Euendolith borings in *Chancelloria* and *Nisusia* from the middle Cambrian (Miaolingian) of North Greenland (Laurentia)

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Borings of microscopic organisms (euendoliths) are described from the Henson Gletscher Formation (middle Cambrian, Miaolingian Series, Wuliuan Stage) of Peary Land, North Greenland (Laurentia). Partially phosphatised sclerites of *Chancelloria* and valves of the brachiopod *Nisusia* reveal abundant casts of borings following dissolution of skeletal calcium carbonate in weak acetic acid. Threads referred to *Scolecia* dominate, occurring together with coccoids (*Planobola*) and the branching *Fascichnus*, in a suite comparable to a lower Cambrian assemblage from the Maidiping Formation of Sichuan, China.

Keywords: Euendoliths, *Chancelloria* spicules, *Nisusia*, Cambrian (Miaolingian Series, Wuliuan Stage), North Greenland, Laurentia.

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Microorganisms including algae, Cyanobacteria and Fungi that bore actively into hard substrates or the calcareous shells and skeletons of living and dead organisms are termed euendoliths (Golubic *et al.* 1981) and have a geological record that extends back to the Palaeoproterozoic (Campbell 1982; Zhang & Golubic 1987; Bengtson *et al.* 2017). At the present day, their activities contribute to the diminution of the penetrated calcareous materials to cryptocrystalline textures through the process of micritisation (MacIntyre & Reid 1978).

The starting point for studies of euendoliths in the ancient rocks of Greenland is the description by Green *et al.* (1988) of microfossils in thin sections of Upper Proterozoic oolites and pisolites from the Eleonore Bay Group of North-East Greenland. Cambrian euendoliths were first reported in Greenland from the Henson Gletscher Formation by Larsen (1989) and described subsequently by Stockfors & Peel (2005a). Borings in ooliths from the Henson Gletscher Formation that are coated by calcium phosphate, and phosphate infilled casts of the tunnels etched free in weak acetic acid were referred to the presumed cyanobacterium *Eohyella* Zhang & Golubic, 1987 (Fig. 1). Their description followed studies by Runnegar (1985) and Runnegar in Bengtson *et al.* (1990) of calcium phosphate infilled borings in the shells of early Cambrian molluscs from Australia, while Li (1997) recorded an assemblage of phosphatised euendolith casts of borings in fragments of the shells of several groups of invertebrates from the lower Cambrian of China.

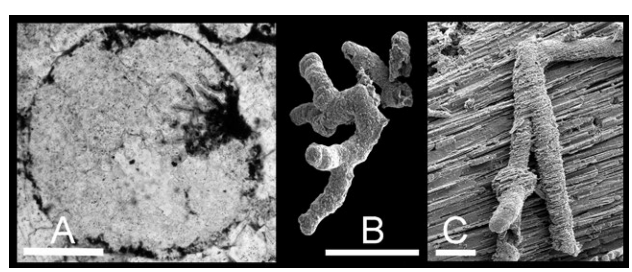

Fig. 1. Preservation of euendoliths in GGU sample 271718, Henson Gletscher Formation, Cambrian (Miaolingian Series, Wuliuan Stage), Løndal, North Greenland. A, *Fascichnus* isp. (*Eohyella* sp). penetrating oolith, MGUH 27656. B, *Fascichnus* isp., internal cast of boring, MGUH 27654. C, calcium phosphate infilled euendolith boring retaining the fine microstructure of the dissolved shell that is reflected in the coarse phosphatic replication of diagenetic aragonite needles now comprising the underlying internal mould. PMU 21439. Scale bars: 10 µm (C); 100 µm (A); 400 µm (B).

Calcium phosphate filled borings formed by euendoliths occur frequently in the calcareous shells of invertebrates from the middle Cambrian Henson Gletscher Formation (Miaolingian Series, Wuliuan Stage) of south-western Peary Land, North Greenland (Fig. 2), although they are uncommon in the helcionelloid molluscs that form the most conspicuous element of the fauna (Peel & Kouchinsky 2022). The mode of preservation is the same as described by Runnegar (1985) and Li (1987), with diagenetic calcium phosphate filling borings within calcareous shells. Routine treatment of limestone samples with weak acetic acid dissolves calcium carbonate, leaving phosphatised casts in the residues.

