • H – PMU 18256 from GGU sample 482337, fractured and repaired valve of *Dictyonina* sp. • I – PMU 39664 from GGU sample 271718, echinoderm holdfast with borings. • K – PMU 21439 from GGU sample 271718, phosphatized internal moulds of euendoliths on chancelloriid. • L – PMU 27656 from GGU sample 271718, phosphate coated (black) oolite penetrated by *Fascichnus* isp. (= *Eohyella* sp.). • M – PMU 27654 from GGU sample 271718, cast of boring *Fascichnus* isp. (= *Eohyella* sp.). Scale bars: 30 µm (G, J, K); 50 µm (C, D, F); 100 µm (M); 200 µm (E, I); 300 µm (A, B); 400 µm (L); 2 mm (H).

bored and covered with dark phosphate prior to their final accumulation (Peel 2023a, fig. 4k, l).

GGU sample 482337 was collected by J.S.P. on 4th August 2006 about 8 m below the top of the Henson Gletscher Formation on the south side of Fimbuldal

(82° 17.7' N, 39° 42' W; Fig. 1A, C). This is locality 3 of Geyer & Peel (2011, figs 2, 5). The sample occurs about 1 m above a thin mass flow bed that appears to be continuous with that overlain by GGU samples 218831 and 271492 in southern Lauge Koch Land (Fig. 1A).

Faunal comparisons

Wuliuan assemblages from the Kuonamka Formation of northern Siberia were described by Kouchinsky *et al.* (2011) but not from the *Ptychagnostus gibbus* Biozone. The underlying *Kuonamkites* Biozone in northern Siberia has not been recognised in North Greenland. A rich fauna of molluscs described by Gubanov *et al.* (2004) from the uppermost beds of the Kuonamka Formation was assigned to the basal Drumian Stage but differs from the current Greenland material most notably in its lack of *Dorispira* (Fig. 16A–I) and *Mellopegma* (Fig. 16Q, S). Yochelcionellids occur in the underlying *Kuonamkites* Biozone and in the base of the overlying Drumian Stage of the Kuonamka Formation, but in Cambrian Series 2, Stage 4 in North Greenland (Peel *et al.* 2016). The bradoriid *Mongolitubulus reticulatus* (Fig. 12E, H, I, F) occurs throughout the *Kuonamkites* Biozone in northern Siberia and in the *Ptychagnostus gibbus* Biozone of North Greenland. Similar, diverse assemblages of sponge spicules to those from North Greenland were described from the Kuonamka Formation (Cambrian Stage 4) by Fedorov & Pereladov (1987), including *Abnormisella*, *Cjulanciella* and *Kuonamia*. *Australispongia* occurs in both localities (Fig. 5C; Kouchinsky *et al.* 2011, fig. 40n–q), while the inflated spicule *Thoracospongia* is represented by different species. *Speciosuspongia* is common in North Greenland, but does not occur in the Kuonamka Formation.

Dorispira is abundant in GGU sample 271718 and the Coonigan Formation of New South Wales (Ordian–Tempeltonian regional stages). The sponge spicules *Celtispongia*, *Thoracospongia* and *Speciosuspongia* occur in Australia and North Greenland (Mehl 1998, Peel 2019). *Galeopsis*, described by Hinz-Schallreuter (1993) from the basal Monastery Creek Formation, Queensland, Australia (Wuliuan Stage; Tempeltonian Regional Stage) is tentatively recorded from North Greenland, as are some Miaolingian hyoliths described by Kruse (2002) from Queensland.

The Brèche à *Micmacca* Member of the High Atlas of Morocco yields a fauna from the Cambrian Stage 4–Wuliuan Stage boundary rich in *Dorispira* and yochelcionellids (Geyer 1986; Mghazli *et al.* 2023) that is slightly older than the North Greenland fauna. Both assemblages include *Protowenella* and the Moroccan material also includes a colonial form that resembles *Tavsenicoralla avannaa* (Mghazli *et al.* 2023, fig. 5r, s).

Hu *et al.* (2021) reported *Dorispira accordionata* (identified as *Oelandiella*), *Chancelloria* and a *Hyo-lithellus* sp. with similar ornamentation to the North Greenland material (Fig. 9A–C) from the Hsuzhuang Formation (Miaolingian) of Henan Province, North China. *Micromitra* (Fig. 14K) also occurs in both Miaolingian faunas.

Skovsted (2006b) and Wotte & Sundberg (2017) described SSF from the Emigrant and Pioche formations (Cambrian Stage 4, Delamaran Regional Stage) of the Great Basin, western USA, that in their content of chancelloriids, hyoliths and molluscs are generally similar to the Wuliuan assemblages from North Greenland. *Mellopegma chelata* occurs in the Emigrant Formation and in North Greenland (Skovsted 2006b, Fig. 16N).

Institutional abbreviations. – GGU – Geologiske Undersøgelse (Geological Survey of Greenland), Copenhagen, Denmark, now the Geological Survey of Denmark and Greenland (GEUS), Copenhagen; MGUH – Natural History Museum of Denmark, Copenhagen; PMU – Museum of Evolution, Uppsala University, Uppsala, Sweden.

Trace fossils

Borings

Circular borings, 100–300 µm in diameter, have been found in a few shell fragments. Those that penetrate through the shell may be of predatory origin (Fig. 3B), but others are likely domiciles (Fig. 3I). Peel (2014) described similar borings in the brachiopod *Botsfordia* sp. from the lower Cambrian Kap Troedsson Formation in south-east Wulff Land.

Euendoliths

Thin sections of GGU sample 271718 (Fig. 3L) reveal widespread boring of ooliths and shell fragments by euendolithic organisms (Stockfors & Peel 2005a). Phosphatized casts of these borings are commonly seen as a result of the dissolution of shell carbonate in residues of the same sample (Fig. 3C, E–G, J, M). Peel (2024a) referred parallel-sided, usually unbranching casts of borings in chancelloriid sclerites and the brachiopod *Nisusia* Walcott, 1905 to *Scolecia* Radtke, 1991 (Fig. 3E, K), making comparisons with lower Cambrian material from Sichuan, China, described by Li (1997). Forms with radiating branching (Fig. 3F, M) previously attributed to the cyanobacterian *Eohyella* sp. by Stockfors & Peel (2005a) were referred to the ichnogenus *Fascicchnus* Radtke & Golubic, 2005. Peel (2024a) compared spherical or slightly oval casts (Fig. 3J) to *Planobola macrogota* Schmidt, 1992, noting also similar specimens from China illustrated by Li (1997).

Ridged galleries in organophosphatic brachiopods described by Stockfors & Peel (2005b) and Peel (2014, fig. 3o) are now known to be ambient inclusion trails of non-organic origin (Yang *et al.* 2017) and not euendolith

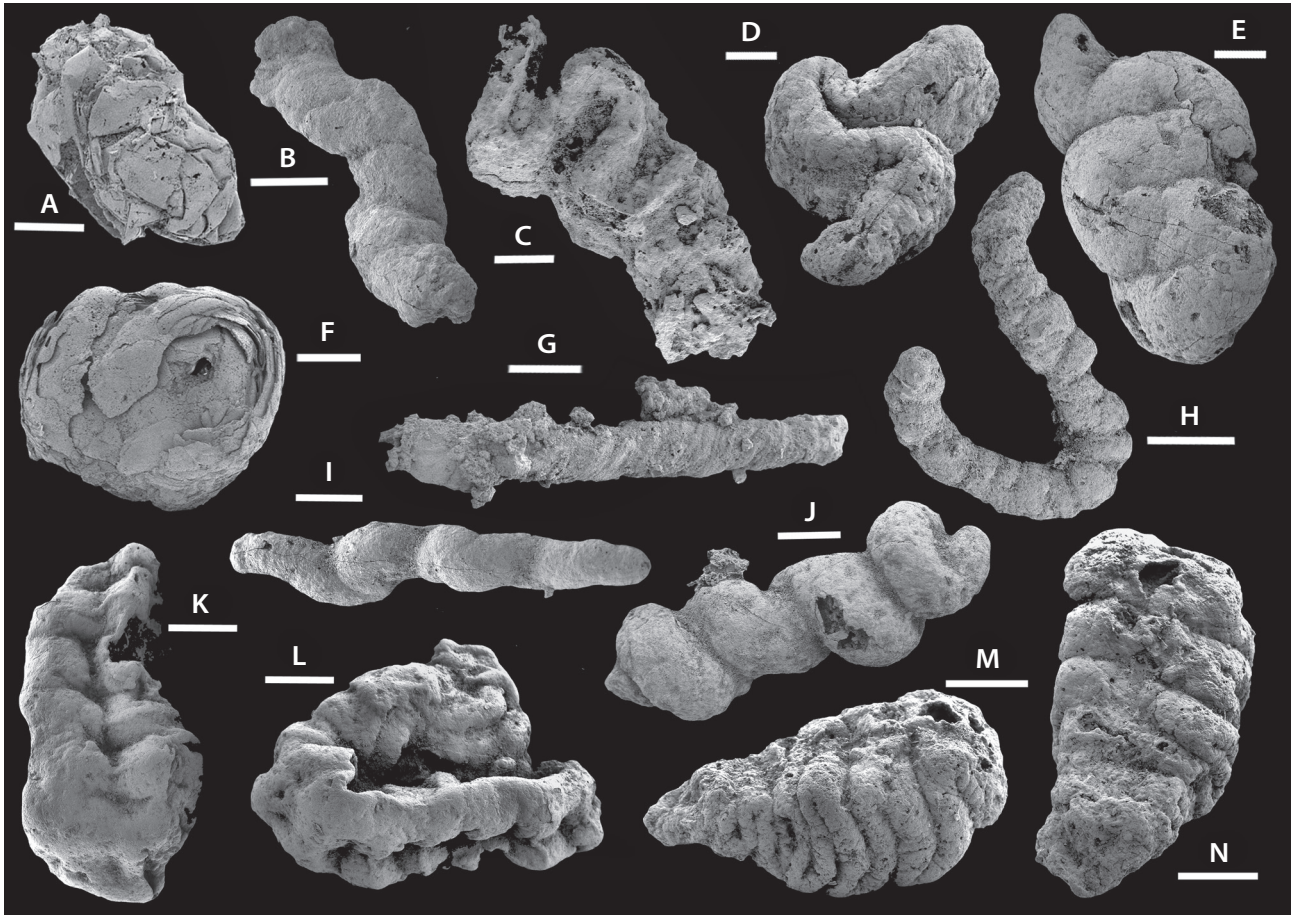


Figure 4. Bromalites from the upper Henson Gletscher Formation Cambrian (Wuliuan Stage), North Greenland. GGU sample 271492 unless stated. • A – coprolite, MGUH 31215 from GGU sample 271718. • B – coprolite, MGUH 31222. • C – orthothecid hyolith cololite, MGUH 31220. • D – orthothecid hyolith cololite, MGUH 31221. • E – orthothecid hyolith cololite, MGUH 31219. • F – coprolite composed of concentrically arranged bradoriid/phosphatocopine fragments, MGUH 31217 from GGU sample 271718. • G – bromalite, MGUH 31213. • H – coprolite, MGUH 31218. • I – coprolite, PMU 18257. • J – spiral coprolite, PMU 18258 from GGU sample 218831. • K, L – cololite, PMU 18259. • M, N – orthothecid hyolith cololite, PMU 18260. Scale bars: 100 µm (A); 200 µm (B–F, H–N); 400 µm (G).

borings, as originally described, although euendolith borings also occur (Peel 2024a). A sphere from GGU sample 271718 (Fig. 3D, G) clearly shows migratory pyrite(?) crystals at the terminations of the ridged galleries.

Coprolites and cololites

Phosphatized bromalites (coprolites and cololites) from the uppermost Henson Gletscher Formation (Wulian Stage) were described by Peel (2015) who interpreted various zigzag folded forms (Fig. 4C–E) as cololites (gut infillings) of orthothecid hyoliths, by comparison with specimens described by Thorall (1935), Runnegar *et al.* (1975), Kruse (1996) and Devaere *et al.* (2014). Shen *et al.* (2014) interpreted similar specimens from southern China, as coprolites (expelled fecal material). A robust specimen, also interpreted as a cololite, tapers to one extremity but has more numerous folds and an overall square cross-

section (Fig. 4M, N). A U-shaped cololite, possibly a folded specimen, has prominent swellings located on each side of a median groove (Fig. 4K, L).

Coprolites include a variety of beaded and spiral forms (Fig. 4B, G–J) and oval pellets composed of compressed fragments of bradoriid and phosphatocopine arthropods (Fig. 4A, F).

Shen *et al.* (2014) described coprolites and cololites of similar age from the lower Gaotai Formation (Wuliuan Stage) in Guizhou, southern China that differ from Henson Gletscher Formation material in including aggregates of numerous faecal pellets and strings rich in palaeoscolecidan sclerites, linguliformean brachiopods and bradoriids. Olempska *et al.* (2023) gave a full description of phosphatized bromalites from the late Cambrian (Furongian Series) of northern Poland, making detailed comparisons with present day coprolites and the Cambrian Stage 4–Miaolingian material from Greenland described by Peel (2015). Multilooped forms interpreted

as coprolites are conspicuous, but orthothecid cololites of the type described by Peel (2015) from the Henson Gletscher Formation (Wuliuan Stage) were not recognised.

Holdfasts

Various holdfasts have been recognised, reflecting organisms attaching themselves on hard substrates. Holdfasts of pelmatozoan echinoderms are common in GGU sample 271718 (Figs 3I, 18L; Clausen & Peel 2012). The cnidarian *Cambroctoconus* Park, Woo, Lee, Lee, Han, Chough & Choi, 2011 displays a similar mode of attachment (Fig. 7F, G), while tubular specimens of *Hyolithellus* Billings, 1872 are often expanded at their base indicating attachment (Fig. 9F, G). Other possible holdfasts appear to have a similar shape in some examples to those described in *Sphenothallus* Hall, 1847 by Peel & Gubanov (2022) but differ in terms of a thick wall penetrated by pores (Fig. 8E–H). A similar wall structure is characteristic of the spherical problematicum *Aetholicopalla* Conway Morris, 1990 in Bengtson *et al.* (1990) from the lower Cambrian of South Australia (Fig. 20A–F), which usually develops some form of attachment to a substrate (Bengtson *et al.* 1990).

Shell repair

Described instances of shell repair following failed predation are uncommon in the Cambrian (Ebbestad *et al.* 2023) but Peel (2014) described a variety of repaired injuries in the linguliformean brachiopod *Botsfordia* Matthew, 1891 from the lower Cambrian Kap Troedsson Formation of North Greenland. A single specimen assigned to *Dictyonina* Cooper, 1942 was crushed during life such that a large central area of the valve is slightly depressed below surrounding shell areas except along the posterior margin (Fig. 3H). Shell formed at the margin, subsequent to the injury shows severe modification and a billowing lobate form similar to that described by Peel (2014, fig. 3I) in *Botsfordia* in shell formed after marginal breakage. Alexander & Dietl (2005) described injuries in burrowing Neogene bivalves resulting from deep burrowing, a mode of life quite distinct from the epibenthic environment envisaged for *Dictyonina*.

Systematic Palaeontology

This published work and the nomenclatural acts it contains have been registered in Zoobank: Zoobank.org:pub:B4ED668D-68AE-4B4B-B236-232E8A60A709

Phylum Porifera Grant, 1836

Discussion. – In North Greenland, Cambrian articulated sponges are only known from mudstones of the Buen Formation (Cambrian stages 3–4; Botting *et al.* 2015, Botting & Peel 2016, Peel & Willman 2018). Disarticulated sponge spicules, in contrast, are widely distributed in acid residues from early–middle Cambrian carbonates (Peel *et al.* 2016; Peel 2017a, 2018a, 2019). Spicules from the Henson Gletscher Formation (Wuliuan Stage) described as form taxa by Peel (2017a, 2019) were mainly derived from GGU sample 271428 and include *Abnormisella insperata* Fedorov, 1987 in Fedorov & Peredalov (1987) (Fig. 5J); *Cjulanciella asimmetrica* Fedorov, 1987 in Fedorov & Peredalov (1987) (Fig. 5D), *Kuonamia fusiformis* (Fedorov, 1987) in Fedorov & Peredalov (1987) (Fig. 5K), *Thoracospongia lacrimiformis* Peel, 2017a (Fig. 5B), *Sanningasopia borealis* Peel, 2019 (Fig. 5H), *Celtispongia dorte* Peel, 2019 (Fig. 5E), *Australispongia? inuak* Peel, 2019 (Fig. 5C) and *Speciosuspongia inughuitorum* Peel, 2019 (Fig. 5F).

Pentactins and stauractins common to most sponge taxa were not named by Peel (2019). The stauractins that dominate GGU sample 271428 are similar to spicules of *Hyalostelia transitiva* Fedorov, 1987 in Fedorov & Peredalov (1987) from the Kuonamka Formation (Cambrian Stage 4, *Oryctocara* Biozone, to Wuliuan Stage) of northern Siberia (Fedorov & Peredalov 1987, Kouchinsky *et al.* 2011). Hexactins here referred to *Kuonamia* Doweld, 2016 were illustrated from the Miaolingian of Queensland, Australia, by Mehl (1998). Stauractins described by Peel (2019) as *Celtispongia dorte* are abundant in the Miaolingian of the Georgina Basin (Mehl 1998, p. 1164).

Thoracospongia lacrimiformis was recognised by Peel (2019) in the Bagrad Formation (Cambrian Series 2, Botoman Regional Stage) of south-eastern Siberia (Sugai *et al.* 2004) while the more globose type species, *Thoracospongia follispiculata* Mehl, 1996, was reported from Wuliuan and Drumian stages (Templetonian–Undilanian regional stages) of Australia (Mehl 1996, 1998). *Thoracispongia* was also described from the Miaolingian Series of Siberia by Kouchinsky *et al.* (2011, 2022).

Basal eumetazoan clade

Order Chancelloriida Walcott, 1920

Family Chancelloriidae Walcott, 1920

Discussion. – The phylogenetic position of chancelloriids is unresolved. Traditionally, they were interpreted as sponges (Walcott 1920) but Goryansky (1973) pointed out that the sclerites are external structures located on the outside of the bag-like body rather than internally within the body wall, as is the case in sponges. Bengtson & Missarzhevsky (1981) proposed *Coeloscleritophora* for Cambrian fossils that show a similar method of for-

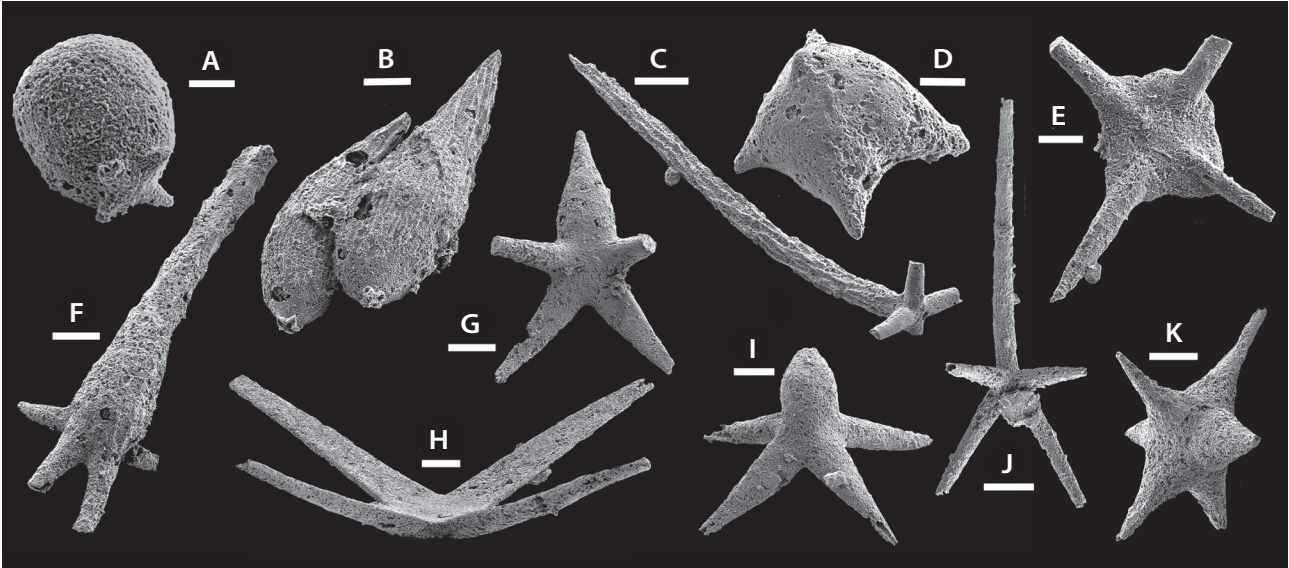


Figure 5. Sponge spicules from the upper Henson Gletscher Formation Cambrian (Wuliuan Stage), North Greenland. All from GGU sample 271428. • A – *Thoracospongia* sp., PMU 34368. • B – *Thoracospongia lacrimiformis* Peel, 2017, PMU 29990, holotype. • C – *Australispongia?* *inuak* Peel, 2019, PMU 34377, holotype. • D – *Cjulanciella asimettrica* Fedorov, 1987 in Fedorov & Peredalov (1987), PMU 34361. • E – *Celtispongia dorte* Peel, 2019, PMU 34372. • F – *Speciosuspongia inughuitorum* Peel, 2019, PMU 34391, holotype. • G, I – *Speciosuspongia* spp., G – PMU 34380, I – PMU 34389. • H – *Sanningasopia borealis* Peel, 2019, PMU 34363. • J – *Abnormisella insperata* Fedorov, 1987 in Fedorov & Peredalov (1987), PMU 34393. • K – *Kuonamia fusiformis* (Fedorov, 1987) in Fedorov & Peredalov (1987), PMU 34399. Scale bars: 50 µm (A); 100 µm (B, C, E–K); 200 µm (D).

mation of hollow aragonitic sclerites to cancelloriids (Bengtson *et al.* 1990, Bengtson & Hou 2001, Bengtson 2005, Porter 2008, Bengtson & Collins 2015). However, the dissimilarity in body plan between the sessile, bag-like cancelloriids and motile forms such as halkieriids argues against a close relationship (Bengtson & Conway Morris 1984). Bengtson & Collins (2015) considered it most likely that Coeloscleritophora is paraphyletic and that the hollow sclerites represent a plesiomorphic eumetazoan character. Botting & Muir (2018) and Cong *et al.* (2018) presented arguments reviewed by Cong (2023) for the assignment of cancelloriids to the sponges, close to the protomonaxonids. Peel (2024b) described internal ray canals in sclerites of *Chancelloria* from the early Cambrian (Stage 4) in North Greenland, noting their similarity with the robust central canal within sclerites of the supposed halkieriid *Sinosachites delicatus* (Jell, 1981) from the early Cambrian of Australia (Jell 1981, Bengtson *et al.* 1990, Vinther 2009).

Peel & Kouchinsky (2024) described the diagenesis of cancelloriid sclerites in GGU samples 271492 and 271718. Peel (2024a) described assemblages of euendoliths in the originally aragonitic sclerites of *Chancelloria* from GGU sample 271718.

Genus *Chancelloria* Walcott, 1920

Type species. – *Chancelloria eros* Walcott, 1920, Walcott Quarry, Ontario, Canada; Cambrian, Miaolingian Series.

Chancelloria sp.

Figure 6B–D

Figured material. – PMU 21447 from GGU 271492, southern Lauge Koch Land; PMU 18261 and PMU 21442 from GGU sample 271718, Løndal.

Discussion. – *Chancelloria* sp. is represented by about 40 broken sclerites in GGU samples 271718 and 271492, most of which display a ray formula of 6–1 (six radiating, usually coplanar, lateral rays and a single central ray on the upper surface). Sclerites with a formula of 7–1 are less common, while rare specimens with 5–1 rays occur in GGU sample 271718. Internal moulds of disarticulated rays are common.