This paper focusses on the assemblage of euendoliths observed in sclerites of the eumetazoan *Chancelloria* Walcott, 1920 (Figs. 3–6), supplementing the material from the same sample (GGU sample 271718) described by Stockfors & Peel (2005a), but comparisons are made with specimens of the calcareous brachiopod *Nisusia* Walcott, 1905 (Fig. 7). Chancelloriids are a widely distributed problematic group of early–middle Cambrian fossils characterised by a bag-like integument studded with external aragonitic sclerites (Bengtson & Hou 2001; Bengtson 2005; Bengtson & Collins 2015; Randell *et al.* 2005; Yun *et al.* 2021). While their overall form is reminiscent of sponges, chancelloriid sclerites are hollow and formed by mineralisation from within (Bengtson 2005, 2015; Peel in press). Complete specimens of chancelloriids are uncommon, but their dissociated sclerites are widespread and often abundant (Bengtson *et al.* 1990: Moore *et al.* 2014, 2019; Kouchinsky *et al.* 2022) Most are stellate in form, with up to eleven lateral rays surrounding a central ray. However, each ray is a separate entity, without internal connection with neighbouring rays in the sclerite, but a basal foramen connects each ray with the soft tissues of the integument (Bengtson & Hou 2001; Bengtson 2015; Yun *et al.* 2021; Peel in press).

Material and methods

GGU sample 271818 was collected on 15th July 1978 from a thin-bedded, phosphatised, bioclastic, dolo-

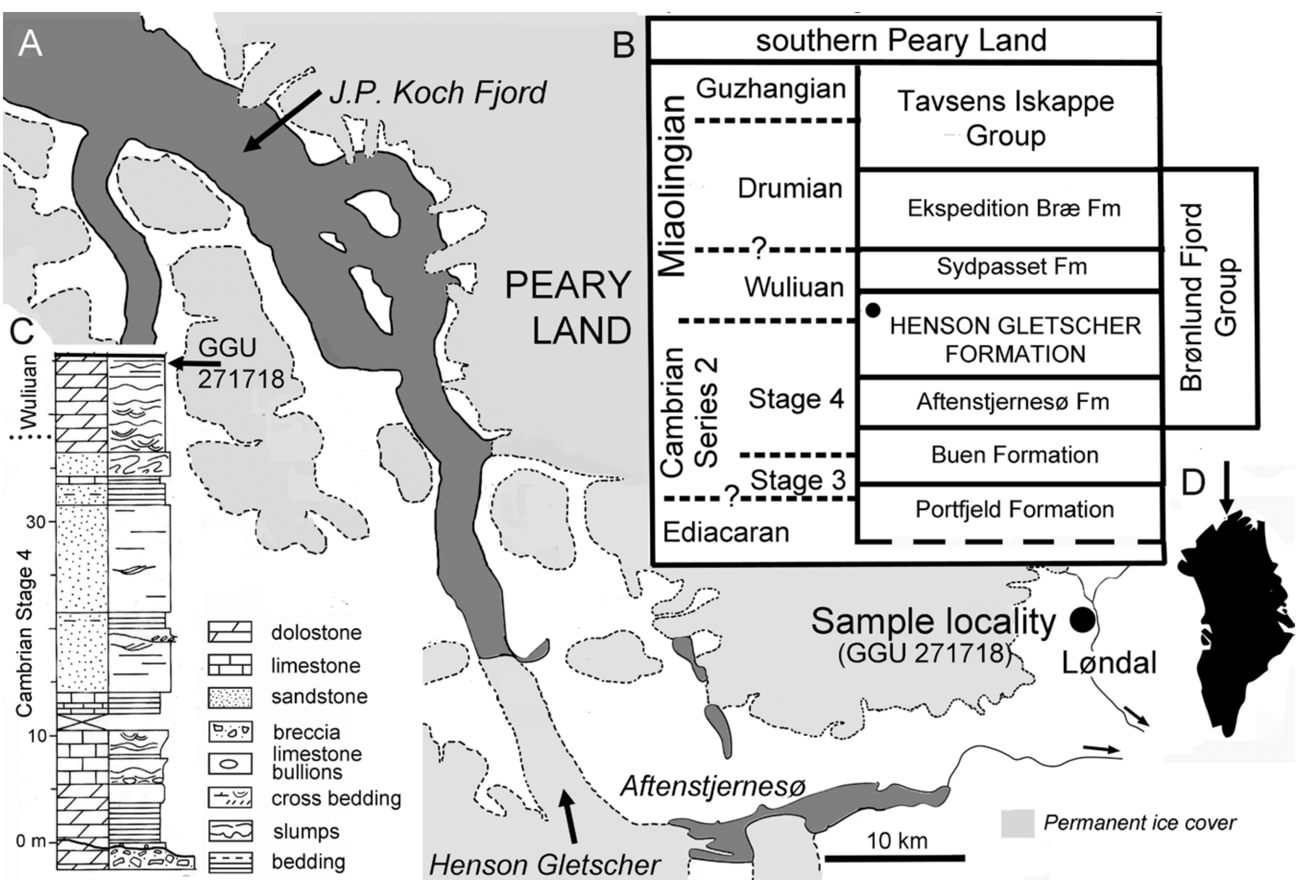

Fig. 2. Geography and geology. **A,** map of the western Peary Land area showing collection locality for GGU sample 271718. **B,** stratigraphic nomenclature in southern Peary Land with location of GGU sample 271718 (black dot). **C,** lithostratigraphic section through the Henson Gletscher Formation in Løndal. **D,** Greenland, arrow locates A.

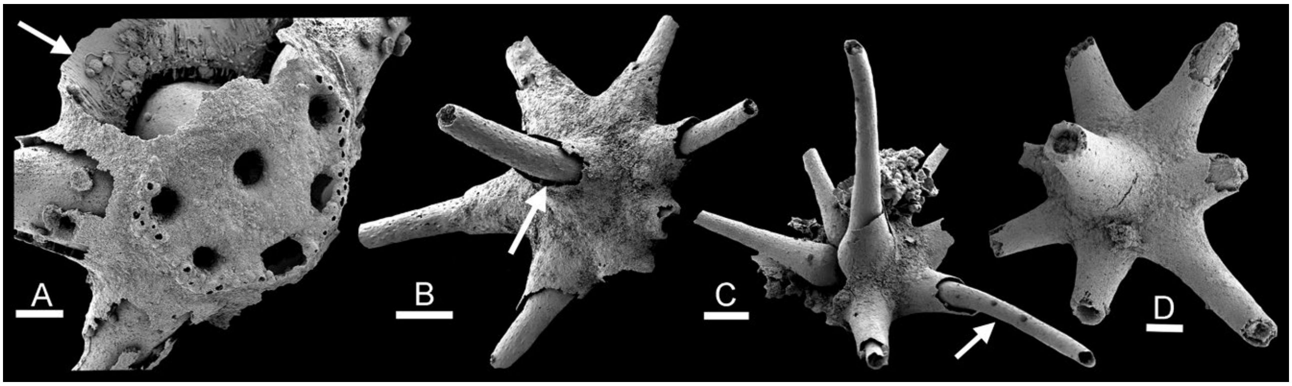

Fig. 3. Phosphatised sclerites of *Chancelloria* from GGU sample 271718, Henson Gletscher Formation, Cambrian (Miaolingian Series, Wuliuan Stage), Løndal, Peary Land. All specimens were treated with weak acetic acid, which dissolved the calcareous shell that is represented by the gap between the internal mould and the external encrustation. **A,** PMU 21440, basal view showing foramina, and the euendolith assemblage (arrow) preserved as internal casts of borings on the phosphatic encrustation of the upper surface of the sclerite. **B,** PMU 21441, upper surface of sclerite showing central ray; arrow locates details in Fig. 5E,G. **C,** PMU 21442, upper surface of sclerite; arrow locates lateral ray with coccoid euendoliths on the internal mould (see Fig. 5B,H). **D,** PMU 21443, upper surface of sclerite. Scale bars: 50 μm (A,D), 100 μm (B,C).