Genus *Allonnia* Doré & Reid, 1965

Type species. – *Allonnia tripodophora* Doré & Reid, 1965. Carteret, Armorican Massif, France; lower Cambrian.

Discussion. – Sclerites of *Allonnia* are rare in the current material and it is likely that most of the morphotypes represent minor elements in cancelloriid scleritomes dominated by other sclerite types (Mehl 1998; Moore *et al.* 2014, 2019; Bengtson & Collins 2015).

Allonnia cf. *tripodophora* Doré & Reid, 1965

Figure 6G

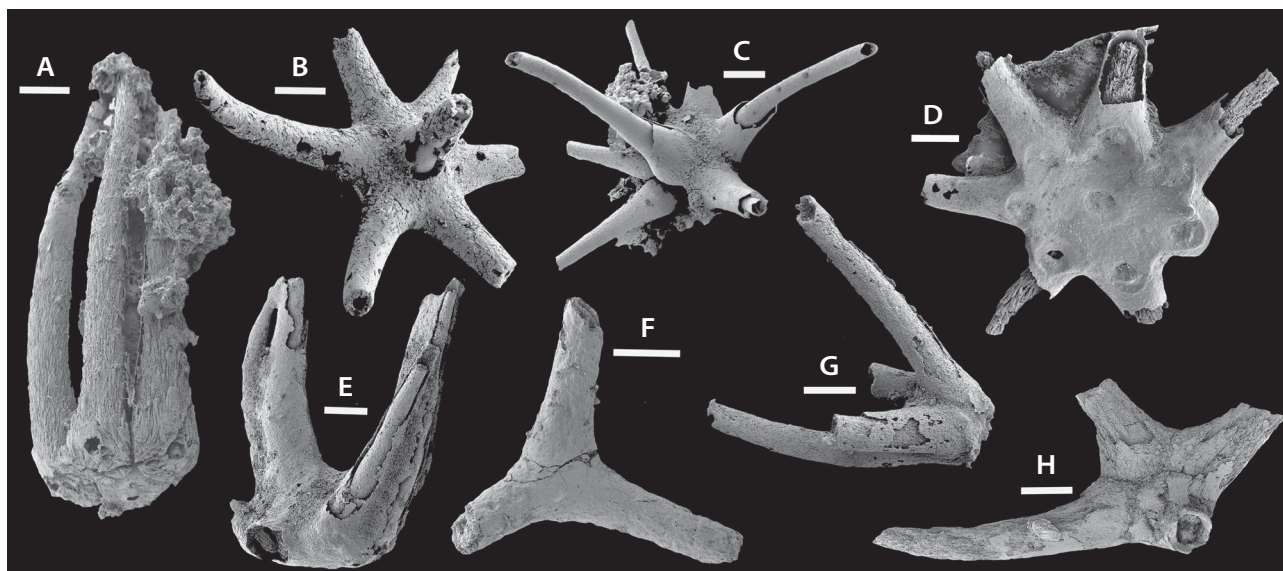


Figure 6. Chancelloriids from the upper Henson Gletscher Formation Cambrian (Wuliuan Stage), North Greenland. GGU sample 271718 unless stated. • A – *Allonnia quadrocornuformis* (Ding & Li, 1992 in Ding *et al.* 1992), PMU 21199. • B–D – *Chancelloria* sp. B – PMU 18261. C – PMU 21442. D – PMU 21447 from GGU 271492. • E – *Allonnia?* sp., PMU 18262 from GGU 271492. • F, H – *Allonnia rossica* (Sayutina, 1988 in Vassiljeva & Sayutina 1988). F – PMU 18263. H – PMU 18264. • G – *Allonnia* cf. *tripodophora* Doré & Reid, 1965, PMU 18265. Scale bars: 100 μ m (C–E, G); 200 μ m (A, B, F, H).

Figured material. – PMU 18265 from GGU sample 271718, Løndal.

Discussion. – *Allonnia tripodophora* Doré & Reid, 1965 is characterised by three steeply inclined rays but examples with four rays, as is the case here (Fig. 6G), have been reported (Moore *et al.* 2014).

***Allonnia quadrocornuformis* (Ding & Li, 1992) in Ding *et al.* (1992)**

Figure 6A

Figured material. – PMU 21199 from GGU sample 271718, Løndal.

Discussion. – The nomenclative history of *Allonnia quadrocornuformis* (Ding & Li, 1992) in Ding *et al.* (1992) was discussed by Peel & Kouchinsky (2024) who compared the single North Greenland specimen with two specimens from the early Cambrian Xinji Formation of Henan Province, China, described by Qian (1989, pl. 68, figs 1–4). *Allonnia quadrocornuformis* has four rays that rise parallel with each other and are perpendicular to the plane of the basal surface, in contrast with other species of the genus, such as *Allonnia tetrahallis* (Jiang, 1982) in Luo *et al.* (1982), in which the rays are steeply inclined but diverging rather than parallel (Moore *et al.* 2014).

***Allonnia rossica* (Sayutina, 1988) in Vassiljeva & Sayutina (1988)**

Figure 6F, H

Figured material. – PMU 18263 and PMU 18264 from GGU sample 271718, Løndal.

Discussion. – *Allonnia* with four rays are usually referred to *Allonnia tetrahallis*, but specimens illustrated by Moore *et al.* (2014, fig. 9) from the early Cambrian Shiyantou Formation of Yunnan, China, and by Devaere *et al.* (2019) from the Puerto Blanco Formation of Sonora, Mexico, have a more swollen basal part of the rays than these rare specimens from North Greenland, as does a specimen illustrated by Peel *et al.* (2016, fig. 6e) from the Henson Gletscher Formation (late Cambrian Stage 4) in Løndal. In *Allonnia rossica* originally described from the early Cambrian (Botoman Regional Stage) of Middle Asia (Vassiljeva & Sayutina 1988, Vasilieva 1998), the rays are more uniformly tapering and less divergent, which is also the case in a morph with three rays (Fig. 6F). A specimen from Cambrian Stage 4 in Løndal that Peel *et al.* (2016, fig. 6g) assigned to *Allonnia tetrahallis* is better placed here for the same reasons.

***Allonnia?* sp.**

Figure 6E

Figured material. – PMU 18262 from GGU 271492, southern Lauge Koch Land.

Discussion. – A single sclerite from GGU sample 271492, an internal mould that is heavily encrusted with calcium phosphate, appears to have six steeply inclined rays arranged in three closely spaced pairs, although

one pair is broken away (Fig. 6E). The internal moulds of the individual rays are unusually slender but display the characteristic fibrous microstructure typical of cancelloriids (Moore *et al.* 2019, Yun *et al.* 2021, Peel & Kouchinsky 2024). Vassiljeva & Sayutina (1998) proposed *Rosella asteroidea* Vassiljeva, 1998 in Vassiljeva & Sayutina (1998) for a cancelloriid from the early Cambrian of Siberia with six lateral rays, but the conical shape of the individual rays and their low inclination suggests that their Siberian form is a *Chancelloria* in which a central ray is absent.

Phylum Cnidaria, Verrill, 1865
Subphylum Anthozoa Ehrenberg, 1834
Class Octocorallia? Haeckel, 1866
Order Cambroctoconida Peel, 2017

Genus *Cambroctoconus* Park, Woo, Lee, Lee, Lee, Han, Chough & Choi, 2011

Type species. – *Cambroctoconus orientalis* Park *et al.*, 2011, from the Changhia Formation of Shandong Province, China, Cambrian, Miaolingian Series, Drumian Stage.

Discussion. – Park *et al.* (2011, 2016) compared *Cambroctoconus* to octocorallians and staurozoans but placed it as a stem-group cnidarian. Peel (2017b) tentatively assigned cambroctoconids to the Octocorallia on account of the octagonal form, eight-fold septation and the pore system, which he compared to the gastrodermal solenia of octocorallians. Growth of *Cambroctoconus orientalis* in crypts within calcimicrobe reefs from the Zhangxia

Formation (Miaolingian) of Shandong Province, China, was described by Ezaki *et al.* (2020, 2023), but this association is not seen in the phosphatized material from North Greenland described by Peel (2017b) where *Cambroctoconus* occurs with bioclastic limestones. Park *et al.* (2011) proposed that *Cambroctoconus* was closely related to cloudinids in a lineage established during the Ediacaran but diversifying through to the Miaolingian.

***Cambroctoconus koori* Peel, 2017b**

Figure 7A–G

Figured material. – PMU 31705, holotype, PMU 31212, PMU 31707 and PMU 31718; PMU 18266, echinoderm plate with remains of attached *Cambroctoconus koori*. All specimens from GGU sample 271718, Løndal.

Discussion. – *Cambroctoconus koori* Peel, 2017b is known from about 50 specimens from GGU sample 271718 that may be to 3 mm tall. They are usually preserved as internal moulds of the calice or phosphatized coralla. They are initially turbinate (Fig. 7A) but become cylindrical with growth (Fig. 7B), with initial attachment to bioclastic fragments (Fig. 7F). Budding has not been observed, although it was described by Park *et al.* (2011) and Ezaki *et al.* (2023) in well preserved silicified specimens of the type species *Cambroctoconus orientalis*. Internal moulds are characterised by eight radial ridges that were formed between the paired septa described from *Cambroctoconus orientalis* by Park *et al.* (2016; Fig. 7A, B, D). Areas between the ridges contain infilled pores.

Cambroctoconus orientalis and *Cambroctoconus kyrgyzstanicus* Peel, 2014 in Geyer *et al.* (2014), the

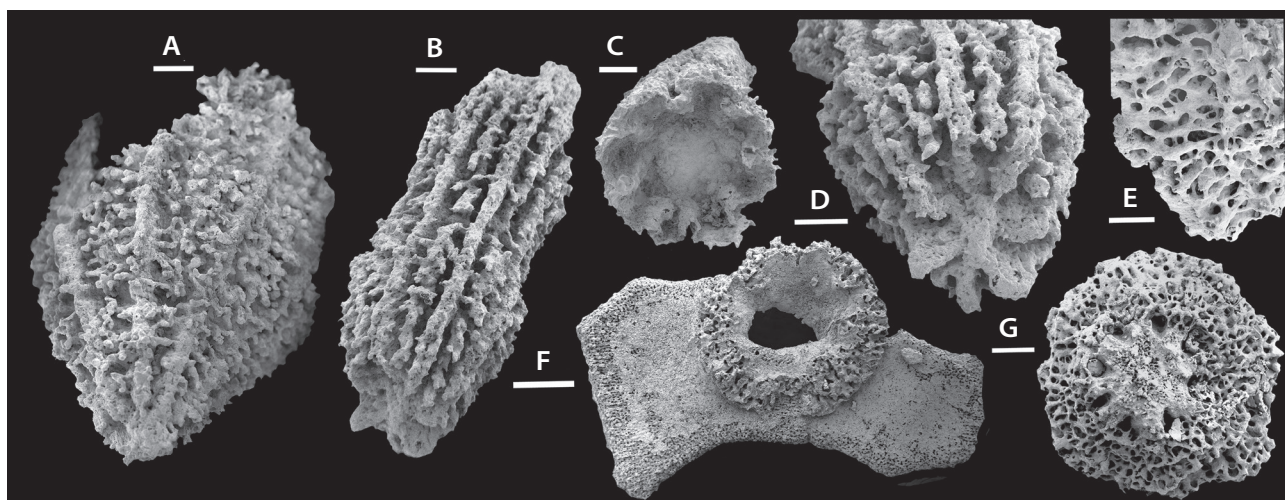


Figure 7. *Cambroctoconus koori* Peel, 2017b from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. GGU sample 271718; A–E, G internal moulds. A – PMU 31705, holotype. B, D – PMU 31718. C – PMU 31707, apertural view showing 8-fold symmetry. E, G – PMU 31212, basal view (G), with detail of pores (E). F – PMU 18266, echinoderm plate with remains of attached *Cambroctoconus koori* with 8-fold symmetry. Scale bars: 40 µm (J); 50µm (D, E, I); 100 µm (C); 200 µm (A, B, D, F, G).

latter described from the Miaolingian Series (Stage 5) of western Kyrgyzstan, are larger than *Cambroctoconus koori* and have a more strongly expressed octagonal form. *Cambroctoconus coreanensis* Park *et al.*, 2016, from the Daegi Formation (Cambrian Series 3, Drumian) of Korea is distinguished by its slender, slightly sinuous form (Park *et al.* 2016).

Coralomorpha Jell, 1984

Discussion. – Coralomorpha is an informal grouping of Cambrian corals and coral-like organisms (Jell 1984; Scrutton 1997, 2015; Debrenne & Reitner 2001; Hicks 2006) that Scrutton (2015) considered were short-lived experiments in cnidarian skeletonization.

Genus *Tavsenicoralla* gen. nov.

LSID. – Zoobank.org:act:870B42F5-42DB-4BB8-A764-910BACA47877

Type species. – *Tavsenicoralla avannaa* sp. nov. from the Henson Gletscher Formation of North Greenland; Cambrian, Wuliuan Stage.

Type horizon and locality. – Upper Henson Gletscher Formation, Løndal, Peary Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – A combination of Hans Tavsen Iskappe and *corallium* (Latin).

Diagnosis. – Multiaxial, with close-packed corallites upto 300 µm in diameter that are oval, often with one or more flattened walls due to close proximity (or shared wall) with adjacent corallites. Maximum observed length of corallites (all broken distally) is about 1 mm. Budding through lateral emergence of daughter corallites that after formation are closed off from the parent corallite internally. Corallites with regular, periodic, shallow constrictions and transverse growth lines. Tabulae and septa not observed. Feminine.

Discussion. – *Tavsenicoralla* gen. nov. differs from the co-occurring *Hensonidendra* gen. nov., described below, by its lack of dichotomous division. Single daughter corallites of *Tavsenicoralla* emerge laterally from the parent corallite (Fig. 8A, D). Internal moulds demonstrate that internal contact between the two corallites was not maintained after budding (Fig. 8B, I, J).

Harklessia Hicks, 2006 from the late lower Cambrian (Stage 4) of Nevada is known from colonies up to 12 cm high and 18 cm wide, preserved in limestone. Corallites have a diameter of 1.2–3.2 mm, about ten times the

dimensions of *Tavsenicoralla*. Hicks (2006, fig. 5.3) illustrated division of a corallite in *Harklessia* without subsequent closing-off of the daughter cell, unlike the complete internal separation of corallites in *Tavsenicoralla* (Fig. 8B, I, J).

Bryomorph, calcareous colonies described by Pruss *et al.* (2022), also from the limestones of the Harkless Formation, are composed of tubes (diameter 40–109 µm) that are smaller than the corallites of *Tavsenicoralla*, but also reproduce by lateral budding. Preservation differences frustrate closer comparison between the two forms. Pruss *et al.* (2022) suggested that the Nevadan material might represent the oldest known mineralized bryozoan, due to similarities with palaeostomate Bryozoa.

***Tavsenicoralla avannaa* sp. nov.**

Figure 8A–D, I, J

LSID. – Zoobank.org:act:A37A3302-613F-45AC-BA88-E29CDAB28B9B

Holotype. – PMU 18267 from GGU sample 271718, Løndal, Henson Gletscher Formation of North Greenland; Cambrian, Wuliuan Stage.

Type horizon and locality. – Upper Henson Gletscher Formation; Cambrian, Miaolingian Series (Wuliuan Stage), Løndal, Peary Land, North Greenland.

Other figured material. – PMU 18268 and PMU 18269 from GGU sample 271718, Løndal.

Etymology. – From *avannaa* (Greenlandic/Kalaallisut), meaning north.

Description. – Type species of *Tavsenicoralla* gen. nov. Multiaxial colonies in which the closely packed corallites are oval in cross-section, but often with one or more flattened walls due to close proximity (or a shared wall) with adjacent corallites. Maximum observed diameter of corallites is about 300 µm, with a maximum observed length of about 1 mm (all corallites are broken distally). Corallites preserve regular, periodic, shallow transverse constrictions (Fig. 8B) and growth lines (Fig. 8A, C). Budding takes place through lateral emergence of daughter corallites (arrows in Fig. 8A, D), which after formation are closed off from the parent corallite internally. Internal septa and tabulae seemingly absent.

Discussion. – All material is broken fragments, so the outer form of the colony is not known. Apart from the holotype (Fig. 8A, C, D), most of the few available specimens are internal moulds in which the tip of the moulds are rounded and clearly separated from adjacent



Figure 8. Cnidaria and holdfasts from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A–D, I, J – *Tavsenicoralla avannaa* gen. et sp. nov., all from GGU sample 271718. A, C, D – PMU 18267, holotype. A – lateral view of colony with arrows indicating budding, enlarged in D. C – sculpture of external surface. B – PMU 18268, internal moulds of adjacent corallites. I, J – PMU 18269, internal moulds of three adjacent corallites. • E–H – holdfasts of *Aetholicopalla adnata* Conway Morris, 1990 in Bengtson *et al.* (1990), all from GGU sample 271492. E, F – PMU 18270. G – PMU 18271. H – PMU 18272, within internal mould of brachiopod. Scale bars: 50 µm (C–E); 100 µm (B, F–J); 200 µm (A).

corallites, including the parent (Fig. 8I). Associations of internal moulds (Fig. 8I, J) often disaggregate into individual corallite moulds as a result of decalcification during sample preparation. Members of an association of disaggregated similar internal moulds were illustrated by Peel *et al.* (2016, fig. 7H–K) from the Henson Gletscher Formation (Cambrian Series 2, late stage 4) in Løndal.

The holotype of *Tavsenicoralla avannaa* preserves the external surface of the corallites and clearly displays lateral budding of daughter corallites (Fig. 8A, arrows with enlargement in 8D) and growth lines that show a slight tendency to flare (Fig. 8C).

Phylum and class uncertain
Order Hyolithelminthida Fisher, 1962
Family Hyolithellidae Walcott, 1886

Genus *Hyolithellus* Billings, 1872

Type species. – *Hyolithus micans* Billings, 1871, lower Cambrian of Troy, New York.

Hyolithellus sp.

Figure 9A–C, F, G

Figured material. – PMU 18273 and PMU 18274 from GGU sample 218831; PMU 18275 and PMU 18276 from GGU sample 271492.

Discussion. – *Hyolithellus* (Fig. 9A–C, F, G) is widely distributed in lower–middle Cambrian strata. It is often interpreted as a cnidarian (Van Iten *et al.* 2014), although Skovsted & Peel (2011) suggested that unusually large specimens in life position from the basal Aftenstjernesø Formation (Cambrian Series 2) of North Greenland may have been stem group annelids. Demidenko (2019) suggested affinity with polychaetes. It is not unlikely that the simple tubes of varying thickness and ornamentation provided domiciles to a variety of organisms. Tubes of *Hyolithellus* are phosphatic and almost parallel sided, with a uniformly circular crosssection, and usually with distinct transverse ornamentation. Most described specimens are broken fragments. A holdfast was described by

Skovsted *et al.* (2021, fig. 11f, g) in a similar species from the Mural Formation, early Cambrian of Alberta, Canada, and additional examples are illustrated here (Fig. 9F, G). The large specimens described by Skovsted & Peel (2011) probably became detached from an original holdfast during growth.

Fragments of Miaolingian specimens from Greenland attain a length of about 3 mm with an inner diameter of the perforated, conical holdfast of about 100 µm (Fig. 9G). Usually, they are ornamented by narrow transverse ridges with concave interareas (Fig. 9A, C) but they are often partially eroded or corroded (Fig. 9B, G). Peel *et al.* (2016, fig. 6j) illustrated similar ornamentation in a specimen from the Henson Gletscher Formation (Cambrian Stage 4, *Bonnina* – *Pagetides elegans* Biozone) in Løndal.

Specimens from the Bastion Formation (Cambrian Series 2) of North-East Greenland described by Skovsted (2006a) have more widely spaced and imbricated transverse growth elements.

Family Torellellidae Holm, 1893

Genus *Torellella* Holm, 1893

Type species. – *Hyolithes laevigatus* Linnarsson, 1871, *Mickwitzia* sandstone, lower Cambrian, Sweden.

Torellella sp.

Figure 9E, H?

Figured specimens. – PMU 18278 from GGU sample 271492 and, tentatively, PMU 18279 from GGU sample 218831, southern Lauge Koch Land.

Discussion. – *Torellella* is widely reported in the Cambrian literature but the type material from the lower Cambrian of Sweden (Holm 1893) is poorly known. Vinn (2006) and Vinn & Mironenko (2021) discussed a possible affinity with *Sphenothallus* Hall, 1847, regarded as a scyphozoan cnidarian (Dzik *et al.* 2017), but Demidenko (2019) supported assignment to polychaetes. A fragment from GGU sample 218831 shows the irregular form often seen in described *Torellella* but has a thicker wall (Fig. 9H).

Genus *Sphenothallus* Hall, 1847

Type species. – *Sphenothallus angustifolius* Hall, 1847 from the Middle Ordovician of New York State.

Sphenothallus sp.

Figure 9D

Figured material. – PMU 18277 from GGU sample 482337, Fimbudal.

Discussion. – Characteristic, trough-like, longitudinal fragments of *Sphenothallus* of the type illustrated by Peel (2021f) from the Silurian of western North Greenland and Skovsted & Holmer (2006) from the lower Cambrian Harkless Formation of Nevada are relatively common in GGU sample 482337. Complete tubes and the distinctive holdfasts described by Dzik *et al.* (2017) and Peel (2021f) have not been observed.

Genus *Coleoloides* Walcott, 1890

Type species. – *Coleoloides typicalis* Walcott, 1890 from the lower Cambrian of Newfoundland.

Coleoloides cf. *typicalis* Walcott, 1890

Figure 9I, J

Figured material. – PMU 18280 from GGU sample 218831, southern Lauge Koch Land, and PMU 18281 from GGU sample 428337, Fimbudal.

Discussion. – Brasier (1984) synonymized numerous of records of *Coleoloides* with the type species *Coleoloides typicalis* Walcott, 1890, noting that the great variation in the number of longitudinal ridges was largely related to the size of the tube. Skovsted (2006a) maintained *Coleoloides prindlei* Lochman, 1956 for specimens from the Bastion Formation of North-East Greenland, as did Peel & Willman (2018), albeit tentatively, for crushed material, from the Buen Formation of Peary Land, North Greenland. The current material is too poor to contribute to the discussion.

Stem-group pentastomids

Genus *Dietericambria* Peel, 2022a

Type species. – *Dietericambria hensoniensis* Peel, 2022a from the Henson Gletscher Formation of North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Dietericambria hensoniensis Peel, 2022a

Figure 10A, B

Figured material. – PMU 39167 from GGU sample 271492, Løndal.

Discussion. – Peel (2022a) described rare vermiform fossils from the upper Henson Gletscher Formation as the oldest known stem-group pentastomids. They are some 15 m.y. older than the exceptionally preserved material from the late Furongian Orsten Lagerstätten in Sweden (Waloszek & Müller 1994, Waloszek *et al.* 2006, Castellani *et al.* 2011). *Dietericambria hensoniensis* is



Figure 9. Tubular fossils from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A–C, F, G – *Hyolithellus* sp. A, C – PMU 18273 from GGU sample 218831. B – PMU 18274 from GGU sample 218831, with holdfast. F – PMU 18275 from GGU sample 271492, with holdfast. G – PMU 18276 from GGU sample 271492, with holdfast. • D – *Sphenothallus* sp., PMU 18277 from GGU sample 482337, longitudinal fragment. • E, H – *Torellella* sp., E, PMU 18278 from GGU sample 271492, H, PMU 18279 from GGU sample 218831. • I, J – *Coleoloides* cf. *typicalis* Walcott, 1889. I – PMU 18280 from GGU 218331, F – PMU 18281 from GGU sample 482337. Scale bars: 100 μ m (F, H); 200 μ m (A–E, G, I–K).

characterised by two pairs of minute cephalic limbs and a median cephalic axial complex in which the mouth has not been identified (Fig. 10A). Isolated hooks from the same collection can be compared to the cephalic grasping hooks of present day eupentastomids (Fig. 10E). Spicules with a central spine and flat ornamented base (Fig. 21G) were compared by Peel (2022a) to the copulatory hooks of males of the present day *Raillietiella frenatus* (Hett, 1915). However, direct association of both structures with *Dietericambria hensoniensis* is lacking.