mitic limestone occurring about 1 m below the top of the Henson Gletscher Formation (Higgins *et al.* 1991; Ineson & Peel 1997; Peel 2023) on the west side of Løndal (82°18′N, 37°00′W; Fig. 2). The limestone contains numerous dark, thin, phosphatised layers, some of which formed hardgrounds. The clastic component includes re-deposited calcareous, phosphatised and silicified shells (Peel 2023, fig. 3), together with ooliths. These, and the accompanying bioclasts were frequently bored by euendoliths and covered by calcium phosphate prior to their final deposition.

The Henson Gletscher Formation of western Peary Land, North Greenland, is a highly fossiliferous unit of shelf carbonates and siliciclastic sediments that accumulated within a prograding complex referred to the Brønlund Fjord Group on the present day southern margin of the transarctic Franklin Basin (Higgins *et al*. 1991; Ineson & Peel 1997; Geyer & Peel 2011; Peel *et al*. 2016). The formation is 47 m thick in Løndal and composed mainly of dark, recessive, bituminous and cherty limestones, dolostones and mudstones, but pale fine-grained sandstones form a prominent middle member.

Fossil assemblages from GGU sample 271718 indicate a middle Cambrian age (Miaolingian Series, Wuliuan Stage), although the formation as a whole ranges from Cambrian Stage 4 to the Drumian Stage across North Greenland (Robison 1984, 1994; Higgins *et al.* 1991; Babcock 1994; Blaker & Peel 1997; Ineson & Peel 1997; Geyer & Peel 2011). The rich fauna from GGU sample 271718 and equivalent localities around the front of Henson Gletscher (Fig. 2) was documented by Clausen & Peel (2012), Peel (2021a,b, 2022a,b, 2023), Peel & Kouchinsky (2022, in press).

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

Preservation. Diagenetic phosphatisation is conspicuous in GGU sample 271718 (Peel 2023). In terms of euendoliths it may be studied in two settings. In thin sections, the diagenetic calcium phosphate is visible as a dark brown coating or the infilling of cavities or borings in calareous ooliths and bioclastic skeletal elements (Fig. 1A). Following dissolution of the calcium carbonate during treatment with weak acetic acid, the calcium phosphate infillings may be etched free (Fig. 1B) or stand in positive relief on phosphatised moulds of the shell interior or encrustations of the exterior (Fig. 1C). Many of the infillings display a fibrous stucture representing traces of the microstructure of the calcareous shells into which the microorganisms bored (Fig. 1C). Golubic *et al.* (1975) noted that this seemed to be mainly a character of Cyanobacteria whereas euendolithic fungi often produced smooth tunnels. Radtke & Golubic (2005) and Wisshak (2012) summarised the organisms producing euendolithic borings and their geological range. The affinity of the boring organisms is not known but cyanobacterians may produce ichnospecies within the ichnogenera noted here (Wisshak 2012).

The borings by euendoliths observed by Larsen (1989) and Stockfors & Peel (2005a) were referred to *Eohyella* Zhang & Golubic, 1987 (Green *et al*. 1988; Larsen 1989; Stockfors & Peel 2005a), which is closely similar in morphology to the present day *Hyella* Bornet & Flahault, 1988. These authors followed biological nomenclature in describing forms characterised by radiating linear cell series (Radtke & Golubic 2005; Fig. 1A) and their casts (Fig. 1B). However the casts are better classified in ichnotaxonomy and referred to the ichnogenus *Fascichnus* Radtke & Golubic, 2005 since similar trace fossils can be produced by a variety of organisms.

Coccoid trace fossils

***Planobola* cf. *macrogota* Schmidt, 1992**

These spherical to slightly oval, coccoid, bodies are in direct contact with the calcium phosphate encrustation of the outer surface of the shell and range in diameter from 7–20 μm. They are common in a *Chancelloria* sclerite with seven radial rays and a central ray (Fig. 3A, 6J–L) and lie closely spaced on the under surface of the calcium phosphate encrustration of the upper surface of the sclerite but are rare on the internal mould. In a specimen of *Nisusia* they occur in abundance on the inner surface of a valve (Fig. 7D). Their surface is fibrous in larger specimens, occasionally granular, irregular, reflecting etching by the borer into the now dissolved aragonitic shell, with strongly aligned crystallites upto about 1 μm in width (Fig. 6L). The interface between the calcium phosphate encrustation (lower surface in Fig. 6J–L located by arrow in Fig. 3A) and the dissolved calcareous shell has the same orientation as the fibrous texture but is composed of much wider crystal laths. The spheres are also present in *Chancelloria* sp. as described by Peel & Kouchinsky (in press) from equivalent strata in the Henson Gletscher Formation on the western side of Henson Gletscher (Fig. 4I).

Infrequently, there appears to be direct connection of the spheres with meandering, occasionally branch-