Total group Priapulida

Genus *Inuitiplaskus* Peel, 2022b

Type species. – *Inuitiplaskus kouchinskyi* Peel, 2022b, from the upper Henson Gletscher Formation of North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Inuitiplaskus kouchinskyi Peel, 2022b

Fig. 10C, D, G, H

Figured material. – PMU 28893 from GGU sample 271492, Løndal.

Discussion. – This single specimen was interpreted by Peel (2022b) as the hatching larva of a priapulid worm after comparison with the much smaller larvae of present day *Priapulius caudatus* Lamarck, 1816 and *Halicryptus spinulosus* Siebold, 1849 described by Janssen *et al.* (2009) and Wennberg *et al.* (2009).

Phylum Euarthropoda Lankester, 1904 (see Ortega-Hernández 2014)

Bivalved arthropods

Discussion. – Peel (2023a) described a number of deformed bivalved arthropods from GGU samples 271492 and 271718 in which the phosphatized valves are partly broken away, revealing internal structures. Both indeterminate bradoriids and phosphatocopids are present. The internal structures are poorly preserved but mineralized sheets that seem to represent phosphatized inner lamellae are common (Peel 2023a, fig. 8a–c, k, l). Other structures include fans of setae and possible limbs (Peel 2023a, fig. 7h, k, l). Fragments, such as broken spines (Fig. 12J) may be derived from bivalved arthropods; they occur together with various other arthropod fragments, such as fragments of abdomen (Fig. 10F).

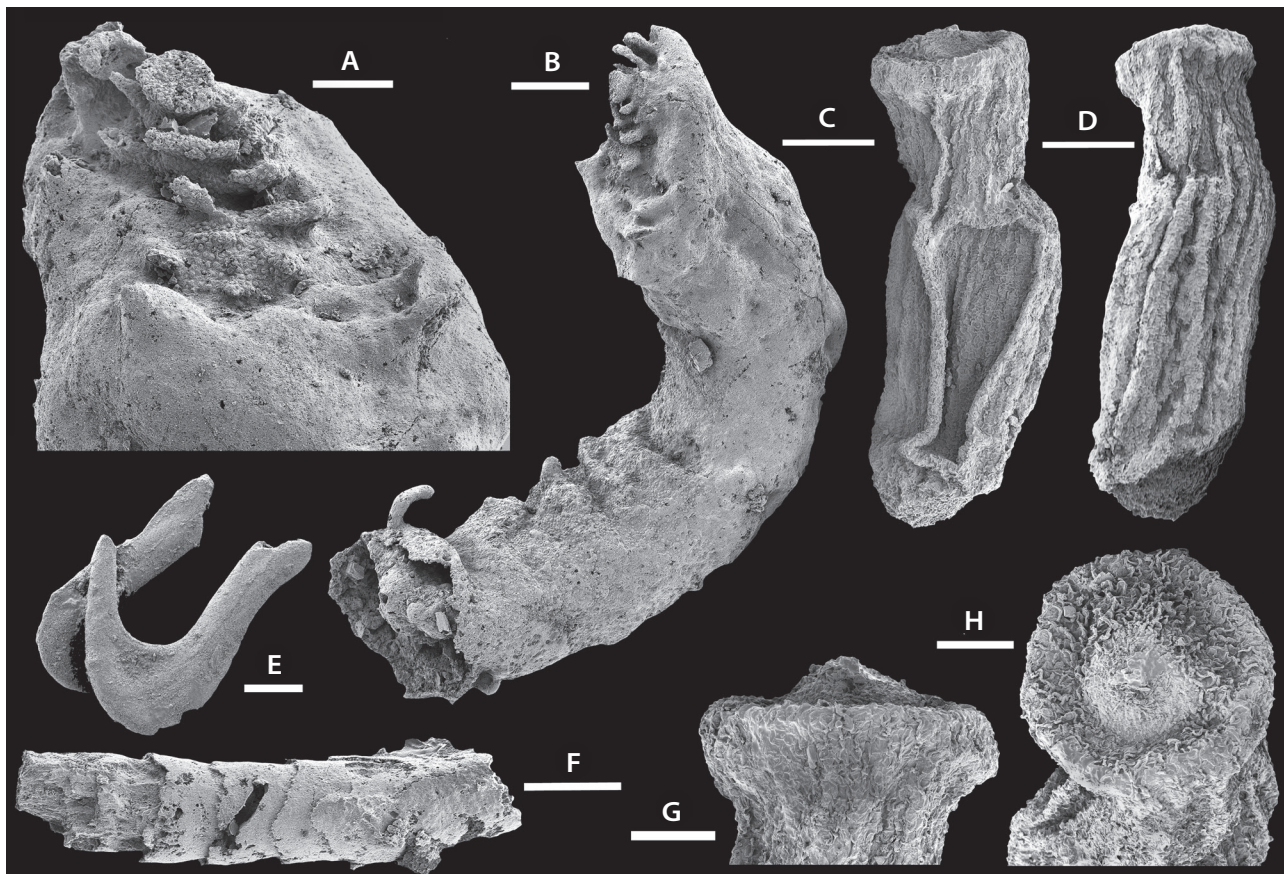


Figure 10. Pentastomid, priapulid and euarthropod from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A, B – *Diatericambria hensoniensis* Peel, 2022c, PMU 39167 from GGU sample 271492, holotype, oblique lateral view with detail of undersurface of the head (A). • C, D, G, H – *Inuitiplaskus kouchinskyi* Peel, 2022b, PMU 28893 from GGU sample 271492, holotype. C, D – lateral views. G – lateral view of anterior rim. H – anterior surface. • E – pentastomid cephalic hooks? PMU 36170 from GGU sample 218831. • F – euarthropod abdomen with telescopic segments, PMU 39678 from GGU sample 271718. Scale bars: 50 μ m (A); 100 μ m (B, E–H); 200 μ m (C, D).

Order Bradoriida Raymond, 1935
Family Beyrichonidae? Ulrich & Bassler, 1931

Genus *Galeopsis* Hinz-Schallreuter, 1993

Type species. – *Galeopsis glabra* Hinz-Schallreuter, 1993, basal Monastery Creek Formation, Queensland, Australia; Cambrian, Miaolingian Series, Wuliuan Stage (Tempeltonian Regional Stage).

Galeopsis? sp.
Figure 11S

Figured material. – PMU 18290 from GGU sample 271718, Løndal.

Discussion. – This single, dorso-ventrally flattened specimen is compared tentatively to *Galeopsis* Hinz-Schallreuter, 1993 on account of the smooth valve with a median spine (Fig. 11S, arrow). However, the type species, *Galeopsis glabra* Hinz-Schallreuter, 1993, has an

unusually tall valve (length:height ratio 1.2:1), seemingly much taller than the specimen from North Greenland.

Family Mongolitubulidae Topper, Skovsted, Harper & Ahlberg, 2013a

Genus *Mongolitubulus* Missarzhevsky, 1977

Type species. – *Mongolitubulus squamifer* Missarzhevsky, 1977 from the lower Cambrian of Mongolia.

Mongolitubulus reticulatus Kouchinsky, Bengtson, Clausen, Gubanov, Malinky & Peel, 2011
Figure 12E, F, H, I

Figured material. – PMU 18292 and PMU 18293 from GGU sample 218831. PMU 39673 from GGU sample 271492. Both samples from southern Lauge Koch Land.

Description. – The two illustrated spines are almost 1 mm long, but their bases are broken. They are initially straight

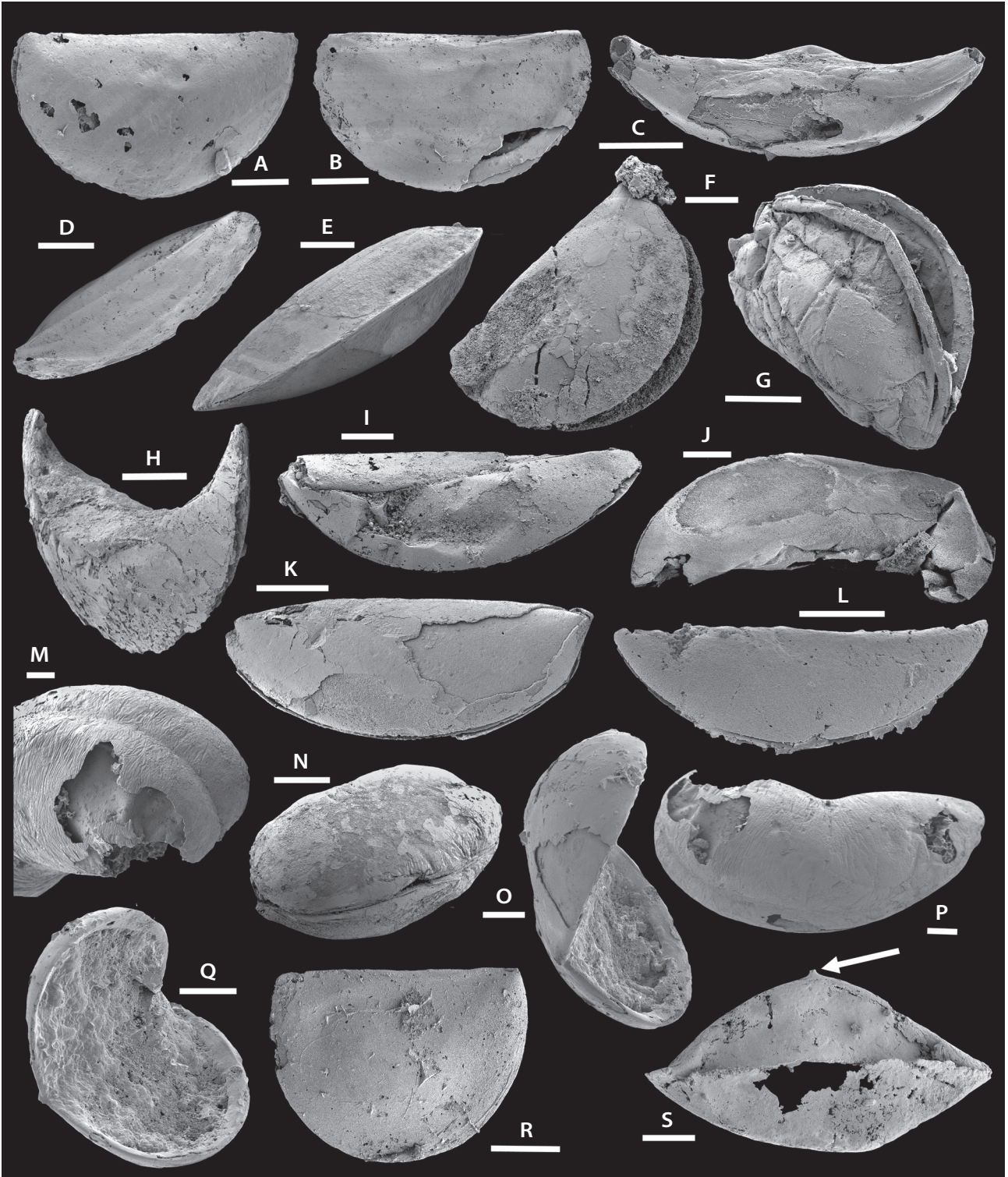


Figure 11. Bivalved arthropods from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. GGU sample 271492 unless stated. • A, B, D–G, O, Q, R – *Dabashanella cf. retrosvinga* Huo, Shu & Fu, 1983 in Huo *et al.* (1983). A – PMU 39680 B, D – PMU 39681, lateral and dorso-lateral views with doublure (B). E – PMU 39682. F – PMU 18282. G – PMU 18283 from GGU 271718. O, Q – PMU 39672 from GGU 271718. R – PMU 18284 from GGU sample 271718. • C, H – *Dabashanella? lunaiformis* sp. nov. C – PMU 39684 from GGU sample 271718. H – PMU 39685. • I, L – *Dabashanella longa* (Zhang, 2023). I – PMU 18285 from GGU 271718. J – PMU 18286, crushed carapace. K – PMU 18287. L – PMU 18288 from GGU sample 271718. • M, P – Bradoriida? sp. indet., PMU 39690 from GGU sample 218331. • N – Phosphatocopida sp. indet., PMU 18289. • S – *Galeopsis?* sp., PMU 18290 from GGU sample 271718, crushed specimen showing lateral spine (arrow). Scale bars: 50 μ m (N, O); 100 μ m (C, E, F, G–M, P–S); 200 μ m (A, B, D).

and slowly tapering, but their robust tips curve through about 90 degrees to a fine, smooth point (Fig. 12E, F, H). Ornamentation consists of a reticulation of sharply defined, irregular, generally six-sided polygons (diameter 5–20 µm) with small tubercles, usually at the point of intersection of the polygon walls. A deformed carapace from GGU sample 271492 displays the same reticulation but retains no indication of the attachment of large spines (Fig. 12F).

Discussion. – *Mongolitubulus reticulatus* Kouchinsky, Bengtson, Clausen, Gubanov, Malinky & Peel, 2011 was described from the Kuonamka Formation (Miaolingian Series, Wuliuan Stage, *Kuonamkites* Biozone of Bol'shaya Kuonamka, northern Siberia (Kouchinsky *et al.* 2011). In North Greenland it is currently known only from the illustrated spines from GGU sample 218831 (Fig. 12E, H, I) and a deformed carapace from GGU sample 271492 (Fig. 12F).

Mongolitubulus squamifer Missarzhevsky, 1977 and *Mongolitubulus henriksenii* Skovsted & Peel, 2001, described in North and North-East Greenland from the lower Henson Gletscher Formation and Bastion Formation, respectively (Peel & Blaker 1988, Skovsted & Peel 2001, Skovsted 2005), have a scale-like spinose ornamentation in contrast to the reticulation of *Mongolitubulus reticulatus*. *Mongolitubulus unispinosa* Topper, Skovsted, Brock & Paterson, 2007 from the lower Cambrian Mernmerna Formation of South Australia developed spines with a similar curvature to *Mongolitubulus reticulatus* from North Greenland, but their ornamentation is also spinose rather than reticulate. Topper *et al.* (2007) considered carapaces, but not spines, assigned to *Mongolitubulus henriksenii* by Skovsted (2005) to be better placed in *Mongolitubulus unispinosa*.

Mongolitubulus spinosus (Hinz, 1987), originally described from the lower Cambrian of the United Kingdom, but subsequently from the upper Emyaksin and lower Kuonamka formations (Atdabanian and Botoman Regional Stages) of northern Siberia (Kouchinsky *et al.* 2015), has an ornamentation resembling that in *Mongolitubulus unispinosa*. Irregular polygons coalesce to form transverse ridges in which the adapical margins are raised and pointed.

Mongolitubulus aspermarchaera Topper, Skovsted, Harper & Ahlberg, 2013a from the Alum Shale Formation (middle Furongian) of Västergötland, southern Sweden, and *Mongolitubulus tunpere* Smith, Brock, Paterson & Topper (2014) from the Wuliuan Stage (Templetonian Regional Stage) of central Australia differ from *Mongolitubulus reticulatus* in that the carapace and large associated spines are mainly ornamented with small tubercles rather than the prominent reticulation of *Mongolitubulus reticulatus*.

Family Svealutidae Öpik, 1968

Genus *Liangshanella* Huo, 1956

Type species. – *Liangshanella liangshanensis* Huo, 1956 from the lower Cambrian of Shaanxi, China.

Liangshanella? qassutit sp. nov.

Figure 12A–C

LSID. – Zoobank.org:act:6C8D9E22-F365-4A2C-942A-68299FAF6CDC

Holotype. – PMU 39671 from GGU sample 218831, southern Lauge Koch Land, Henson Gletscher Formation, Wuliuan Stage.

Type horizon and locality. – Upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – From qassutit (Greenlandic/Kalaallisut), meaning fishing net, referring to the polygonal ornamentation.

Diagnosis. – Postplete, uniformly convex shields without lobes; incipient admarginal brim. Ornamentation of polygonal rounded ridges.

Description. – Postplete, equivalved, bivalved carapace, with height about two thirds of length, and shields that are uniformly convex, without lobes. Free margin smoothly curved, without marked changes in curvature. Greatest height is at about two thirds of length; greatest length (about 400 µm as preserved) at about three quarters of the height (Fig. 12A, B). Free margin with very narrow admarginal groove and brim; doublure absent but fine grooves immediately adjacent to the margin on the inner surface (Fig. 12C). Dorsum shallowly convex in lateral profile (Fig. 12A), with straight hinge (arrow in Fig. 12B). Posterior cardinal corner sharply angular; anterior cardinal corner with short, upwardly directed spine (Fig. 12C, the broken spine arrowed). Ornamentation consists of ridges in an irregular pattern of equidimensional polygons near the posterior margin but the polygons become elongate towards the antero-dorsal extremity.

Discussion. – The assignment of the only known specimen to *Liangshanella* Huo, 1956, first illustrated by Peel (2023a, fig. 5a), is arbitrary on account of the lack of a well-developed admarginal brim and groove and the presence of polygonal ornamentation, although *Liangshanella? sayutinae* (Melnikova, 1988), as illustrated by Melnikova *et al.* (1997) from the lower Cambrian of Transbaikalia

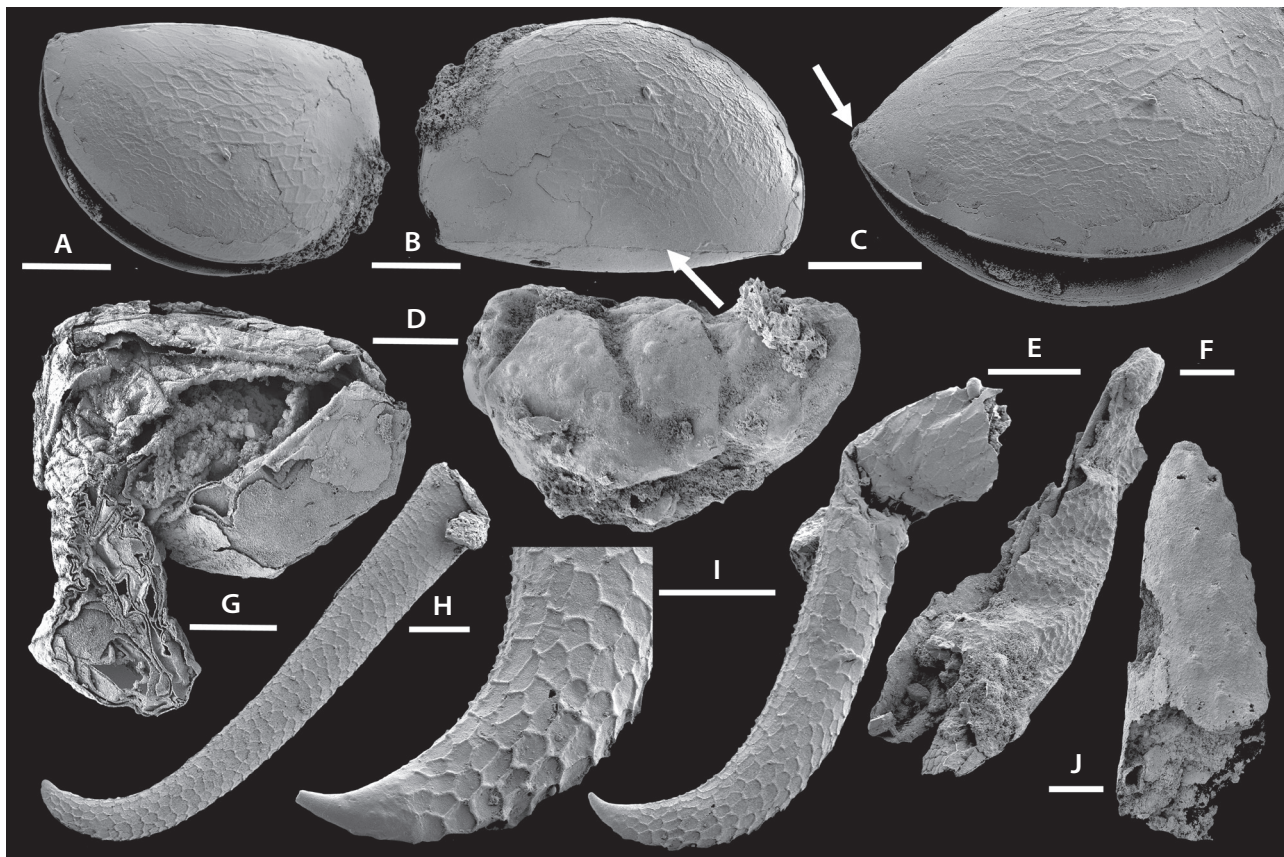


Figure 12. Bivalved arthropods from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. From GGU sample 218831 unless stated. • A–C – *Liangshanella? qassutit* sp. nov., PMU 39671 from GGU sample 218831, holotype. Arrow in B indicates the hinge line; arrow in C indicates the broken cardinal spine. • D – Bradoriid sp. indet. 1, PMU 18291 from GGU sample 271492. • E, F, H, I – *Mongolitubulus reticulatus* Kouchinsky, Bengtson, Clausen, Gubanov, Malinky & Peel, 2011. E, I – PMU 18292 from GGU sample 218831. F – PMU 39673 from GGU sample 271492. H – PMU 18293 from GGU sample 218831. • G – Hymenocarine arthropod sp. indet., PMU 39694 from GGU sample 271718. • J – Bradoriid? spine, PMU 18294 from GGU sample 271718. Scale bars: 50 µm (I); 100 µm (A–C, E–H, J); 200 µm (D).

and Skovsted (2006a) from the Bastion Formation of North-East Greenland has a relatively narrow brim. The posterior margin in the latter material from North-East Greenland has a pronounced angulation not present in *Liangshanella? qassutit*. *Liangshanella? nivalis* Peel, Streng, Geyer, Kouchinsky & Skovsted, 2016 from the lower member of the Henson Gletscher Formation (Cambrian Series 2, Stage 4) in Løndal is delimited by its prominent admarginal brim and lack of polygonal ornamentation. The prominent polygonal ornamentation is not seen in other species of *Liangshanella* but similar ornamentation was illustrated by Wrona (2009, fig. 15) in a preplete specimen from lower Cambrian erratics in West Antarctica that he referred to *Dabashanella? sp. 2*. The presence of thin, generally exfoliated layers near the free margin in the holotype may suggest that ornamentation is more weakly developed on the outermost shield laminae.

Liangshanella? qassutit differs from *Dabashanella* cf. *retroswinga* Huo, Shu & Fu, 1983 in Huo *et al.* (1983) (Fig. 11A, B, R) in its apparent lack of a broad doublure, more globose form and the polygonal ornamentation

Bradoriid sp. indet. 1

Figure 12D

Figured material. – PMU 39679 from GGU sample 271492, southern Lauge Koch Land.

Discussion. – This deformed and poorly preserved specimen is ornamented with low, irregularly distributed tubercles of variable size (Peel 2023a, fig. 5k).

Bradoriida? sp. indet.

Figure 11M, P

Figured material. – PMU 39690 from GGU sample 218831, southern Lauge Koch Land.