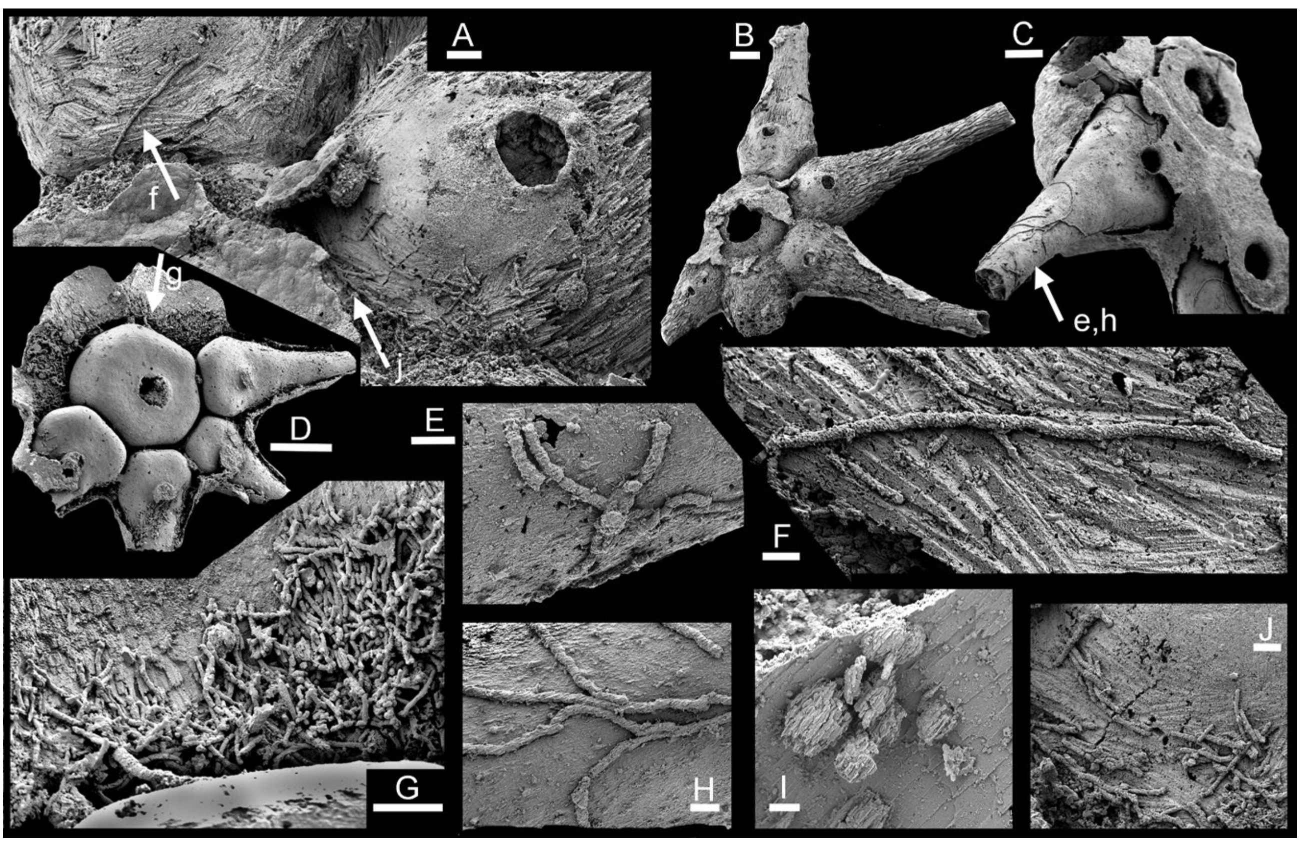

Fig. 4. Euendoliths in *Chancelloria* sclerites. Henson Gletscher Formation, Cambrian (Miaolingian Series, Wuliuan Stage), Løndal, Peary Land. All specimens are preserved as calcium phosphate internal moulds and external encrustations after dissolution of calcium carbonate in weak acetic acid. GGU sample 271718 unless stated. **A,B,F,J,** PMU 21444, basal view with foramina (B), enlarged in (A), to show replicated acicular microstructure of inner shell surface overlain on the internal mould by infilled borings of *Scolecia*, with detail in F and J (located by arrows f and j in A). **C,E,H,** PMU 21445, oblique basal view with internal mould of lateral ray; arrow locates details of *Scolecia* (E,H). **D,G,** PMU 21446, basal view of internal mould; arrow g locates detail of dense mass of *Scolecia* (G). **I,** PMU 21447, infillings of coccoid borings attached to external encrustation of sclerite wall; note microstructure of broad laths on wall. Henson Gletscher Formation at front of Henson Gletscher, after Peel & Kouchinsky (in press). Scale bars: 5 μm (F,H,I); 7 μm (E); 10 μm (J); 20μm (A,G); 50 μm (C); 100 μm (B,D).

ing traces (Figs. 6L, 7D) of both the narrow and wider forms of *Scolecia*. However, both the connected and solitary coccoids occur together (Figs. 5A, 7D).

These spherical microborings are compared to *Planobola macrogota* Schmidt, 1992, which has similar, near perfectly spherical coccoids, although these are typically much larger (Wisshak *et al.* 2008, fig. 5G,H). Illustrations by Wisshak *et al.* (2008) do not show the pronounced fibrous texture inherited from the surrounding substrate seen in most of the Greenland specimens.

A related coccoidal form with widely spaced hemispheres and a more granular texture occurs along the length of the cast of a lateral ray showing the fine fibres and protruberances characteristic of many chancelloriid internal moulds (Fig. 3C, 5B,H; see Yun *et al.* 2021; Peel & Kouchinsky in press, fig. 1). The proximal part of the same ray shows a sphere in contact with the cast but connected to the outer calcium phosphate layer by a broad stalk (Fig. 5G). It resembles *Cavernula coccidia* Glaub, 1994, as illustrated by Wisshak *et al.* (2008, fig. 6A,B)

Li (1997) referred similar spherical coccoids to *Graviglomus* Green, Knoll & Swett, 1988, originally described from ooliths from the Proterozoic Eleonore Bay Formation of North-East Greenland. Green *et al.* (1988, fig. 9.9) illustrated a series of laterally juxtaposed specimens with a U-shaped longitudinal profile in thin section, while recognising that single specimens also occurred. The Henson Gletscher specimens are more perfectly spherical (Figs. 4I, 6L, 7D), as are the specimens illustrated by Li (1997).

Scolecia Radtke, 1991

***Cunicularius* Green, Knoll & Swett, 1988**

Rarely branching borings of uniform width that occur as rounded ridges on internal moulds from the early Cambrian Maidiping Formation of Sichuan, China,

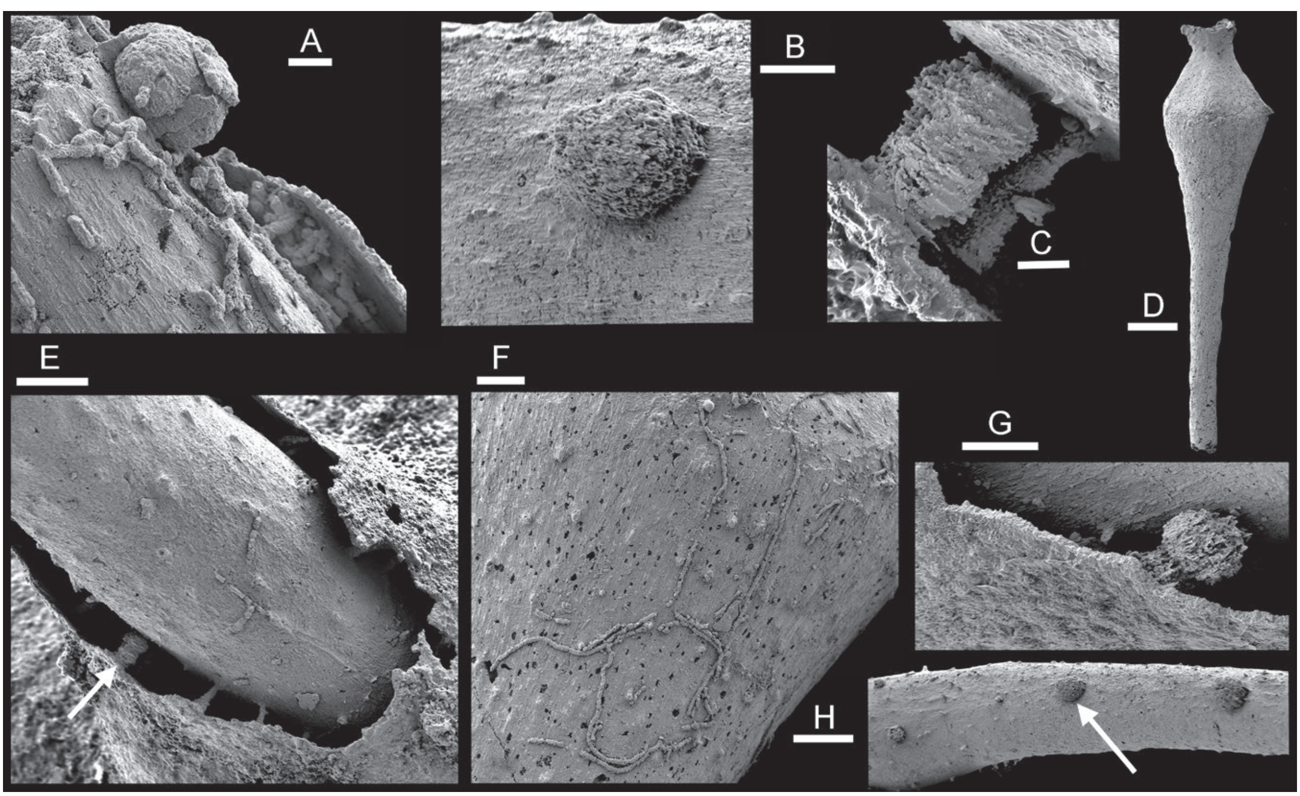

Fig. 5. Euendoliths in *Chancelloria* sclerites, GGU sample 271718. Henson Gletscher Formation, Cambrian (Miaolingian Series, Wuliuan Stage), Løndal, Peary Land. All specimens are preserved as calcium phosphate internal moulds and external encrustations after dissolution of calcium carbonate in weak acetic acid. **A,** PMU 21448, internal mould of cocoid boring and short segments of *Scolecia* on longitudinally striated lateral ray; note internal moulds perpendicular to internal mould surface indicating borings that penetrated the shell (now dissolved). **B,G,H,** PMU 21442, details from Fig. 3C with hemispherical coccoids and stalked coccoid (G). **C,E,** PMU 21441, upper surface of sclerite (Fig. 3B arrow) showing wide perpendicular boring penetrating into the shell (now dissolved) from the outer surface (lower left); note fibrous texture on internal mould reflecting shell microstructure . **D,F,** PMU 21449, internal mould of central ray oriented with base at top (D), with detail of *Scolecia* (F). Scale bars: 5 μm (A,B,C); 10 μm (G); 20 μm(E,F,H); 100 μm (D).