Discussion. – Peel (2023a, fig. 7n–p) interpreted this specimen as the phosphatized internal mould of the integument of a univalved carapace. The inflated form stands in contrast to the deformation seen in most specimens in equivalent samples and suggests very early

mineralization. The median ventral groove (Fig. 11M) represents the line of junction between opposing lateral shields, but the preserved surface of the internal mould continues across it without break. The lack of an inner doublure supports tentative assignment to Bradoriida.

Order Phosphatocopida Müller, 1964
Family Dabashanellidae Zhao, 1989

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

Type species. – *Dabashanella hemicyclica* Huo, Shu, & Fu, 1983 in Huo et al. (1983), lower Cambrian Stage of China.

Discussion. – The systematic history of Dabashanellidae Zhao, 1989 and its nominative genus was reviewed by Peel (2023a) who noted that *Dabashanella* Huo, Shu, & Fu, 1983 in Huo et al. (1983) was univalved and possessed a well-developed doublure (Fig. 11B). *Dabashanella*, especially *Dabashanella* cf. *retroswinga* Huo, Shu, & Fu, 1983 in Huo et al. (1983), is common in GGU samples 218831, 271492 and 271718 but most specimens are deformed.

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

Figure 11A, B, D–G, O, Q, R

Figured material. – PMU 18282 and PMU 39680–39682 from GGU sample 271492, southern Lauge Koch Land. PMU 18283, PMU 18284 and PMU 39672 from GGU sample 271718, Løndal.

Discussion. – Peel (2023a) compared the North Greenland material with specimens from the lower Cambrian Heilinpu Formation of Yunnan, China, described by Huo et al. (1983) and summarized other literature. *Dabashanella hemicyclica* Huo, Shu, & Fu, 1983 in Huo et al. (1983), as illustrated by Hou et al. (2002, fig. 25), is characterised by short cardinal spines not seen in the Greenland material, although Melnikova & Mambetov (1990) assigned specimens with short cardinal spines from the lower Cambrian of Tien-Shan to *Dabashanella retroswinga*. Hou et al. (2002) placed numerous genera and very many species established in China as junior synonyms of *Dabashanella hemicyclica*, including *Dabashanella retroswinga*.

***Dabashanella longa* (Zhang, 2023)**

Figure 11I–L

Figured material. – PMU 18286 and PMU 18287 from GGU sample 271492, southern Lauge Koch Land. PMU 18285 and PMU 18288 from GGU sample 271718, Løndal.

Discussion. – *Dabashanella longa* Zhang, 2023 was originally described from the lower Cambrian Shuijingtuo Formation of Hubei Province, China (Zhang 2023). Specimens from the upper Henson Gletscher Formation of North Greenland are more than twice as long as high, proportionately longer than in the type material. In lateral perspective the ventral margin is shallowly convex, varying from symmetrical (amplete) to steepened at the presumed anterior. The dorsal surface in lateral profile varies from straight to shallowly convex, but this curvature is easily affected by deformation. Terminations are acute, but not spinose. A doublure is present but its width is not known; Zhang (2023) stated that it is 10% of the height. The carapace surface is smooth.

Phaseolella curvata Zhang, 1987 was originally described from the lower Cambrian Shuigoukuo Formation of Henan Province, China (Zhang 1987) but the genus was regarded as a junior synonym of *Dabashanella* by Hou et al. (2002). In overall form, the crescentic carapace is similar to *Dabashanella longa* but the longitudinal dorsal profile is concave. The development of concave curvature of the dorsal surface between its two extremities is a common deformational feature in phosphatocopids (Hou et al. 2002), including the upper Henson Gletscher Formation (Peel 2023a, fig. 5g), although this is not immediately visible in Zhang's (1987, fig. 13) illustrations.

***Dabashanella? lunaiformis* sp. nov.**

Fig. 11C, H

2023a Phosphatocopida spp. indet. – Peel, p. 112, fig. 7f, g.

LSID. – Zoobank.org:act:C661B7EF-9136-48FF-9F2D-715C3A9126C1

Holotype. – PMU 39685 from GGU sample 271492, Henson Gletscher Formation, southern Lauge Koch Land; Cambrian, Miaolingian Series, Wuliuan Stage.

Type horizon and locality. – Upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – From *lunae* (Latin), meaning crescent moon, referring to the lateral profile.

Other figured material. – PMU 39684 from GGU sample 271718, Løndal.

Description. – Univalve, amplete, with length more than twice the height at the median point. Ventral margin shallowly convex in lateral view, continuing into terminations that extend high above the shallowly concave dorsal surface (Fig. 11H) to give the crescent moon

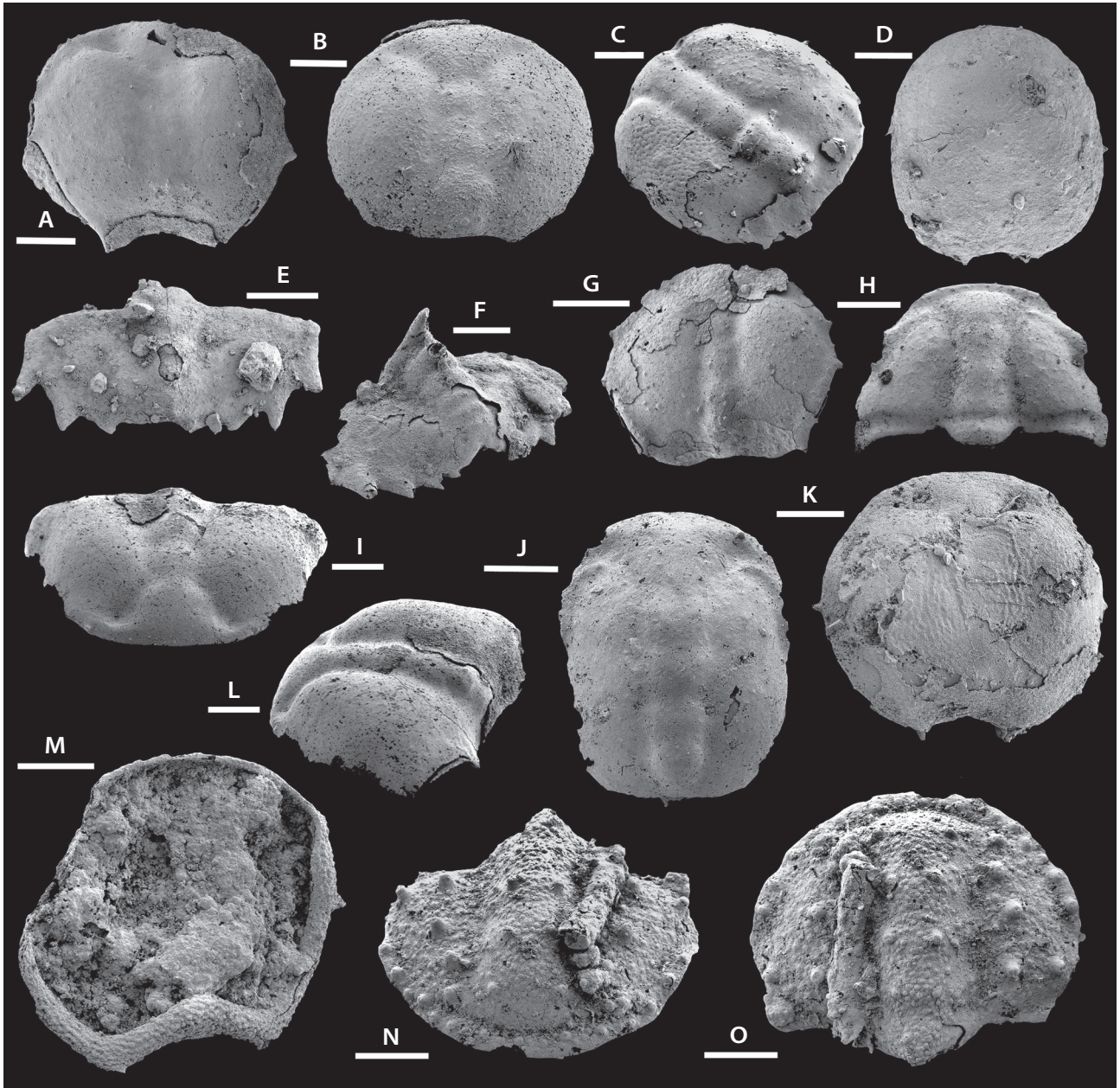


Figure 13. Trilobite early growth stages from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. GGU sample 271718 unless stated. A – PMU 18295 from GGU sample 271492. B – PMU 18296 from GGU sample 271492. C – PMU 18297. D – PMU 18298. E, F – PMU 18299 from GGU sample 271492. G – PMU 18300. H – PMU 18301. I, L – PMU 18302. J – PMU 18303. K – PMU 18304. M – PMU 18305 from GGU sample 271492. N, O – PMU 18306. Scale bars: 100 μ m (A–D, I–M); 200 μ m (E–H, N, O).

appearance. Doublure present but poorly known. Carapace may be inflated on each side adjacent to dorsal zone of flexure at their mid-point (Fig. 11C). Carapace smooth.

Discussion. – Specimens of *Dabashanella? lunaiformis* sp. nov. are rare. It is only tentatively referred to the genus on account of its prominent distal terminations. *Dabashanella hemicyclica*, the type species of *Dabashanella*, has a much shorter carapace and lacks the strongly upturned terminations. *Dabashanella curvata* (Zhang, 1987) from

the early Cambrian Shuigoukou Formation of Xichuan, Henan Province, China, has an elongate, shallowly crescentic carapace but lacks the strong tapered and upturned terminations seen in the Greenland species. The dorsal surface of *Dabashanella longa* from the Shuijingtuo Formation of Hubei Province, China, (Zhang 2023) has a straight to shallowly convex longitudinal profile.

Phosphatocopida sp. indet.

Figure 11N

Figured material. – PMU 18289 from GGU sample 271492, southern Lauge Koch Land.

Discussion. – This strongly inflated specimen is interpreted as an internal mould comparable to *Bradoriida?* sp. indet. (Fig. 11M, P), but the presence of an internal doublure along the free margin supports interpretation as a phosphatocopid.

Hymenocarine arthropod sp. indet.

Fig. 12G

Figured material. – PMU 39694 from GGU sample 271718, Løndal.

Discussion. – A short, segmented abdomen extends beyond the postero-lateral margins of the deformed carapace (Fig. 12G) in a specimen referred to Bivalved arthropod sp. indet. by Peel (2023a). The phosphatized internal structures were described by Peel (2023a, fig. 8g–j).

Class Trilobita Walch, 1771

Discussion. – Disarticulated sclerites of agnostids (Fig. 2), some of which were cited by Robison (1984), and trilobites often cover bedding surfaces in GGU sample 271492. Some 10–15 species appear to be present but this millimetre-sized material is not described herein. Acid residues of this sample and GGU sample 271718 contain numerous well-preserved protaspids and small meraspids, some of which are illustrated here (Fig. 13). *Corynexochid* anaprotaspids and early and late meta-protaspids dominate (Fig. 13A–C, G, I–L) but smooth ptychopariid anaprotaspids are also well represented (Fig. 13D). Distinctive forms include a spinose small meraspid pygidium (Fig. 13E, F) and a tuberculate oryctocephalid cranidium (Fig. 13N, O).

On the basis of the agnostids, this horizon is assigned to the *Ptychagnostus gibbus* Biozone (Babcock *et al.* 2007, fig. 2) and characteristic forms are illustrated in Figure 2. *Ptychagnostus intermedius* (Tullberg, 1880) of Robison (1984) was reassigned to *Ptychagnostus sinicus* Lu, 1957 by Ahlberg *et al.* (2007).

Phylum Lobopodia Cavalier-Smith, 1998

Genus *Microdictyon* Bengtson, Matthews & Missarzhevsky, 1986

Type species. – *Microdictyon effusum* Bengtson, Matthews & Missarzhevsky, 1986 from the lower Cambrian of Ma-lyj Karatau.

***Microdictyon* sp.**

Figure 19A, B

Figured material. – PMU 18340 from GGU sample 271492, southern Lauge Koch Land.

Discussion. – Peel in Kouchinsky *et al.* (2011, p. 39) tentatively reported the onychophoran (lobopod) *Microdictyon robisoni* Bengtson, Matthews & Missarzhevsky, 1986 from the Henson Gletscher Formation (*Ptychagnostus gibbus* Biozone) of North Greenland, although Peel *et al.* (2016) described *Microdictyon robisoni* from the slightly older *Ovatoryctocara granulata* assemblage (Cambrian Series 2, latest Stage 4) in Løndal. The currently described inflated, oval specimen from GGU sample 271492 lacks the tall, mushroom-shaped nodes of *Microdictyon robisoni* such that the oval caps to the nodes are only slightly elevated above the underlying reticulate frame (Fig. 19A, B). The central part of each cap is raised with a flattened upper surface and this may show traces of tubercles (Fig. 19A). The terminal caps in specimens of *Microdictyon robisoni* illustrated by Kouchinsky *et al.* (2011, figs 28, 29) from the Kuonamka Formation (*Kuonamkites* Biozone) differ in being inclined obliquely to the stem of the node. In a fragment from the Kuonamka Formation assigned by Kouchinsky *et al.* (2011, fig. 31) to *Microdictyon sphaeroides* Hinz, 1987, the nodes also lack a long stem, as in the Løndal specimen (Fig. 19A, B). However, the central area of the caps is strongly elevated and asymmetric in contrast to *Microdictyon* sp. Kouchinsky *et al.* (2011) suggested that the asymmetry of the node caps may reflect the orientation of the sclerites along the dorsum of the onychophoran, but such asymmetry is not present in the single available specimen from GGU sample 271492.

Topper *et al.* (2013b) described evidence of moulting based on conjoined lobopodian sclerites assigned to *Onychodictyon* sp. that were collected from 23 m above the base of the lower member of the Henson Gletscher Formation (82° 09' N, 42° 25' W; Geyer & Peel 2011, fig. 4) in Freuchen Land, North Greenland (Fig. 1F). The sclerites showed repetition of the basal circum-marginal area. Moulting in *Microdictyon* from China described by Chen *et al.* (2024) revealed stacking of several sclerites resulting from incomplete detachment of the old sclerites following formation beneath of the new sclerite. Similar repetition around the periphery of the specimen of *Microdictyon* sp. from GGU sample 271492 (Fig. 19B) is also attributed to a single phase of moulting.

Phylum Chaetognatha? Leuckart, 1854
'Protoconodonta'



Figure 14. Conodonts and juvenile brachiopods from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. GGU sample 271718 unless stated. • A, D, E, H – *Gapparodus* cf. *bisulcatus* (Müller, 1959). A – PMU 18307. D – PMU 18308 from GGU sample 218831. E – PMU 18309 from GGU sample 482337. H – PMU 18310. • B, C – *Paibiconus* cf. *proarcuratus* Dong, 1993. B – PMU 18311. C – PMU 18312. • F, I – *Hertzina* cf. *elongata* Müller, 1959. F – PMU 18313 from GGU sample 271492. I – PMU 18314. • G – *Hagionella* sp. – PMU 18315. • J, N – juvenile rhynchonelliformean brachiopods. J – PMU 18317 from GGU sample 271492. N – PMU 18316. • K – *Micromitra* sp., PMU 18318 from GGU sample 482337. • L, M – bostfordioid brachiopods. L – PMU 18319. M – PMU 18320. Scale bars: 100 µm (A, G, I, L, M); 200 µm (C–F, H, J, K); 300 µm (B).

Genus *Gapparodus* Abaimova, 1978

Type species. – *Hertzina*? *bisulcata* Müller, 1959 from the Cambrian of Sweden.

Gapparodus cf. *bisulcatus* (Müller, 1959)

Figure 14A, D, E, H

Figured material. – PMU 18307 and PMU 18310 from GGU sample 271718, Løndal; PMU 18308 from GGU sample 218831, southern Lauge Koch Land; PMU 18309 from GGU sample 482337, Fimbuldal.

Discussion. – Slender cones of *Gapparodus* cf. *bisulcatus* compare closely with specimens from the *Bergeroniellus expansus* Biozone (late Botoman Stage, Cambrian Stage 4) and the *Kuonamkites* Biozone (Cambrian Stage 5) of the

Kuonamka Formation in northern Siberia (Kouchinsky *et al.* 2011, 2015). Broken specimens are difficult to distinguish from *Gumella cuneata* Müller & Hinz, 1991. The *Gapparodus bisulcatus*–*Westergaardodina brevidens* Biozone of Drumian Stage (Cambrian Series 3) age, was the lowest of four conodont biozones recognised by Dong & Bergström (2001), but *Gapparaodus bisulcatus* ranges down into the early Cambrian in northern Siberia, Greenland and China (Yang *et al.* 2015). Laurentian occurrences were reported previously from the middle Cambrian (Miaolingian Series) by Clark & Robison (1969) and Landing (1974).

Genus *Hagionella* Xie, 1990

Type species. – *Protohertzina*? *cultrata* Missarzhevsky, 1977 from the lower Cambrian of Siberia.

***Hagionella* sp.**

Figure 14G

Figured material. – PMU 18315 from GGU sample 271718, Løndal.

Discussion. – *Hagionella* sp. is known only from a few broken elements in GGU samples 218331 and 271718 that show the characteristic blade-like flange on the supra-apical surface of large specimens (Fig. 14G). Well preserved specimens of the type species, *Hagionella cultrata* (Missarzhevsky, 1977), were described by Peel *et al.* (2016) from lower levels in the Henson Gletscher Formation (Cambrian Series 2, late Stage 4; *Ovatoryctocara granulata* assemblage) on the western side of Løndal. Kouchinsky *et al.* (2011, 2015) described *Hagionella cultrata* from the *Kuonamkites* Biozone (Cambrian, Wuliuan Stage) from the Kuonamka Formation and the underlying Emyaksin Formation (Cambrian Stage 3, *Delgadella anabara* Biozone) in Siberia. Qian *et al.* (2004) reviewed records from China, Siberia, Kazakhstan and Mongolia, see also Yang *et al.* (2015).

Genus *Hertzina* Müller, 1959

Type species. – *Hertzina americana* Müller, 1959 from the Cambrian of Nevada, USA.

***Hertzina* cf. *elongata* Müller, 1959**

Figure 14F, I

Figured material. – PMU 18313 from GGU sample 271492, southern Lauge Koch Land; PMU 18314 from GGU sample 271718, Løndal.

Discussion. – Rare specimens of *Hertzina elongata* Müller, 1959 were described by Peel *et al.* (2016) from Cambrian Stage 4 (*Ovatoryctocara granulata* assemblage in Løndal), but they are more slender and with a less acute transverse profile of the supra-apical surface than the Wuliuan Stage material.

Genus *Paibiconus* Dong, 1993

Type species. – *Paibiconus proarcuatus* Dong, 1993 from the Cambrian, Miaolingian Series (Drumian Stage)–early Furongian Series of South China.

***Paibiconus* cf. *proarcuatus* Dong, 1993**

Figure 14B, C

Figured material. – PMU 18311 and PMU 18312 from GGU sample 271718.

Discussion. – *Paibiconus proarcuatus* Dong, 1993 is distinguished by the sharp, median, costa on the supra-apical surface of the slender simple cone-shaped element. Type material illustrated by Dong (1993) and Dong & Bergström (2001) has a more slender form than the slightly older Greenland material and expands more abruptly close to the base. In *Paibiconus* cf. *proarcuatus* the element expands more gradually as the base is approached (Fig. 14C) and, in lateral view (Fig. 14B), shows a greater rate of expansion.

Phylum Brachiopoda Duméril, 1806

Discussion. – Rhynchonelliformean and linguliformean, mainly acrotretid, brachiopods are common in the current samples but are not described herein. In acid residues, small internal moulds of the calcareous rhynchonelliformeans may show rich assemblages of the phosphatised galleries of euendoliths (Peel 2024a). Juvenile linguliformeans are common in acid residues (Fig. 14J–N).

Clade Pan-Brachiopoda Carlson & Cohen, 2020

Class Stenothecoida Yochelson, 1960

Discussion. – Peel (2021d) described stenothecoids from the upper Henson Gletscher Formation (Wuliuan Stage) of North Greenland based on phosphatized internal moulds, rare silicified shells and crack-out material in limestone. Evidence of fibrous pedicle attachment beneath the apex (posterior) of internal moulds of juveniles about 1 mm in length (Fig. 15B, G) supported a relationship with brachiopods rather than the affinity with molluscs that was suggested by Yochelson (1969). Johnston & Streng (2021) proposed that stenothecoids represent a stem group of panbrachiopods following detailed morphological analysis of silicified material from British Columbia, Canada.

Genus *Stenothecoides* Resser, 1938

Type species. – *Stenotheca elongata* Walcott, 1884, Prospect Peak, Eureka District, Nevada, USA; Cambrian, Miaolingian Series, Wuliuan Stage.

***Stenotheca* cf. *elongata* Walcott, 1884**

Figure 15D

Figured material. – MGUH 33948 from GGU sample 271492.

Discussion. – This internal mould was described in detail by Peel (2021d) who compared it to *Stenothecoides* cf. *elongata* of Rasetti (1954) from the upper Mount Whyte

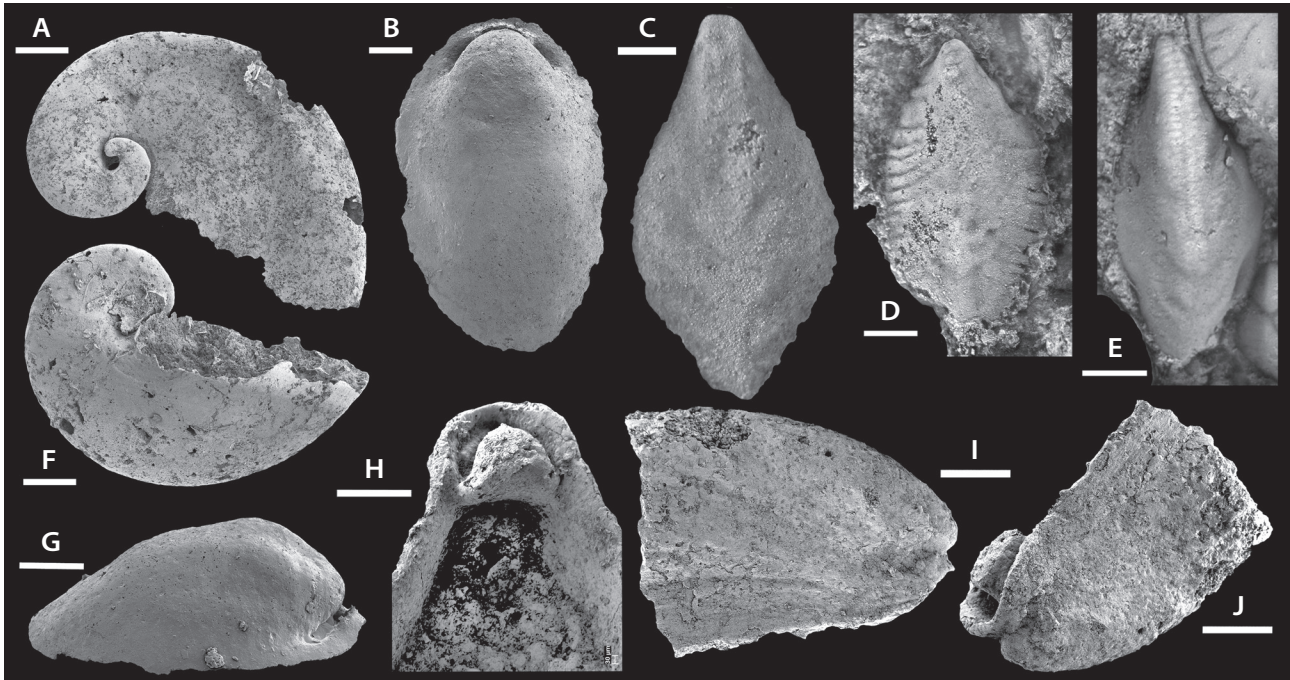


Figure 15. *Costipelagiella* and stenothecids from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A, F – *Costipelagiella* cf. *nevadense* Skovsted, 2006b from GGU sample 271718, internal moulds. A – PMU 39178. F – PMU 39175. • B, C, G–J – *Stenothecoides terraglaciei* Peel, 2021d. B – PMU 38317 from GGU sample 271492, internal mould of juvenile. C – PMU 38315 from GGU sample 271718, internal mould. G – PMU 38320 from GGU sample 271492, juvenile internal mould. H–J – PMU 38323, silicified specimen, ventral valve. • D – *Stenotheca* cf. *elongata* Walcott, 1884, MGUH 33948 from GGU sample 271492. • E – *Stenothecella* cf. *sibirica* Aksarina, 1978 in Aksarina & Pelman (1978), MGUH 33949 from GGU sample 271492. Scale bars: 100 µm (B, G); 200 µm (A, F, H–J); 500 µm (C, D); 1 mm (E).

Formation (early Wuliuan Stage) of British Columbia. It differs in preservation from silicified material of *Stenotheca elongata* in Laurentia described in detail by Johnston & Streng (2021).

***Stenothecoides terraglaciei* Peel, 2021d**

Figure 15B, C, G–J

Figured material. – PMU 38315, internal mould, and PMU 38323, silicified specimen, both from GGU sample 271718, Løndal. PMU 38317 and PMU 38320 are juvenile internal moulds from GGU sample 271492, southern Peary Land.

Discussion. – The abundant internal moulds of *Stenothecoides terraglaciei* Peel, 2021d from GGU sample 271718 (Fig. 15C) lack the closely spaced radiating grooves on the dorso-lateral flanks of internal moulds preserved in limestone of *Stenotheca* cf. *elongata* from GGU sample 271492 (Fig. 15D).

Genus *Stenothecella* Aksarina, 1978 in Aksarina & Pelman (1978)

Type species – *Stenothecella sibirica* Aksarina, 1978 in Aksarina & Pelman (1978), Kuznetskiy Alatau, Siberia;

lower Cambrian, (Cambrian Stage 4, Lenian Regional Stage).

***Stenothecella* cf. *sibirica* Aksarina, 1978 in Aksarina & Pelman (1978)**

Figure 15E

Figured material – MGUH 33949 internal mould from GGU sample 271492, southern Lauge Koch Land.

Discussion. – Peel (2021d) noted that this elongate stenothecoid from GGU sample 271492, with about twenty pairs of muscle scars along the dorsal mid-line, represented the youngest example of a genus otherwise known from Cambrian Series 2 in Siberia and Mongolia (Esakova & Zhegallo 1996, Korovnikov *et al.* 2018).

Phylum Mollusca Cuvier, 1797
Class Helcionelloida Peel, 1991a
Order Helcionellida Geyer, 1994

Figured material. – PMU 39181, PMU 39185, PMU 39186, PMU 39188, PMU 39193, PMU 39195, PMU 39197, PMU 39199, PMU 39200, PMU 39206, PMU 39210, PMU 39211, PMU 39221, PMU 39227–39229,

PMU 39232, all from GGU sample 271718, Løndal. PMU 39204 from GGU sample 271492 and PMU 39209 from GGU sample 218331, both from southern Lauge Koch Land.

Discussion – Peel & Kouchinsky (2022) and Peel (2023b), described 20 species of helcionellid molluscs, some with muscle scars, see also Peel & Berg-Madsen (2023), from the Wuliuan Stage of North Greenland. The fauna compares closely with that of the Coonigan Formation of Australia (Runnegar & Jell 1976) of similar age (see discussion of the age of the Coonigan Formation in Peel & Kouchinsky 2022, p. 75). It is dominated by seven species of *Dorispira* Parkhaev, 2010 in Parkhaev & Demidenko (2010), with prominent transverse rugae: *Dorispira accordionata* (Runnegar & Jell, 1976) (Fig. 16E); *Dorispira* cf. *arguta* (Resser, 1939) (Fig. 16C); *Dorispira avannga* Peel & Kouchinsky, 2022 (Fig. 16B); *Dorispira?* *penecyrano* (Runnegar & Jell, 1976) (Fig. 16F); *Dorispira septentrionalis* Peel & Kouchinsky, 2022 (Fig. 16I); *Dorispira tavsenensis* Peel & Kouchinsky, 2022 (Fig. 16H) and *Dorispira tippik* Peel & Kouchinsky, 2022 (Fig. 16A, D, G). The Australian Miaolingian species *Mellopegma schizocheras* Vendrasco, Kouchinsky, Porter & Fernandez, 2011 (Fig. 16Q) is also common and occurs together with *Mellopegma chelata* (Skovsted, 2006b) (Fig. 16N), originally described from the Emigrant Formation of Nevada (Cambrian Series 2, Stage 4). *Mellopegma* cf. *georginense* Runnegar & Jell, 1976 is rare (Fig. 16S). The strongly coiled *Erugoconus acuminatus* Peel & Kouchinsky, 2022 (Fig. 16M) and the upright *Tavseniconus erectus* Peel & Kouchinsky, 2022 (Fig. 16L) are both common in GGU sample 271718. Other, uncommon species include *Sermegiconus polaris* (Peel, 2021e) (Fig. 16J), *Hensoniconus siku* (Peel & Kouchinsky, 2022) (Fig. 16R), *Vendrascospira troelseni* Peel & Kouchinsky, 2022 (Fig. 16O) and *Vendrascospira frykmani* Peel & Kouchinsky, 2022.

Class uncertain

Order Pelagiellida MacKinnon, 1985

Discussion – Evidence from shell structure presented by Kouchinsky (2000), Vendrasco *et al.* (2010) and Li *et al.* (2017, 2021) prompted Peel & Kouchinsky (2022) to reject the suggestion by Landing *et al.* (2021) that the familiar and widely distributed helically coiled fossils generally referred to *Pelagiella* Matthew, 1895 were annelids and not molluscs. However, the significance of bristles (setae) protruding from the aperture in specimens of *Pelagiella exigua* Resser & Howell, 1938 from the Kinzers Formation (Cambrian Series 2, Stage 4) of Pennsylvania by Thomas *et al.* (2020) is not adequately resolved.

Genus *Costipelagiella* Horný, 1964

Type species. *Costipelagiella zazvorkai* Horný, 1964, Skryje Formation, Czech Republic; Cambrian, Miaolingian Series.

Costipelagiella cf. *nevadense* Skovsted, 2006b

Figure 15A, F

Figured material – PMU 39175 and PMU 39178 from GGU sample 271718, Løndal.

Discussion – Smooth internal moulds of pelagiellids are common in GGU sample 271718, but rare traces of prominent comarginal rugae (Peel & Kouchinsky 2022, fig. 6i) prompted assignment to *Costipelagiella* Horný, 1964.

Phylum uncertain

Class Hyolitha Marek, 1963

Discussion. – Hyoliths in the current material are usually preserved as broken internal moulds of conchs, so that details of the aperture and external ornamentation are lacking. Protoconchs are common in the acid residue of GGU sample 271718 (Fig. 17N, Q). Opercula, which are of primary importance for identification, have not been recognised in processed samples, although they occur commonly in other North Greenland Cambrian samples (Peel *et al.* 2016, Peel 2021e). A notable exception is provided by the unique occurrence of an in-place operculum in *Protowenella flemingi* Runnegar & Jell, 1976 from GGU sample 218831 (Fig. 17L; Peel 2021c). As is generally the case, the systematic links between micromorphic and macromorphic hyolith taxa are poorly established, as is the ontogenetic development of most micromorphic species.

Order Orthothecida Marek, 1966

Family Circothecidae Missarzhevsky, 1969 in Rozanov *et al.* (1969)

Genus *Conotheca* Missarzhevsky, 1969 in Rozanov *et al.* (1969)

Type species. – *Conotheca mamillata* Missarzhevsky, 1969 in Rozanov *et al.* (1969); lower Cambrian of Siberia.

Discussion. – As noted by Qian & Bengtson (1989), Bengtson *et al.* (1990), Malinky & Skovsted (2004) and Devaere *et al.* (2013, 2014), specific determination of species of *Conotheca* Missarzhevsky, 1969 in Rozanov *et al.* (1969) is mainly dependant on the characters of the operculum. Unfortunately, hyolith opercula have not been recovered from the processed samples.



Figure 16. Helcionelloid molluscs from the upper Henson Gletscher Formation Cambrian (Wuliuan Stage), North Greenland. Internal moulds from GGU sample 271718, Løndal, unless stated. • A, D, G – *Dorispira tippik* Peel & Kouchinsky, 2022. A – PMU 39186. Note grooves on umbilical wall. D – PMU 39185, lateral view. G – PMU 39188, antero-dorsal view. • B – *Dorispira avannga* Peel & Kouchinsky, 2022, PMU 39197, holotype. • C – *Dorispira* cf. *arguta* (Resser, 1939), PMU 39193. • E – *Dorispira accordionata* (Runnegar & Jell, 1976), PMU 39181. • F – *Dorispira*? *penecyrano* (Runnegar & Jell, 1976), PMU 39200. • H – *Dorispira tavsensis* Peel & Kouchinsky, 2022, PMU 39195, holotype. • I – *Dorispira septentrionalis* Peel & Kouchinsky, 2022, PMU 39199. • J – *Sermegiconus polaris* (Peel, 2021e), PMU 39210 from GGU sample 218331, Lauge Koch Land. • K – *Helcionella*? sp., PMU 39209 from GGU sample 218331, Lauge Koch Land. • L – *Tavseniconus erectus* Peel & Kouchinsky, 2022, PMU 39229, holotype. • M – *Erucoconus acuminatus* Peel & Kouchinsky, 2022, PMU 39232. • N – *Mellopegma chelata* (Skovsted, 2006b), PMU 39228. • O – *Vendrascospira troelseni* Peel & Kouchinsky, 2022, PMU 39211, holotype. • P – *Parailsanella* sp., PMU 39204 from GGU sample 271492, Lauge Koch Land. • Q – *Mellopegma schizocheras* Vendrasco, Kouchinsky, Porter & Fernandez, 2011, PMU 39221. • R – *Hensoniconus siku* (Peel & Kouchinsky, 2022), PMU 39206. • S – *Mellopegma* cf. *georginense* Runnegar & Jell, 1976, PMU 39227. Scale bars: 100 µm (F, J, N, R); 200 µm (A, B, D, I, L, O, Q); 300 µm (K); 400 µm (C, E, G, H, M, P); 600 µm (S).

***Conotheca* sp.**

Figure 17A, R

Figured material. – PMU 18321 from GGU sample 271718, Løndal.

Discussion. – The internal mould is almost straight, with an overall expansion rate of about 10 degrees, and with slight curvature of the pointed apex towards the left side of the illustration (Fig. 17A, detail in R). The pointing of the apex may reflect internal shell deposition within the conch, but see discussion by Liu *et al.* (2020).

The conch of *Conotheca mammilata* Missarzhevsky, 1969 in Rozanov *et al.* (1969), as illustrated by Peel & Gubanov (2022, fig. 3b, j) from the Bystraya Formation (Cambrian Series 2) of eastern Transbaikalia (Zabaykalsky Krai), Siberia, is wider, but the extreme apex is similar in shape to *Conotheca* sp. Some specimens of *Conotheca australiensis* Bengtson, 1990 in Bengtson *et al.* (1990) from the lower Cambrian Parara Limestone of South Australia also preserve a similar tapered apex, but in others the apex is bluntly rounded as a result of breakage at an apical septum (Bengtson *et al.* 1990, fig. 143h–j). Specimens from Cambrian Series 2 in North-East Greenland, assigned to the Australian species by Malinky & Skovsted (2004, fig. 14), are curved towards the apex, which is usually broken away.

Family Turcuthecidae Missarzhevsky, 1989

Genus *Loculitheca* Sysoev, 1968

Type species. – *Circotheca anulata* Sysoev, 1959 from the lower Cambrian (Atdabanian Regional Stage) of Kotuy, Siberia.

***Loculitheca*? sp.**

Figure 17G

Figured material. – PMU 18331 from GGU sample 271718, Løndal.

Discussion. – While resembling internal moulds of some species of the widely distributed lower Cambrian *Cupitheca* Duan, 1984, this specimen compares closely with *Loculitheca kunka* Kruse, 2002 from the Monastery Creek Member (Beetle Creek Formation; Wuliuan–Drumian stages) of Queensland in terms of its slight curvature and apical septation (Kruse 2002, Moore & Porter 2018).

Family Tetrathecididae Sysoev, 1968

Genus *Holmitheca* Sysoev, 1968

Type species. – *Holmitheca obvia* Sysoev, 1968 from the lower Cambrian (late Tommotian Stage) of the Siberian Platform.

***Holmitheca* sp.**

Figure 18D

Figured material. – PMU 18338 from GGU 271718, Løndal.

Discussion. – This single specimen has a broken aperture and a preserved length of 1.6 mm. A slightly swollen protoconch and irregular (slightly deformed?), upturned early growth stage (length 300 µm) is followed abruptly by the development of two longitudinal, rounded angulations that divide the dorsal surface into three flat to shallowly concave surfaces that are most conspicuous near the aperture. The ventral surface is seemingly flat or shallowly convex; dorsal ornamentation of fine transverse growth lines.

Holmitheca quadricostata (Shaler & Foerste, 1888) from the Brigus Formation (Cambrian Series 2, Stage 3), as illustrated by Malinky & Geyer (2024, fig. 16e–o) has a more slender conch with the dorsal angulations more closely together. *Holmitheca* sp. of Malinky & Geyer (2019, fig. 8j–m) from the Browns Pond Formation (Cambrian Series 2, Stage 4) of New York State has more strongly delimited dorsal angulations and a fine rib in the median dorsal concavity. An internal mould from the early Wuliuan Stage of Queensland referred to *Holmitheca*? sp. by Kruse (2002) has a more rectangular cross-section than the Henson Gletscher specimen and greater apical angle. ‘*Hyolithes*’ *conularoides* Tate, 1892, as figured by Bengtson *et al.* (1990) and Wrona (2003) from the lower Cambrian of South Australia and western Antarctica, respectively, has a much wider apical angle, with the dorsal angulations correspondingly closer to the median line.

Family Protowenellidae Peel, 2021c

Genus *Protowenella* Runnegar & Jell, 1976

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

Discussion. – Peel (2021c) described an in-place operculum in *Protowenella* from GGU sample 218831 (Fig. 17L) indicating that this tightly coiled isostrophic taxon was an orthothecid hyolith and not a monoplacophoran, helcionelloid or gastropod, as previously supposed (Runnegar & Jell 1976; Berg-Madsen & Peel 1978;

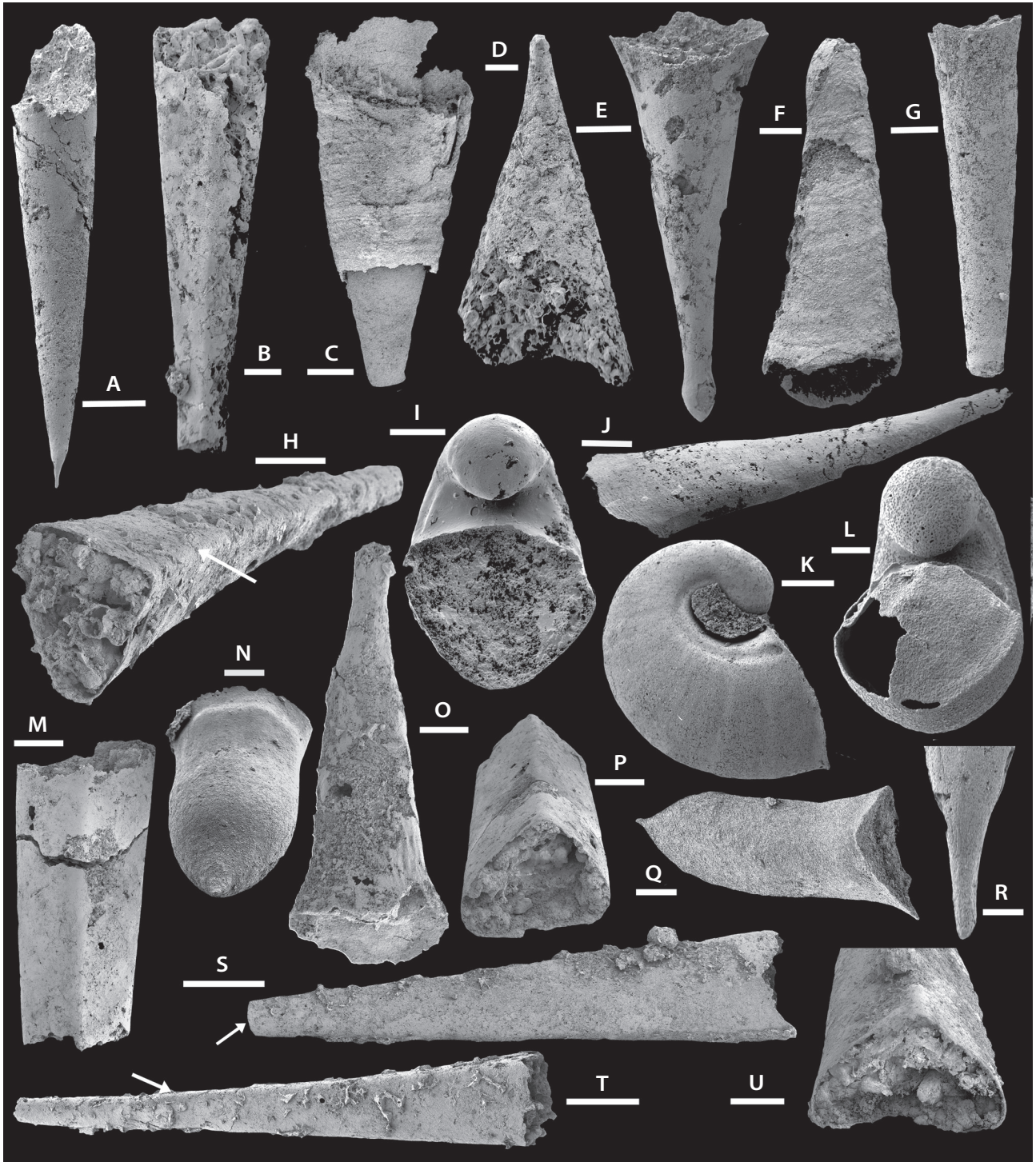


Figure 17. Hyoliths from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. Internal moulds from GGU sample 271718 unless stated. • A, R – *Conothea* sp., PMU 18321 with detail of apex (R). • B, H, M, P, S–U – *Yuku?* *tjurtu* Kruse, 2002. B – PMU 18322, internal mould, dorsal view. H, T – PMU 18323, oblique dorsal (H) and lateral (T) views with median dorsal angulation arrowed. M, P – PMU 18324, dorsal (M) and aperturo-dorsal (P) views. S, U – PMU 18325, lateral (S) and aperturo-dorsal (U) views, with apical septum arrowed. • C – Hyolithida sp. I, PMU 18326, dorsal view, partly exfoliated specimen. • D – ‘*Hyolithes*’ cf. *obesus* Holm, 1893, PMU 18327, dorsal view. • E – *Microcornus?* cf. *delicatus* He & Pei, 1984 in He *et al.* (1984), PMU 18328, dorsal view. • F, J – *Parakorilithes?* sp. F – PMU 18329, ventral surface, partly exfoliated. J – PMU 18330 from GGU sample 271492, lateral view with ventral surface uppermost. • G – *Loculitheca?* sp., PMU 18331, lateral view with septate apex. • I, K, L – *Protowenella flemingi* Runnegar & Jell, 1976. I – PMU 38331, apertural view. K – PMU 38330, lateral view. L – PMU 38329 from GGU sample 218831, with operculum in place. • N, Q – hyolith protoconchs. N – PMU 18332. Q – PMU 18333. • O – *Crestjahitus groenlandicus* sp. nov., PMU 18234, internal mould, early growth stage. Scale bars: 30 μ m (Q, R); 50 μ m (L, M); 100 μ m (F, K, I, O); 200 μ m (E, G, H, J); 300 μ m (A–D); 400 μ m (N, P).

Peel 1991a, b; Parkhaev 2008). *Protowenella* has a cosmopolitan distribution, mainly in the Miaolingian, with records extending from Antarctica to North Greenland (Claybourn *et al.* 2019, Peel 2021c).

***Protowenella flemingi* Runnegar & Jell, 1976**

Figure 17I, K, L

Figured material. – PMU 38329 from GGU sample 218831, PMU 38330 and PMU 38331 from GGU sample 271718.

Discussion. – Internal moulds of *Protowenella flemingi* Runnegar & Jell, 1976 are common in GGU samples 218831, 271492 and 271718, showing the characteristic circumbilical channels on the umbilico-lateral walls (Fig. 17I, K). Comparisons with other species from Cambrian Series 2 and the Miaolingian Series from Spain, New Zealand, Maly Karatau (Kazakhstan) and China were given by Peel (2021c).

Order Hyolithida Sysoev, 1957

Family Parakorilithidae Qian, 1989

Genus *Parakorilithes* He & Pei, 1984 in He *et al.* (1984)

Type species. – *Parakorilithes mammillatus* He & Pei, 1984 in He *et al.* (1984) from the lower Cambrian of North China.

***Parakorilithes?* sp.**

Figure 17F, J

Discussion. – The longitudinal convex curvature of the dorsal surface promotes assignment to *Hyptiotheca* Bengtson, 1990 in Bengtson *et al.* (1990), which was considered to be a junior synonym of *Parakorilithes* He & Pei, 1984 in He *et al.* (1984) by Pan *et al.* (2019), but the distinctive operculum has not been found. The conch is ornamented with comarginal growth lines and faint longitudinal striations. The two specimens differ in the transverse convexity of the ventral surface, from shallowly convex (Fig. 17J) to flattened in the fragment of the apex (Fig. 17F).

Family Crestjahitidae Sysoev, 1968

Genus *Crestjahitus* Sysoev, 1968

Type species. – *Crestjahitus compressus* Sysoev, 1968 from the lower Cambrian of Siberia.

***Crestjahitus groenlandicus* sp. nov.**

Figure 17O, 18A–C, E–G

LSID. – Zoobank.org:act:376C7A42-2B79-441B-B3A5-78BAC5DDB676

Holotype. – PMU 18337 from GGU sample 271718, Løndal.

Type horizon and locality. – Upper Henson Gletscher Formation, Løndal, Peary Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. – PMU 18334–PMU 18234 from GGU sample 271718, Løndal.

Etymology. – From Greenland (Danish, Groenland).

Diagnosis. – Conch orthoconic, with an overall apical angle of about 15 degrees and dorsum shallowly concave in lateral view, with an oxygonal aperture; dorsum transversely uniformly convex; ventral surface shallowly convex, almost flat; ligula hemispherical. Dorsum covered with transverse, rounded ribs with concave spaces between.

Description. – The conch increases slowly in apical angle from the tapered apex towards the aperture, sometimes with slight flaring visible on the internal mould during growth (Fig. 18C), and with concave longitudinal curvature of the dorsal surface (Fig. 18G); overall apical angle 15 degrees. The protoconch is seemingly parallel-sided, and about 300 µm in length, followed by a doubling in width to the initially slightly expanding conch (Fig. 17O). The aperture is seemingly oxygonal and the ligula hemispherical in dorsal view (Fig. 18A). The uniformly convex dorsum passes rapidly around lateral extremities onto the shallowly convex, almost flat, ventral surface. Dorsal ornamentation consists of transverse, rounded ribs with concave interspaces equal in width to 1–3 ribs.

Discussion. – The type species, *Crestjahitus compressus* Sysoev, 1968, as illustrated by Rozanov *et al.* (2010, pl. 41, figs 1–3), has a larger apical angle and more acute lateral angulations. *Crestjahitus* sp. of Malinky (2014) from the Miaolingian (Marjum Regional Stage) of Montana also has a wider apical angle, with much coarser transverse dorsal ornamentation adapically. *Crestjahitus? danianus* (Matthew, 1884) in Walcott (1884) from the Cambrian of New Brunswick, illustrated by Kruse & Hughes (2016, fig. 10), differs from *Crestjahitus groenlandicus* in having an oval cross-section and ornamentation of closely spaced, irregular, fine growth lines. *Crestjahitus?* sp. of Kouchinsky *et al.* (2011, fig. 11j–l) from the Kuonamka Formation (early Drumian Stage) of northern Siberia displays similar transverse dorsal ornamentation to *Crestjahitus groenlandicus* but has a swollen, slightly upturned protoconch.

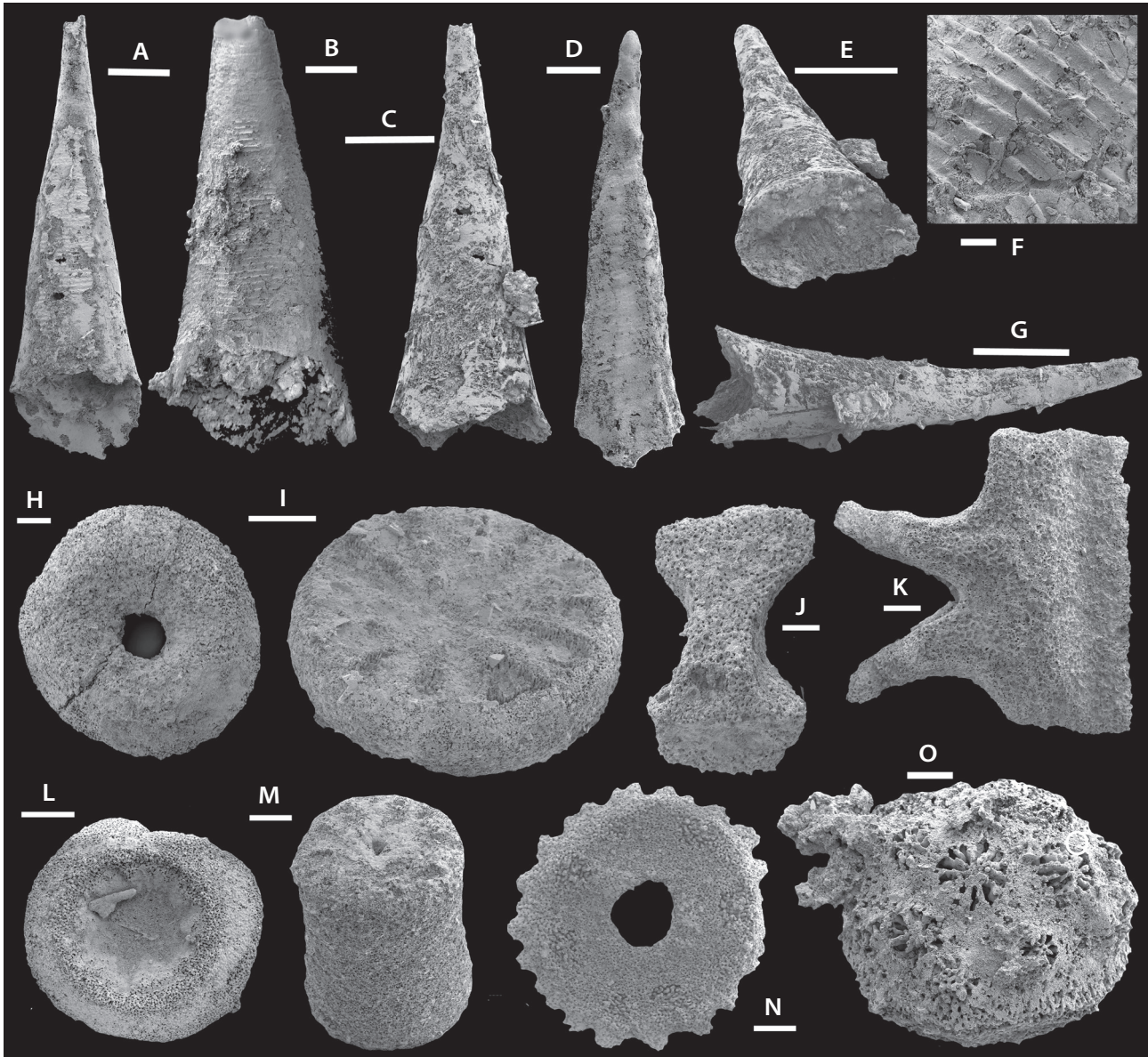


Figure 18. Hyoliths and echinoderm plates from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. GGU sample 271718. • A–C, E–G – *Crestjähitus groenlandicus* sp. nov. A – PMU 18335. B, F – PMU 18336, with detail of ornamentation (F). C, E, G – PMU 18337, holotype in dorsal (C), oblique apertural (E) and lateral (G) views. • D – *Holmitheca* sp., PMU 18338, slightly oblique dorsal view. • H–O – echinoderm plates. H – MGUH 30252, holomeric columnal. I – MGUH 30241, holomeric columnal. J – MGUH 30286, edrioasteroid ambulacral flooring plate. K – MGUH 30237, edrioasteroid ambulacral flooring plate. L – MGUH 30239, discoidal holdfast. M – MGUH 30244, tall holomeric columnal. N – MGUH 30249, holomeric columnal. O – PMU 18339, multi-spine thecal plate. Scale bars: 100 μ m (C, H, J, O); 200 μ m (A, B, D, F, G, I, K, M, N); 300 μ m (E, L).

Family Angusticornidae Sysoev, 1968

Genus *Yuku* Kruse, 2002

Type species. – *Yuku tjurtu* Kruse, 2002 from the Gowers Formation, Queensland, Australia; Cambrian, Miaolingian Series, Drumian Stage.

Discussion. – Kruse (2002) assigned *Yuku* to the hyolithid Family Angusticornidae Sysoev, 1968 following his

description of an orthogonal aperture. Placement of the present material is tentative since evidence of a ligula has not been seen, although undamaged apertures have not been observed.

Yuku? tjurtu Kruse, 2002

Figure 17B, H, M, P, S–U

Figured material. – PMU 18322–PMU 18325 from GGU sample 271718, Løndal.

Description. – The largest fragment (Fig. 17B) is an internal mould with a preserved length of about 3.5 mm and greatest width of about 950 µm. Initially, the triangular conch is almost parallel-sided, but thereafter it expands slowly with straight sides. A second specimen (Fig. 17H, T with arrows indicating the median dorsal angulation) displays the slightly concave, longitudinal curvature of the dorsal surface of the conch and shows gradual development of the triangular cross-section from a sub-circular early growth stage; the protoconch is not preserved. The apical area of a third internal mould is truncated by a transverse septum (Fig. 17S, arrow). Width is slightly greater than height in the triangular cross-section (Fig. 17H, P), where the pronounced median dorsal angulation is flanked by flat to shallowly concave dorso-lateral surfaces. The ventral surface is usually flat but may become shallowly concave in the latest preserved growth stage (Fig. 17U). Evidence of a ligula not observed. Operculum not known. Dorso-lateral surfaces with traces of transverse growth lines.

Discussion. – In the shape of the conch the specimens from the Henson Gletscher Formation compare closely with *Yuku tjurtu* Kruse, 2002 from the *Ptychagnostus gibbus* Biozone –earliest Drumian Stage of Queensland, Australia (Kruse 2002), but the presence of the ligula described by Kruse (2002) has not been demonstrated in the broken specimens. Cross-sections illustrated by Kruse (2002, fig. 27d, g) indicate that on the outer surface the angulations are acute, in comparison to their rounded form in internal moulds. *Nganki wumirri* Kruse, 1990a from the Tindall Limestone (Wuliuan Stage) of Northern Territory, Australia, has a similar triangular cross-section but a larger apical angle (Kruse 1990a, b).

Family undetermined

Genus *Microcornus* Mambetov, 1972

Type species. – *Microcornus parvulus* Mambetov, 1972 from the lower Cambrian of Malyj Karatau.

Discussion. – Kruse (2002) discussed the relationship between *Gerkella* Malinky & Sixt, 1990, originally described from the Carboniferous of Iowa, USA, and *Microcornus* Mambetov, 1972 from the lower Cambrian of Tien Shan, Kazakhstan, with reference to material from the Gowers Formation (Wuliuan–Drumian stages) of Queensland, Australia.

Microcornus? cf. *delicatus* He & Pei, 1984 in He *et al.* (1984)

Figure 17E

Figured material. – PMU 18328 from GGU sample 271718, Løndal.

Discussion. – Peel & Gubanov (2022) tentatively referred *Parakorilithes delicatus* He & Pei, 1984 in He *et al.* (1984), originally described from the Xinji Formation of Henan Province, China, to *Microcornus* while describing hyoliths from the Bystraya Formation (Cambrian Series 2) of Transbaikalia. The illustrated internal mould (Fig. 17E) is more slender than early growth stages of *Microcornus eximius* Duan, 1984 as illustrated by Bengtson *et al.* (1990) and Gravestock *et al.* (2001) from the lower Cambrian of South Australia. It compares closely to the early growth stages of *Gerkella? thuka* Kruse, 2002 from the *Ptychagnostus gibbus* Biozone and Drumian Stage of Queensland (Kruse 2002) in terms of its rate of expansion, but has a less pronounced protoconch.

Genus undetermined

Hylolithes cf. *obesus* Holm, 1893

Figure 17D

Figured material. – PMU 18327 from GGU sample 271718, Løndal.

Discussion. – This specimen is distinguished by its high apical angle, flattened ventral surface and slightly upturned apex, in which it is closely similar to the paralectotype of Holm (1893), illustrated by Malinky & Berg-Madsen (1999) from the Guzhangian Stage of Sweden.

Hylolithida sp. 1

Figure 17C

Figured material. – PMU 18326 from GGU sample 271718, Løndal.

Discussion. – This partly exfoliated specimen with transverse growth lines can be compared to an indeterminate hylolithid figured by Kouchinsky *et al.* (2011, fig. 13b–d) from the Kuonamka Formation (Wuliuan Stage, *Kuonamkites* Biozone).

Phylum Echinodermata Klein, 1734

Echinoderm plates

Figures 18H–O; 21A, B

Figured material. – MGUH 30237 and MGUH 30286, edrioasteroid ambulacral flooring plates; MGUH 30239, discoidal holdfast; MGUH 30241, MGUH 30244, MGUH 30249 and MGUH 30252, holomeric columnals; PMU 39664, holdfast; PMU 18339, multi-spine thecal plate;

PMU 18359, spinose thecal plate. All specimens from GGU sample 271718, Løndal.

Discussion. – Disarticulated plates and columnals of echinoderms are diverse and very common in GGU sample 271718. They were described in detail by Clausen & Peel (2012) who considered the presence of polymeric pelmatozoan stem elements and holdfasts (Fig. 3I) to be particularly noteworthy.

Phylum uncertain

Order Tommotiida Missarzhevsky, 1970

Family Kelanellidae Missarzhevsky & Gregorieva, 1981

Discussion. – Tommotiidan sclerites are common in GGU sample 482337 from Fimbuldal, occurring both as SSF in acid residues and as large examples about 10 mm in length in hand specimens. They occur only rarely in GGU samples 271492 and 271718. The Wuliuan material from North Greenland compares closely with sclerites described from Kuznetskiy Alatau, southern Siberia (Amgan Regional Stage, latest Stage 4) by Missarzhevsky & Gregorieva (1981) and assigned to *Sonella* Missarzhevsky & Gregorieva, 1981 and *Tesella* Missarzhevsky & Gregorieva, 1981. *Tesella* was spelt as *Tessella* by Qian (1989), Parkhaev & Demidenko (2010) and Devaere *et al.* (2014). Schopf & Klein (1992) considered *Sonella* to be a junior synonym of *Tesella* but Esakova & Zhegallo (1996) considered *Tesella* to be a junior synonym of *Sonella*, although Missarzhevsky (1989) and Qian (1989) had maintained their separate identities.

Sonella and *Tesella* were treated as junior synonyms of *Kelanella* Missarzhevsky, 1966 in Rozanov & Missarzhevsky (1966) by Devaere *et al.* (2014), a genus characterised by conspicuous septation within the sclerite inner cavity (Fig. 19J). They were incorporated into the scleritome of *Kelanella altaica* Missarzhevsky, 1966 in Rozanov & Missarzhevsky (1966), based on material from the early Cambrian of the Montagne Noire, southern France, an opinion restated by Yang *et al.* (2015) and Devaere & Skovsted (2021, p. 165). The composition of the French scleritome seems secure, but its identity with the type material of *Kelanella altaica* is equivocal. *Kelanella altaica*, the type species of *Kelanella*, was originally described from the late Atdabanian Regional Stage (Cambrian Series 2, Stage 3) of Altai-Sayan but only a single type of sclerite was illustrated (Rozanov & Missarzhevsky 1966, pl. 11, fig. 6, pl. 13, figs 9, 10). However, additional material was described by Novozhilova *et al.* (2019) from the lower Cambrian of Tyva (Tuva) in southern Siberia. Pending full description of the material from the Henson Gletscher Formation, the synonymy of *Tesella* and *Sonella* proposed by Schopf & Klein (1992), see also Geyer *et al.* (2014), is maintained,

but the assignment to *Kelanella altaica* and synonymy with *Kelanella* proposed by Devaere *et al.* (2014) is left in abeyance.

Family Kelanellidae was not employed by Bengtson *et al.* (1990) or Devaere *et al.* (2014), although maintained by Esakova & Zhegallo (1996) and Novozhilova *et al.* (2019).

Genus *Tesella* Missarzhevsky & Gregorieva, 1981

Type species. – *Tesella deplanata* Missarzhevsky & Grigorieva, 1981, from Mt. Sladkiye Koren'ya, Kuznetsk Alatau Range, southern Siberia, Russia; lower Cambrian (Stage 4), from the early part of the Amgan Regional Stage.

Discussion. – Missarzhevsky & Gregorieva (1981) established one species of *Sonella* and four species of *Tesella* from Mt. Sladiye Koren'ya, all of which are considered to be constituents of the same scleritome. Esakova & Zhegallo (1996, p. 116) inadvertently cited *Sonella deplanata* Missarzhevsky & Gregorieva, 1981 as the type species of *Sonella*; it is the type species of *Tesella* Missarzhevsky & Gregorieva, 1981. The type species of *Sonella* is *Sonella rostriformis* Missarzhevsky & Gregorieva, 1981. The Siberian material was derived from Cambrian Series 2, Stage 4 (Devaere & Skovsted 2021) and thus is older than the Wuliuan material from North Greenland. However, specimens attributed to *Tesella* were later found in 'Upper Amgan' (Wuliuan Stage) rocks in Kyrgyzstan (Geyer *et al.* 2014).

Tesella deplanata Missarzhevsky & Gregorieva, 1981

Figure 19C–K

Figured material. – PMU 18341–18346 from GGU sample 482337.1.

Description. – Sclerite type A (Fig. 19D, E, I, K) is strongly curved, expanding away from the overhanging apex, but also asymmetric with the apex lying to the right in the illustrated view of the outer surface (Fig. 19I). The convex outer surface is ornamented by about 12 longitudinal ridges of variable relief and spacing, crossed over by regularly spaced transverse elements that may extend into nodes at the point of crossing (Fig. 19K). Individual cells within the resultant reticulate pattern have concave sides and may show fine longitudinal or transverse striation (Fig. 19D). The concave inner surface of the sclerite is poorly known.

Sclerite type B has shallowly curved sclerites with sub-parallel sides and an oval, almost slit-like transverse aperture (Fig. 19C, G, H). The shallowly convex upper surface carries a median longitudinal ridge of variable

relief that passes across shallowly concave surfaces towards the rounded lateral extremities. It is crossed by transverse ribs of variable spacing and relief. The under surface (Fig. 19C) is shallowly concave and dominated by transverse ridges.

Sclerite type C is similar in its narrowly tapering form to sclerite type B but has a sub-triangular cross-section and more prominent sculpture (Fig. 19F).

Sclerite type D (Fig. 19J) is represented by a fragment of a strongly flattened sclerite viewed from the underside, which is ornamented by rounded, transverse ribs (left side of figure). The upper side is viewed from its inner surface and has prominent longitudinal grooves (corresponding to acute ridges on the exterior) separated by broad, convex interareas (concave on the exterior). Transverse internal septae show an interlocking pattern.

Discussion. – Sclerite type A corresponds to the sclerite *Sonella rostriformis* of Missarzhevsky & Grigorieva (1981) but similar shaped sclerites occur in other taxa (e.g. Devaere *et al.* 2014, fig. 7k). A sclerite referred by Qian (1989, pl. 37, fig. 1) to *Sonella jinshaensis* (Yuan & Zhang 1983) from the lower Cambrian Tongying Formation of Hubei, China, lacks longitudinal ridges on the lateral area. Sclerites described by Yuan & Zhang (1983) from the lower Cambrian of south-west China are generally narrower and have more prominent nodes at the crossing points in the ornamentation.

Sclerite type C resembles the early growth stages of *Tesella trilateralis* Missarzhevsky & Grigorieva, 1981. Sclerite type D is a fragment readily assigned to *Tesella deplanata* Missarzhevsky & Grigorieva, 1981.

Problematica

Genus *Aetholicopalla* Conway Morris, 1990 in Bengtson *et al.* (1990)

Type species. – *Aetholicopalla* Conway Morris, 1990 in Bengtson *et al.* (1990) from the Parara Limestone of South Australia; lower Cambrian.

***Aetholicopalla adnata* Conway Morris, 1990 in Bengtson *et al.* (1990)**

Figure 20A–G

Figured material. – PMU 18347, PMU 18349, PMU 18350, PMU 18352 and PMU 18353 from GGU sample 271492, southern Lauge Koch Land; PMU 18351 from GGU sample 271718, Løndal.

Discussion. – *Aetholicopalla* Conway Morris, 1990 in Bengtson *et al.* (1990) was described in detail from the Parara Limestone of South Australia by Bengtson *et al.* (1990).

Specimens from the available acid residues from North Greenland extend the range of *Aetholicopalla* into the Miaolingian. They show the double wall structure with the two phosphatized layers joined by hollow, tubular pillars that was considered to be characteristic of the genus (Fig. 20E, with arrow locating the pillars). The tubular pillars are manifested on the outer surface by numerous circular pores (Fig. 20A–G) and therefore form tubules connected to the interior of the sphere. Specimens are usually sub-spherical, but flattened surfaces (Fig. 20A) or impressions (arrow in Fig. 20E) indicate attachment to a substrate or slight diagenetic compression. A series of attached fragments or holdfasts with the double walls joined by pillars (Fig. 8E–H) likely represents broken specimens of *Aetholicopalla*, similar to specimens illustrated by Bengtson *et al.* (1990, fig. 215).

In discussing the wall structure of *Aetholicopalla*, Conway Morris, 1990 in Bengtson *et al.* (1990) acknowledged that the two phosphatized layers connected by tubules may represent phosphatic encrustation on the inner and outer surfaces of a now dissolved single calcareous (?) wall penetrated by tubules, rather than replacement of two separate walls. This interpretation is favoured here.

Devaere *et al.* (2021) described *Aetholicopalla adnata* from the lower Cambrian (Terreneuvian) of northern Iran, listing earlier literature. Wotte & Sundberg (2017) referred two spheres from the lowermost Emigrant Formation (Cambrian Series 2, Delamarian Regional Stage) to *Archaeooides* cf. *A. granulata* Qian, 1977 rather than *Aetholicopalla* on account of their lack of double wall structure and absence of evidence of attachment to a substrate. Skovsted (2006b) had previously described, but did not name, six specimens from higher in the formation at the same locality (Split Mountain, Nevada). He noted that they differed from *Aetholicopalla* in possessing fewer pores, but material from North Greenland shows similar variation in the number and relative size of pores (Fig. 20A–G). As noted above, the double wall structure of *Aetholicopalla adnata* is likely a diagenetic artifact.

Aetholicopalla is often compared to *Archaeooides* Qian, 1977 and related genera (Xian *et al.* 2024) in which the outer surface of the probable algae is covered by closely spaced nodules or spines. Xian *et al.* (2024) noted that *Aetholicopalla* is delimited by its double wall structure, but this is here considered to be a diagenetic effect, requiring a re-assessment of the relationship. Luzhnaya (2024) reported a double wall structure in *Gaparella* Missarzhevsky, 1981 in Missarzhevsky & Mametov (1981), a genus generally considered to be a junior synonym of *Archaeooides*, see also Luzhnaya *et al.* (2023).

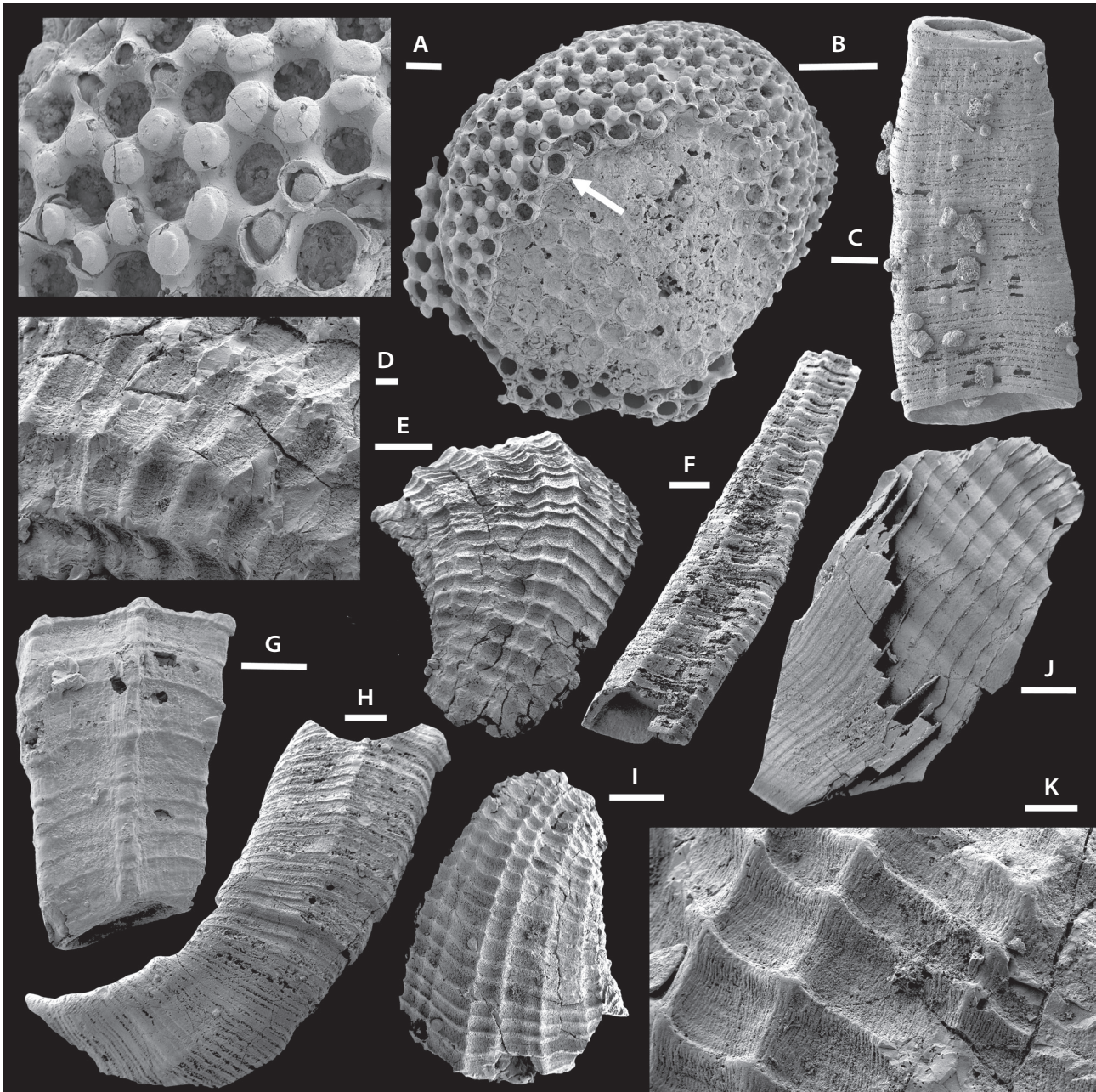


Figure 19. Lobopodian and tommotiid sclerites, Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A, B – *Microdictyon* sp., PMU 18340 from GGU sample 271492; arrow in B locates enlargement A. • C–K – *Tesella deplanata* Missarzhevsky & Grigorieva, 1981 from GGU sample 482337. C, G, H – sclerite type B. C – PMU 18341. G – PMU 18342. H – PMU 18343. D, E, I, K – sclerite type A, PMU 18344. F – sclerite type C, PMU 18345. J – sclerite type D, PMU 18346, fragment showing septation in sclerite interior. Scale bars: 50 μ m (D); 100 μ m (G, K); 200 μ m (B, C, F); 300 μ m (A); 400 μ m (E); 500 μ m (J).

Parasols and perforated plates

Figure 21A–J

Figured material. – PMU 36171 and PMU 18364 from GGU sample 271492, southern Lauge Koch Land. PMU 18360 from GGU 218831, southern Lauge Koch Land. PMU 18361–PMU 18363 and PMU 18359 from GGU sample 271718, Løndal.

Discussion. – Peel (2022a) noted the similarity in morphology between one of the sclerites illustrated here from GGU sample 271492 (Fig. 21G, J) and the copulatory spicules of males of the present day pentastomid *Raillietiella orientalis* (Hett, 1915) described by Kelehear *et al.* (2011, fig. 4c). The sclerite occurs in the same sample as the oldest known stem-group pentastomid *Dietericambria hensoniensis* Peel, 2022c, although

there is no conclusive evidence of its relationship to *Dietericambria hensoni*. The circular plate has a shallowly convex basal (?) surface about 200 µm in diameter that is covered with small rounded tubercles. The opposing surface is flattened and seemingly lacks the tubercles, but carries a prominent perpendicular tubular spike (Fig. 21G).

In a similar specimen from GGU sample 218831 (Fig. 21C), from the same horizon in southern Lauge Koch Land, the spike divides into three tapering branches of unequal length. In other specimens from GGU samples 271492 and 271718 the plate lacks the tuberculate lower surface (Fig. 21H). In this sclerite elongate tubercles extend radially from the margin indicating a polygonal outline to the sclerite unlike the circular form in Fig. 21G. The sclerite is hollow, suggesting encrustation of an originally calcareous skeletal element. Other plates from GGU sample 271718, also encrustations, display perforations representing small circular spines distributed on the upper surface of the circular plate around the large central spike (Fig. 21E, F). In one figured example with abundant perforations (Fig. 21D, I), a central spike is not present.

A stellate plate from GGU sample 271718 (Fig. 21A, B) has widely spaced spatulate spines radiating from the periphery and a prominent, hollow, central spine. The phosphatized outer wall of the central spine is composed of closely spaced, fine, parallel rods representing closely spaced pores in the original, presumed calcareous material. Transverse connections between adjacent longitudinal rods (Fig. 21A, arrow) indicates stereome structure and the echinoderm affinity of the plate.

Genus *Laugephakos* gen. nov.

LSID. – Zoobank.org:act:309DBC75-EB1D-4C8F-A613-B80D34B3C9FE

Type species – *Laugephakos groenlandicus* sp. nov., from the Henson Gletscher Formation of North Greenland; middle Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – From Lauge Koch Land and *phakos* (Greek, lens), reflecting the lenticular cross-section. Masculine.

Diagnosis. – Slender, straight, seemingly calcareous tubes known from phosphatized internal moulds, with lenticular cross-section; varied ornamentation of longitudinal ridges and threads crossed by transverse growth lines.

Discussion. – All available specimens are broken distally but characterized by their lenticular cross-section and

perfectly straight shells of uniform width. In lateral view, specimens of *Laugephakos* may be superficially reminiscent of phosphatic tubes of *Hyolithellus*, which have a circular cross-section, but most are delimited by the dominance of longitudinal ribs. The relationships of *Laugephakos* are not known.

Laugephakos groenlandicus sp. nov.

Figure 23A–F, I, J

LSID. – Zoobank.org:act:17DBC470-E66C-4399-AB68-146D0EFDA4E4

Holotype. – PMU 18372 from GGU sample 218831, southern Lauge Koch Land.

Type horizon and locality. – Upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. – PMU 18370, PMU 18371, PMU 18373 and PMU 18374 from GGU sample 271492, southern Lauge Koch Land.

Etymology. – From Greenland (Danish, Groenland).

Description. – Straight, almost parallel, seemingly calcareous tubes up to an observed length of about 1.5 mm; lenticular in cross-section with maximum diameter of about 80 µm (both in the broken holotype, Fig. 23C, D). Ornamentation dominated by longitudinal ridges, varying between specimens in width and spacing; more prominent ribs usually separated by concave interspaces with finer ribs (Fig. 23C). Transverse growth lines variably expressed, sometimes with periodic constrictions or slight flaring (Fig. 23F, I).

Discussion. – Ribs in *Coleoloides* cf. *typicalis* (Fig. 9I, J), which differs in the calcareous shell having a circular cross-section, are more closely spaced than in most specimens of *Laugephakos groenlandicus* and show less variation in pattern. Specimens of *Hyolithellus* sp. differ in being circular in cross-section, often slightly curved or slightly irregular in form (Fig. 9A–C, F, G) and dominated by transverse ribs and growth lines. Holdfasts or unbroken terminations are not known in *Laugephakos groenlandicus*.

Genus *Cambrocoryne* Peel, 2023a

Type species. – *Cambrocoryne lagenamorphia* Peel, 2023a from the Henson Gletscher Formation of North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

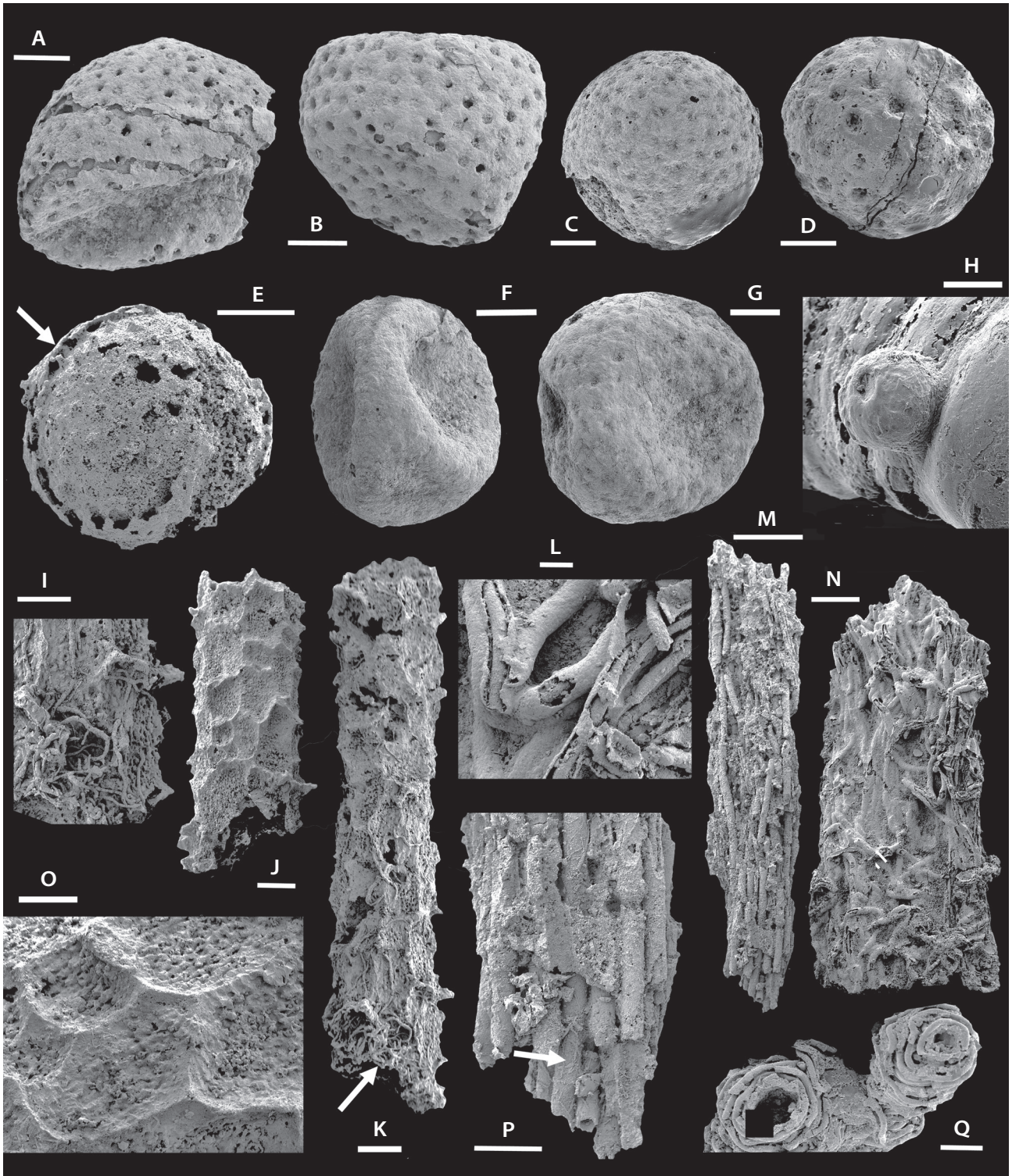


Figure 20. Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. GGU sample 271492 unless stated. • A–G – *Aetholicopalla adnata* Conway Morris, 1990 in Bengtson *et al.* (1990). A – PMU 18347. B – PMU 18348. C – PMU 18349. D – PMU 18350. E – PMU 18351 from GGU sample 271718, arrow indicates pillars between inner and outer walls. F – PMU 18352. G – PMU 18353. • H – spherical epibiont attached to sclerite of tommotiid, PMU 18354 from GGU sample 482337. • I–K, O – cellulose rods. I, K – PMU 18355 with encrusting *Girvanella* sp., arrow in K indicates location of I. J, O – PMU 18356. • L, N, Q – *Girvanella* sp. from GGU sample 271718. L, N – PMU 18357. Q – associated with MGUH 27652. • M, P – *Subtifloria* sp., PMU 18358 from GGU sample 271718, arrow in O indicates fine fungal filaments. Scale bars: 20 µm (L, O); 30 µm (H); 50 µm (A, Q); 100 µm (B–G, I, P); 200 µm (J, K, M, N).

***Cambrocoryne lagenamorph* Peel, 2023a**

Figure 23G, H

Figured material. – PMU 39697 and PMU 39699 from GGU sample 271718.

Discussion. – *Cambrocoryne lagenamorph* Peel, 2023a resembles a phosphatized wiwaxiid sclerite from the Monastery Creek Formation, (Wuliuan Stage, *Ptychaognostis gibbus* Biozone) in the Georgina Basin of Australia figured by Porter (2004, fig. 11.7). However, the Australian specimen lacks the massive thickening and circular cross-section of *Cambrocoryne lagenamorph*, being flattened, with rounded terminations and stronger longitudinal ridges. Peel (2023a) made fanciful morphological comparisons of *Cambrocoryne lagenamorph* to some Silurian thelodont trunk scales and the Mesozoic–Recent foraminiferan *Lagena* Walker & Jacob, 1798 in Kanmacher (1798), but the affinity of the North Greenland specimens remains unknown.

Spheres

Figures 3D, G, 23K–N

Figured material. – PMU 18251 from GGU sample 218831; PMU 18375–18377 from GGU sample 271492, both samples from southern Lauge Koch Land. PMU 18254 from GGU sample 271718, Løndal.

Discussion. – Spheres of the type often referred in the literature to *Olivoides* Qian, 1977 or *Markuelia* Val'kov, 1983 (e.g. Donoghue *et al.* 2006, Pyle *et al.* 2006, Dong *et al.* 2010, Peel 2021e) occur in all samples and usually have a diameter of about 500–700 μm . They are smooth, sometimes wrinkled (Fig. 23L), and may be perforated (Fig. 23N, arrow). When broken, the outer wall in some displays a radial, fibrous fabric of diagenetic calcium phosphate (Fig. 23K), while the outer surface may be marked by ambient inclusion trails (Fig. 3D, G) and euendoliths. Rare specimens display phosphatised threads of the type illustrated by Stockfors & Peel (2005b), Pyle *et al.* (2006) and Peel & Willman (2022), and indeterminate structures possibly representing soft parts, as in *Markuelia hunanensis* Dong & Donoghue, 2004 in Dong *et al.* (2004), illustrated by Dong *et al.* (2010, text-fig. 3e–g).

Spherical epibiont

Figure 20H

Figured material. – PMU 18354 from GGU sample 482337, Fimbuldal.

Discussion. – Tommotiid sclerites from GGU sample 482337. Fimbuldal, often form the substrate for spheroidal

epibionts with a diameter of 30–50 μm . The spheres are composed of solid amorphous phosphate, often with an irregular concentric outer zone. Their surface texture is usually irregular due to diagenetic phosphate growth between adjoining sediment grains, but many specimens display a pore 5–10 μm in diameter (Fig. 20H).

Cellulate rods

Figure 20I–K, O

Figured material. – PMU 18355 and PMU 18356 from GGU sample 271492, southern Lauge Koch Land.

Discussion. – The robust fragments of rods are characterised by a cellular surface structure in which acute ridges delimit concave depressions that are finely tuberculate, with the tubercles often arranged in rows. Individual cells within this pattern are generally equidimensional but vary greatly in size from 50–300 μm in diameter. The structure shows superficial similarity to the surface texture of sclerites of conodontiform *Rhombocorniculum* Walliser, 1958 (Kouchinsky *et al.* 2011), but the ornamentation seen within the depressions suggests that they may form elements within tommotiid scleritomes (Fig. 19D, E, I, K).

Phylum Cyanobacteria Stanier ex Cavalier-Smith, 2002
Family Cyanophyceae Schaffner, 1909, *incertae sedis*

Genus *Girvanella* Nicholson & Etheridge, 1878

Type species. – *Girvanella problematica* Nicholson & Etheridge, 1878, Stinchar Limestone, Girvan, southern Scotland; Upper Ordovician.

***Girvanella* spp.**

Figure 20I, K, L, N, Q

Figured material. – PMU 18357 and a specimen associated with MGUH 27652 from GGU sample 271718, Løndal.

Discussion. – Tangled masses of parallel-sided filaments encrusting bioclasts (e.g. Fig. 20I, K) have an external filament diameter of about 20 μm . The phosphatised core is separated from an outer phosphatised encrustation by a gap equivalent to the now dissolved calcareous sheath (Fig. 20L).

Girvanella masses are widely distributed in decalcified residues of Cambrian limestones from North Greenland. An unusual specimen from GGU sample 271718 displays threads that were tightly wrapped around an unknown rod (Fig. 20Q). *Girvanella lianiformis* Peel, 2018 from the Ekspedition Bræ Formation (Drumian Stage) of southern Freuchen Land, North Greenland, has filaments about 40 μm in diameter intertwined around the branches of the

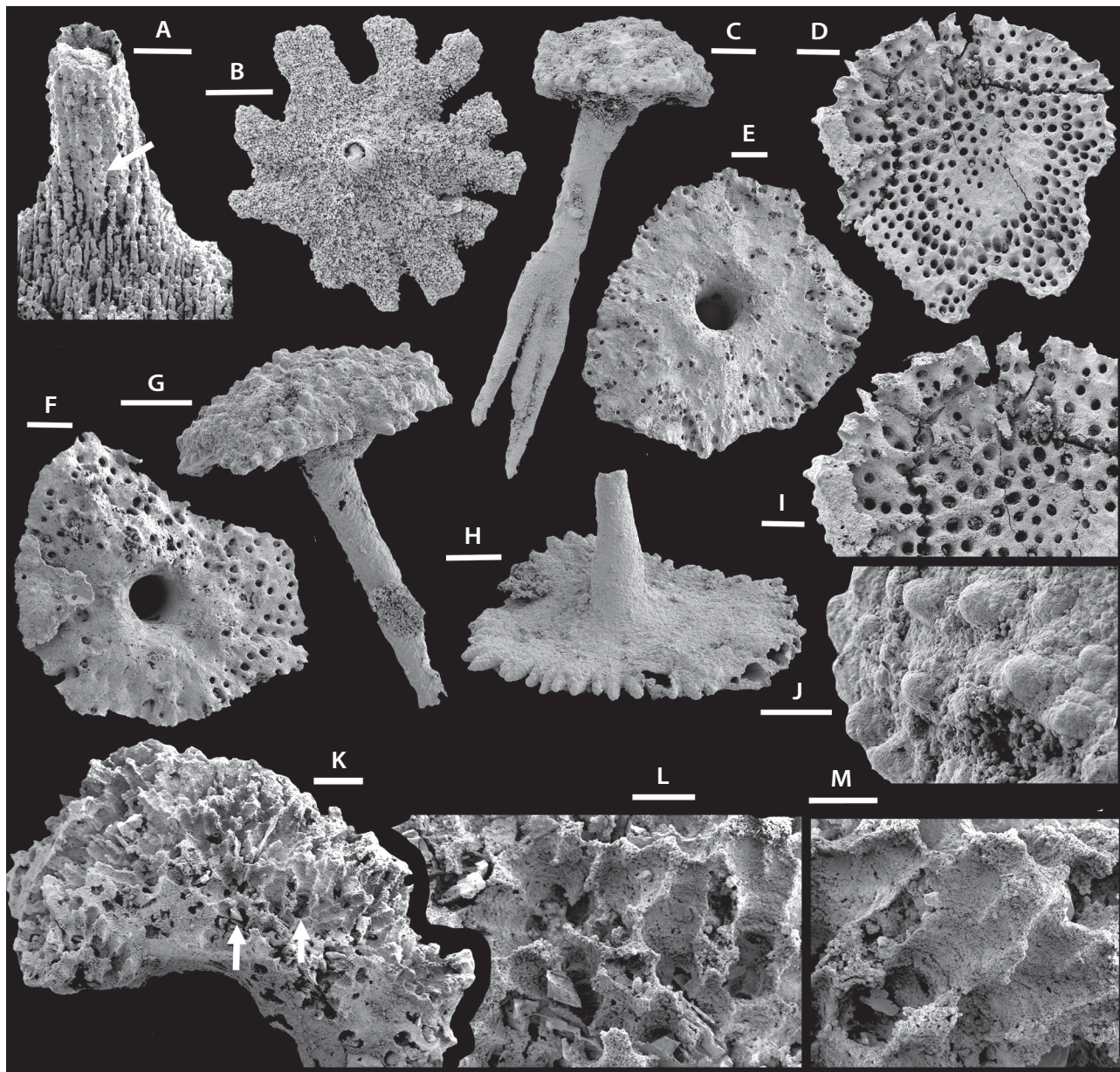


Figure 21. Problematica from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A–J – parasols and perforated plates. A, B – PMU 18359 from GGU sample 271718, with detail of stereome (arrow in A) on central spine. C – PMU 18360 from GGU sample 218831. D, I – PMU 18361 from GGU sample 271492. E – PMU 18362 from GGU sample 271718. F – PMU 18363 from GGU sample 271718. G, J – PMU 36171 from GGU sample 271492. H – PMU 18364 from GGU sample 271492. • K, L, M – *Epiphyton* sp., PMU 18365 from GGU sample 271718. Scale bars: 20 µm (J); 30 µm (I); 50 µm (A, C, D, F–H, L, M); 100 µm (E, K); 200 µm (B).

dendritic epiphytacean *Orpikania freucheni* Peel, 2018, to which it is attached with conical holdfasts. *Girvanella pituutaq* Peel, 2018, from the same formation and locality, differs in having straight filaments 60–80µm in diameter that are collectively twisted together into a rope.

Genus *Subtifloria* Maslev, 1956

Type species. – *Subtifloria delicata* Maslev, 1956, lower Cambrian of Siberia.

Subtifloria sp.

Figure 20M, P

Figured material. – PMU 18358 from GGU sample 271718, Løndal.

Discussion. – *Subtifloria* is characterised by bundles of straight, tubular filaments with a calcified sheath in contrast to the irregularly coiled or folded filaments of *Girvanella*. The single specimen from GGU sample 271718 has

a preserved length of 2 mm and consists of a bundle of about 20 non-branching tubular filaments in which the phosphatized external sheath has an external diameter of 20–30 μm (Fig. 20M, P). The external surface of the sheath is crossed by irregular fine ridges with a diameter of about 2 μm that are interpreted as fungae (Fig. 20P, arrow).

Subtifloria is mainly described from the lower Cambrian (Maslev 1956, Meshkova 1983, Rozanov *et al.* 2010, Wrona & Zhuravlev 1996). *Subtifloria* sp. described by Feng *et al.* (2010) from the Devonian of South China has calcified filaments with an average external diameter of 23 μm and a mean wall thickness of 6 μm , similar in dimensions to material assigned to *Subtifloria delicata* Maslev, 1956 from the Ediacaran of China by Min *et al.* (2020). *Subtifloria delicata* of Liu *et al.* (2021) from the Ordovician of North China has thinner walls (3 μm).

Family Epiphytaceae Korde, 1959

Genus *Epiphyton* Bornemann, 1886

Type species. – *Epiphyton flabellatum* Bornemann, 1886 from the lower Cambrian of Sardinia.

Discussion. – Riding (1991) noted that described Cambrian specimens of the multiaxial, dendritic *Epiphyton* were usually solid and micritic in composition. Other preservational varieties include tubular and coccoidal forms (Min *et al.* 2019, Zhang *et al.* 2019) but all may be strongly influenced by the high levels of calcification and diagenetic mineralization that are characteristic of many Lower Palaeozoic occurrences (Pratt 1984, 2001). Pratt (1984) proposed that the branches of *Epiphyton* were produced by stacking of colonies of coccoid cells and this hypothesis was supported by Zhang *et al.* (2019) following examination of Miaolingian Series thrombolites from North China. However, as discussed below under *Hensonidendra* gen. nov., Luchinina & Terleev (2008) assigned to *Epiphyton* material from the lower Cambrian of eastern Siberia with numerous transverse internal structures interpreted as thin cells.

Riding (1991) assigned *Epiphyton* to Cyanobacteria, but Luchinina & Terleev (2008) supported earlier suggestions that it was a red alga (Rhodophyta). Liu *et al.* (2016) favoured placement as Microproblematica. Zhang *et al.* (2019) followed Pratt (1984) and others in concluding that *Epiphyton* represents stacks of calcified coccoid cyanobacteria.

Epiphyton sp.

Figure 21K–M

Figured material. – PMU 18365 from GGU sample 271718.

Discussion. – Phosphatized, irregular hemispherical masses, perhaps redeposited clasts, about 1 mm in diameter preserve external moulds of short-branched dendritic colonies assigned to *Epiphyton* (Fig. 21K–M). The original calcified dendritic colonies that were dissolved during sample preparation had individual branches 40–60 μm in diameter; their outer surface is annulated. Branching is by simple dichotomous division (Fig. 21L). The annulation is similar to that illustrated by Min *et al.* (2019, fig. 3) in phosphatized specimens from the Neoproterozoic Dengying Formation of Shaanxi Province, China, that they assigned to *Epiphyton*. Min *et al.* (2019) regarded the transverse annulation as an external feature. The dominant, coarse annulations (length of individual annulations = 10–15 μm) are overlain by a pattern of fine transverse striations (Min *et al.* 2019, fig. 3b, 4d), but these are not seen in the more coarsely preserved Greenland specimens. The annulation likely reflects cell structure, with the shape of the cells and branches modified by postmortal degradation and variable diagenetic mineralization, but see discussion of *Hensonidendra* gen. nov., below.

Peel (1988b, fig. 8) demonstrated that early phosphatization, in the spiruliniform *Jiangispirellus groenlandicus* Peel, 1988b from the Ediacaran of North Greenland, can produce uniform, pristine, moulds of cells (diameter 50 μm , length 8 μm) in the phosphatized trichomes, but also replicas of degraded, dead specimens. In both cases, phosphatization was restricted to the peripheral area of the trichome such that individual preserved fossils were tubular after dissolution of calcium carbonate during preparation (Peel 1988b, Willman *et al.* 2020).

Epiphytiform Problematica

Genus *Hensonidendra* gen. nov.

LSID. – Zoobank.org:act:3F319FBF-B5C9-43ED-88FC-07DF24296231

Type species. – *Hensonidendra tavsénica* sp. nov., from the Henson Gletscher Formation of North Greenland; middle Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – A combination of Henson Gletscher Formation and the branching form. Feminine.

Diagnosis. – Multiaxial dendritic to almost hemispherical colonies up to a maximum observed height of 3 mm. Closely spaced circular or polygonal tubules, up to about 100 μm in diameter, branch dichotomously at a low angle by simple division into two subequal daughter tubules that continue growth in close proximity to each other. Wall growth by internal accretion of steeply inclined laminae

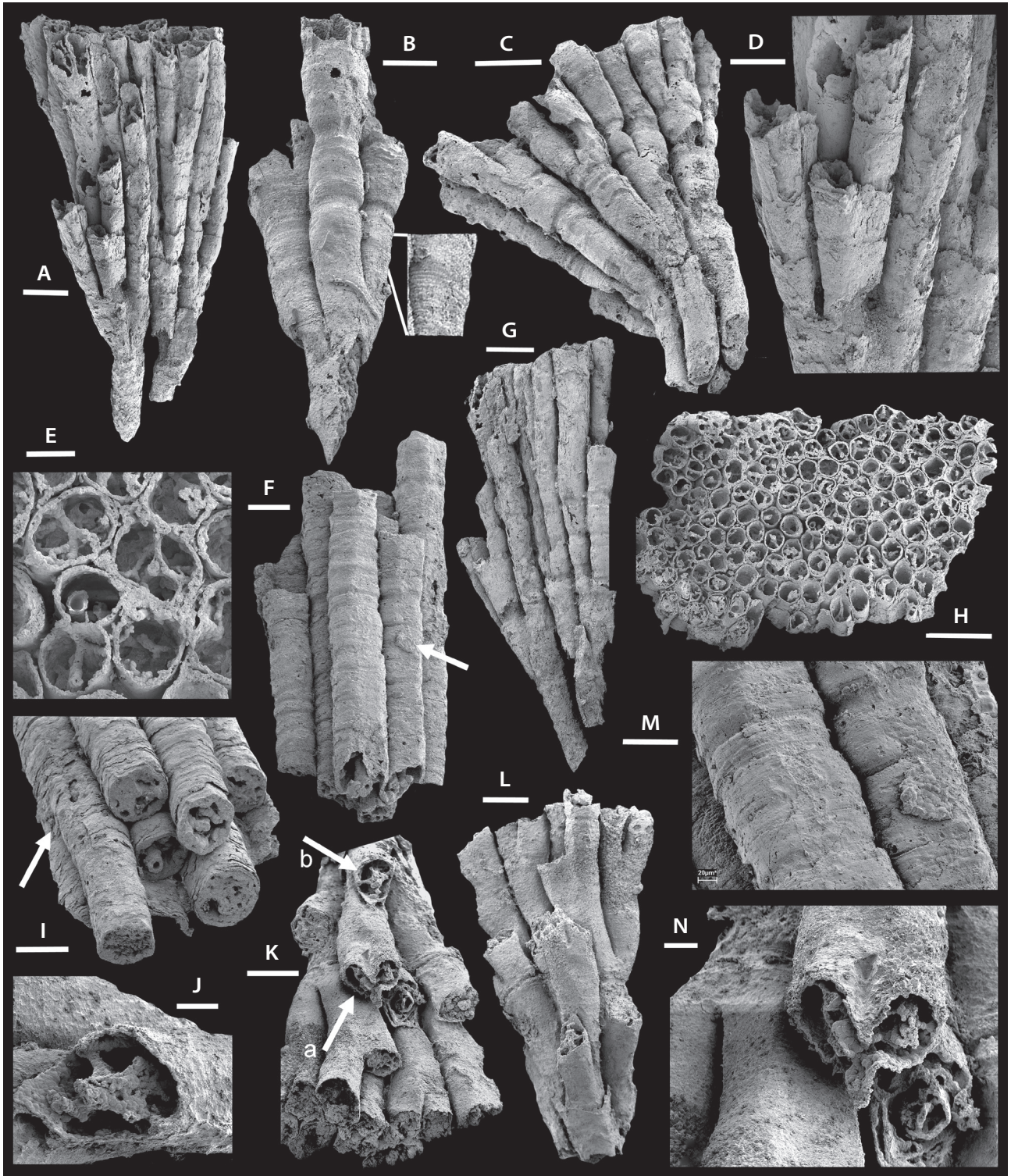


Figure 22. Multiaxial colonies from GGU sample 271492, the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A–E, G, H, J–L, N – *Hensonidendra tavszenica* gen. et sp. nov. A, D, G – PMU 18366, lateral view (detail in D) showing mode of growth with accretion within the calice. B – PMU 18367 showing period growth constrictions, surface detail in inset. C – PMU 18368, lateral view with transverse constrictions emphasised by incomplete phosphatisation or corrosion in acid. E, H – PMU 38172, cross-section with detail (E); note phosphatized cryptoendoliths within calices. J–L, N – PMU 38171/2, opposing lateral views (K, L) with detail of branching point (N, arrow a in K) and cryptoendoliths with spherulitic growth within calice (J, arrow b in K). • F, I, M – *Tavsenicoralla hensoniensis* sp. nov. PMU 18369 with detail of fine transverse ridges/growth lines (M, located by arrow in F). Arrow in I locates dichotomous branching point; flattened surfaces of cryptoendoliths within calices indicate presence of tabulae (now dissolved). Scale bars: 50 μ m (J, M, N); 100 μ m (B, D, F, I); 200 μ m (A, C, G, K, L); 500 μ m (H).

forming cone-shaped growth increments (Figs 22A, D, M). External surface with periodic transverse grooves and constrictions separated by fine transverse ridges/growth lines. Internal structure poorly known, but transverse tabulae present in one species.

Discussion. – A variety of problematic multiaxial and dendritic organisms of similar overall morphology has been described from Ediacaran and Cambrian strata (Korde 1973; Riding 1991; Zhuravlev *et al.* 1993; Scrutton 1997; Cunningham *et al.* 2015, 2017; Pruss *et al.* 2022), usually from thin sections in carbonate rocks. Records of phosphatized material, such as the current Greenland material, are less common (*e.g.* Wrona 2004, Luchinina & Terleev 2008, Luchinina & Zhegallo 2016, Peel 2018b, Min *et al.* 2019). The preservational differences frustrate comparison since critical morphological features such as cell structure and internal septa and tabulae are generally not preserved within the phosphatized tubules/corallites, but see Peel (1988b) and Castellani *et al.* (2018) for examples of the phosphatized preservation of cell structure in cyanobacteria.

The dichotomous branching and small diameter of the tubules favour interpretation of *Hensonidendra* as an epiphytacean, but these display a variety of internal structures, and presumably growth mechanisms, within the branches that may suggest polyphyletism (Pratt 1984, Luchinina & Terleev 2008, Min *et al.* 2019, Peel 2018b, Zhang *et al.* 2019). The cone-shaped, accretionary, growth increments of *Hensonidendra tavszenica* sp. nov. (Fig. 22A, D) suggest interpretation as a cnidarian, but most described Cambrian cnidarians (coralomorphs) have corallites with a larger (millimetre scale) diameter (Zhuravlev *et al.* 1993, Hicks 2006). However, other groups of tubular Cambrian small shelly fossils with a similar tube diameter to *Hensonidendra*, such as anabaritids and hyolithelminths, are often interpreted as cnidarians (Kouchinsky *et al.* 2017).

Of the coralomorphs listed by Hicks (2006), *Harklessia yuenlingensis* Hicks, 2006 from the Harkless Formation (late Cambrian Stage 4) of Nevada resembles *Hensonidendra* in terms of overall form and corallite morphology. It is distinguished, however, by its cerioid corallites with slightly meandrine corallite walls and a corallite diameter of 1.2–3.2 mm, much larger than the 100 µm of *Hensonidendra*. *Hensonidendra* is similar to bryomorphic colonies from the Harkless Formation described by Pruss *et al.* (2022) but the tubules in the latter lack the dichotomous branching of *Hensonidendra*.

Tavsenicoralla gen. nov., a coralomorph from GGU sample 271718, is distinguished by its nondichotomous branching, with daughter corallites arising laterally, one at a time, from the parent corallite (Fig. 8 A–D, I, J). In this respect it is similar to the bryomorph of Pruss *et al.*

(2022). The periodic transverse constrictions and growth lines in *Tavsenicoralla* (Figs 8B, 22F, M) suggest a similar mode of growth to *Hensonidendra*.

The notion of branches of *Epiphyton* forming as series of stacked coccoid colonies of cells advanced by Pratt (1984) and elaborated by Zhang *et al.* (2019) envisages the formation of a series of generally convex-up transverse surfaces crossing the branch with the addition of each colony. It is inherent in the models of morphological integration advanced by Pratt (1984, fig. 3) and Riding (1991, fig. 3), and the structure can be discerned in *Epiphyton* sp. from GGU sample 271718 (Fig. 21K–M). It is well seen in the septate *Chabakovia* Vologdin, 1939 as illustrated by Voronova & Radionova (1976, pl. 6, fig. 1) and Cherchi & Schroeder (1985). This calcification of the surface of the individual coccoids as they are sequentially stacked to form the branches contrasts markedly with the series of stacked cones with internal accretion evident in the wall structure of *Hensonidendra tavszenica* (Fig. 22A, D).

The stacked series of convex-up coccoid cell colonies is not seen in *Epiphyton durum* Korde, 1961 of Luchinina & Terleev (2008, pl. 1), from the early Cambrian (Tommotian Regional Stage) of eastern Siberia. This has branches about 70 µm in diameter, without an outer wall, that widen distally to about 110 µm; it is considered to be a species of *Gordonophyton* Korde, 1973. The branches are banded into darker and lighter areas and are composed of flat, transverse, plate-like structures (cells?), the margins of which are seen as lines 2–4 µm apart. The outer surface of well-preserved specimens of *Hensonidendra tavszenica* (Fig. 22B and inset) displays similarly-sized transverse sculpture. Fine, transverse ridges/growth lines are also present on the individual primary growth increments in *Hensonidendra hensoniensis* gen. et sp. nov. (Fig. 22F, I, M) from GGU sample 271492, but these are more widely spaced than those illustrated by Luchinina & Terleev (2008).

Direct comparison of the fine transverse ridges in *Hensonidendra tavszenica* (Fig. 22B and inset) with the putative cell boundaries in *Gordonophyton durum* of Luchinina & Terleev (2008, pl. 1) might suggest a grouping of thin cells in *Hensonidendra tavszenica* into growth packages delimited by the coarser growth increments, perhaps as a result of environmental periodicity. However, interpretation as growth lines on the developing coarser increments is more likely even though packaging of putative cells is seen in *Gordonophyton durum* in the alternation of dark and paler bands (Luchinina & Terleev 2008, pl. 1).

The stacking of individual cells, each of which extends across the full diameter of the branch in *Gordonophyton durum*, into packages is dissimilar from the arrangement of cells within individual coccoids in the model of stacked coccoid capsules in *Epiphyton* envisaged by Zhang *et al.* (2019, figs 8, 9). This might imply that the putative cells seen in *Gordonophyton durum* could represent

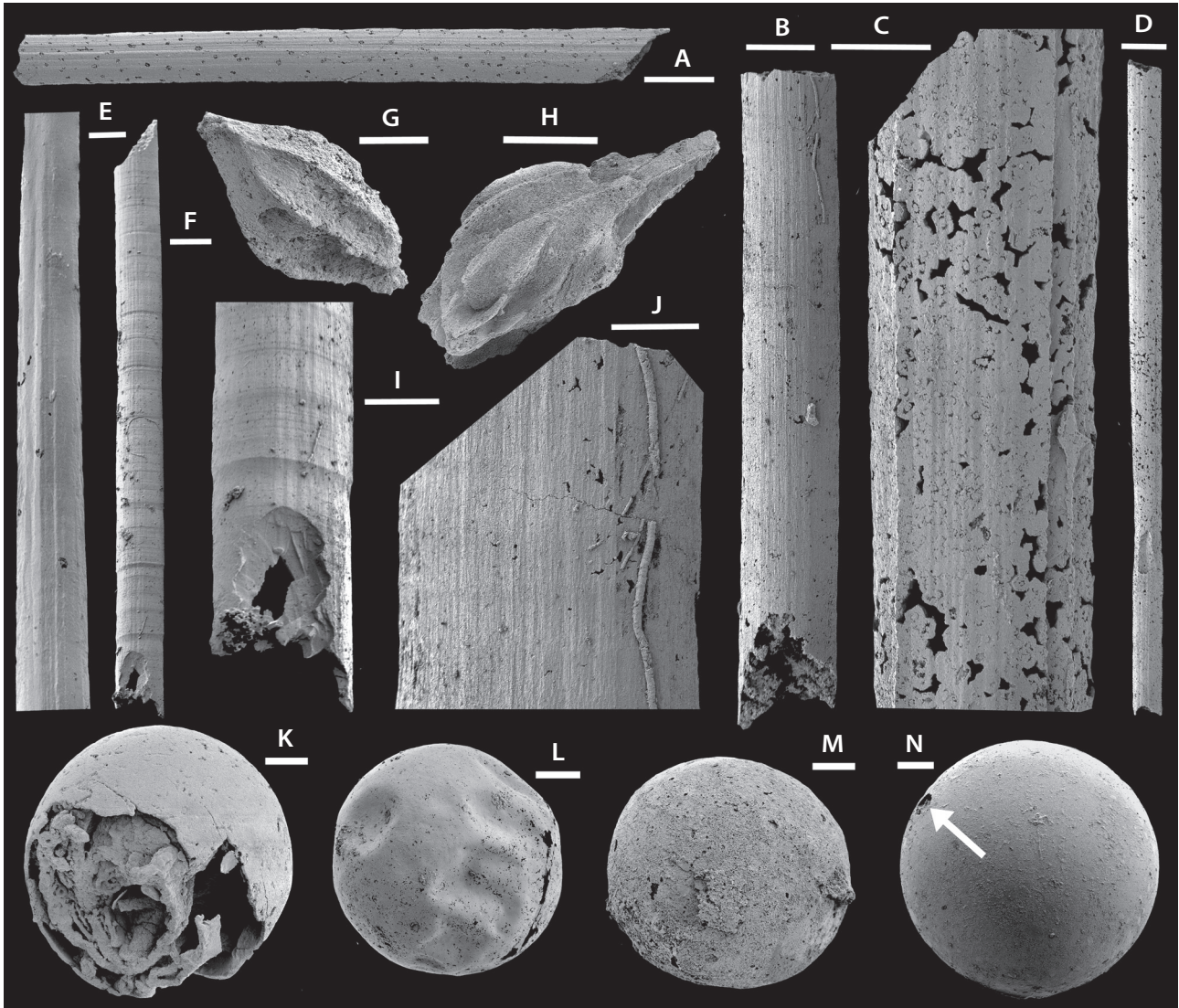


Figure 23. Problematica from the upper Henson Gletscher Formation, Cambrian (Wuliuan Stage), North Greenland. • A–H, I, J – *Laugephakos groenlandicus* sp. nov., from GGU sample 271492 unless stated. A – PMU 18370. B, J – PMU 18371. C, D – PMU 18372 from GGU sample 218831. E – PMU 18373. F, I – PMU 18374. • G, H – *Cambrocoryne lagenamorpha* Peel, 2023a from GGU sample 271718. G – PMU 39699. H – PMU 39697, holotype. • K–N – spheres from GGU sample 271492 unless stated. K – PMU 18375. L – PMU 18376. M – PMU 18377. N – PMU 18251 from GGU sample 218831. Scale bars: 30 μ m (C, E); 50 μ m (I–K, N); 100 μ m (A, B, D, F, G, L, M); 200 μ m (H).

degraded, largely flattened, coccoid colonies of cells in which the outer colony wall was rapidly mineralized while the inner content was lost, an interpretation that could be strengthened by the presence of fine transverse sculpture on the stacked ‘coccoids’ in the phosphatized Ediacaran material that Min *et al.* (2019, fig. 4d) assigned to *Epiphyton*. However, the consistently uniform shape of the putative cells in the branches of *Gordonophyton durum* argues against simple postmortal degradation, suggesting that this growth form is different from the stacked coccoid colonies of Pratt (1984) and Zhang *et al.* (2019). *Gordonophyton durum*, *Epiphyton* and *Hensonidendra* have fundamentally different growth patterns, suggesting that they probably are not closely related to each other.

Bija Vologdin, 1932, originally described from the lower Cambrian (Botoman Regional Stage) of southern Siberia, was considered to be either a chaetetid or a solenoporacean by Scrutton (1997), but as a cyanobacterian by Liu *et al.* (2016); occurrences are listed by Pruss *et al.* (2022). As illustrated by Voronova & Radionova (1976, pl. 16, figs 1–4), the rather strongly recrystallised narrower corallites appear to be cerioid rather than phacelloid, as are specimens described by Liu *et al.* (2016) from the Ordovician of the Tarim Basin, northwest China. Pruss *et al.* (2022) described a bryomorph form similar to *Bija* from the Harkless Formation (Cambrian Series 2, Stage 4) of Nevada, which they interpreted as a possible mineralized bryozoan. *Hensonidendra* differs by its

dichotomous budding structure, in contrast to the parent–daughter relationship of the Nevadan form. Budding episodes in *Hensonidendra tavsénica* (Fig. 22L) also occur more frequently than in the Nevadan bryomorph (Pruss *et al.* 2022, fig. 5).

***Hensonidendra tavsénica* sp. nov.**

Figure 22A–E, G, H, J–L, N

LSID. – Zoobank.org:act:0142731E-8456-4338-B2B8-3B8448B3E7C8

Holotype. – PMU 18366 from GGU sample 271492.

Type horizon and locality. – Upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. – PMU 18367, PMU 18368, PMU 38172, PMU 3871/2 from GGU sample 271492, southern Lauge Koch Land.

Etymology. – From Hans Tavsén Iskappe (Fig. 1A).

Diagnosis. – Type species of *Hensonidendra* with closely spaced circular tubules up to about 100 µm in diameter; branches often with periodic transverse constrictions (Fig. 22B, C). Internal structures not observed.

Description. – The multiaxial, dendritic to almost hemispherical colonies attain a maximum observed height of 3 mm. The closely spaced circular tubules (diameter up to about 100 µm) branch dichotomously at a low angle by simple division into two subequal daughter tubules that continue growth in close proximity to each other. Branching occurs at intervals from about 300–600 µm (Fig. 22A, C, L). Growth of the outer wall is achieved by internal accretion of steeply inclined laminae that form cone-shaped growth increments (Figs 22A, D, M). Growth increments tend to be separated by transverse constrictions and of uniform length in each branch, with incremental lengths of 150–300 µm. Their external surfaces are ornamented with fine, transverse ridges and growth lines (Fig. 22B and inset). Original internal structures are not known.

Discussion. – Although common in GGU samples 271492 and 271718, most specimens in residues consist of bunches of a few tubules representing fragments of the broken colony (Fig. 22A, C). However, transverse sections may display more than 100 tubules (Fig. 22H). The outer wall of phosphatized tubules has a smooth surface, with preservation of fine transverse (growth?) lines in well preserved specimens from GGU sample 271492,

while the inner wall is irregular and coated with patches of spherulitic diagenetic mineralization. Specimens often display periodic constrictions (Fig. 22B, C) which may be emphasized by corrosion or etching. Phosphatized cryptoendoliths (and possibly euendoliths) are often conspicuous within the now decalcified tubules (Fig. 22E, J, K, N).

The epiphytacean *Orpikania* Peel, 2018b, from the Ekspedition Bræ Formation (Drumian Stage) of North Greenland is known from dendritic tubular fragments that are similar in diameter to those of *Hensonidendra tavsénica*, but the overall form of its colonies is not known. In contrast to the accretionary growth ornamentation of *Hensonidendra tavsénica* (Fig. 22A, D), the outer surface of *Orpikania* displays stacked, cylindrical segments interpreted as cell structure by Peel (2018b).

***Hensonidendra hensoniensis* sp. nov.**

Figure 22F, I, M

LSID. – Zoobank.org:act:88D2882F-2A19-42ED-9FF3-D62BF2CB08D6

Holotype. – PMU 18369 from GGU sample 271492, southern Lauge Koch Land.

Type horizon and locality. – Upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – From Henson Gletscher (Fig. 1A).

Diagnosis. – A species of *Hensonidendra* with closely juxtaposed, mainly polygonal, parallel-sided branches, and simple transverse internal partitions.

Description. – Multiaxial colonies in which the closely packed tubules are mainly polygonal in cross-section, but do not share common walls with adjacent corallites. Individual tubules are of uniform width with a diameter of about 100 µm and a maximum observed length of about 1 mm (all are broken distally). Budding is dichotomous (arrow in Fig. 22I). Tubule growth is periodic, with each growth stage originating by internal accretion within the previous stage, the junction marked by a shallow transverse constriction (Fig. 22I, F, M). Each growth stage is ornamented with growth lines (Fig. 22M). Tubules with simple transverse internal partitions.

Discussion. – The presence of transverse internal partitions (tabulae) in the decalcified tubules is likely demonstrated by the termination of phosphatized diagenetic cryptoendoliths at flat surfaces (Fig. 22I), although the tabulae themselves are not preserved (Fig. 22I).

Hensonidendra hensoniensis sp. nov. differs from the much more abundant type species *Hensonidendra tavsénica* sp. nov. in the polygonal shape of its tubules and their more uniform width. Tabulae have not been observed in *Hensonidendra tavsénica* but this may be a diagenetic feature.

Acknowledgements

Samples were collected during the North Greenland Project (1978–1980) of Grønlands Geologiske Undersøgelse (GGU; Geological Survey of Greenland, now a part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen. Some primary images were made by Mark R. Blaker (Keele), Sébastien Clausen (Lille) and Artem Kouchinsky (Stockholm). Jon R. Ineson (GEUS) provided measured sections through the Henson Gletscher Formation. Andrej Yu. Zhuravlev (Moscow) kindly provided information concerning some Siberian material. Marissa Betts (Armidale), Jan Ove R. Ebbestad (Uppsala) and journal editors are thanked for their comments concerning the submitted manuscript.

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