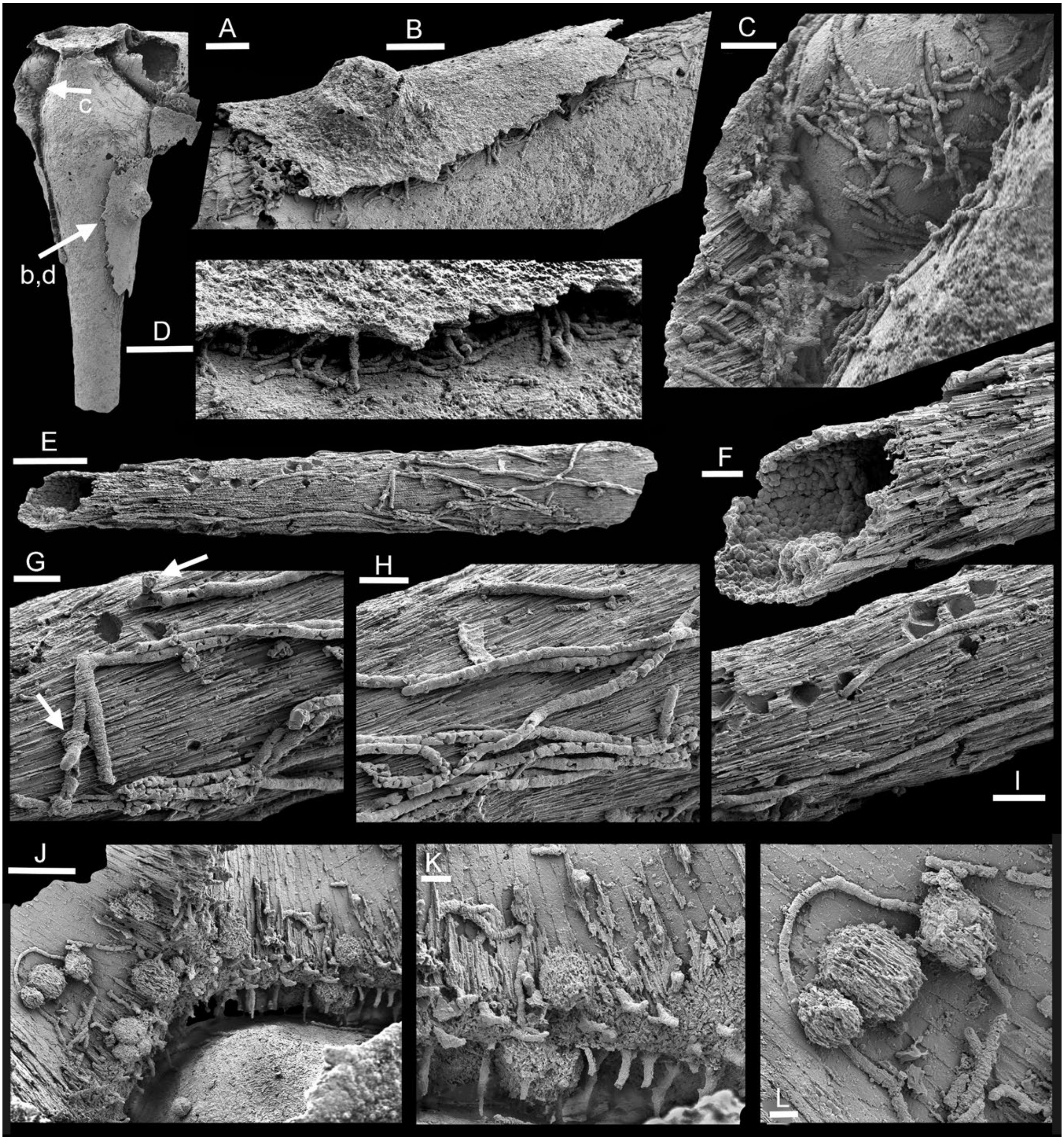

Fig. 6. Euendoliths in *Chancelloria* sclerites, GGU sample 271718. Henson Gletscher Formation, Cambrian (Miaolingian Series, Wuliuan Stage), Løndal, Peary Land. All specimens are preserved as calcium phosphate internal moulds and external encrustations after dissolution of calcium carbonate in weak acetic acid. **A–D,** PMU 21450, internal mould of central ray with patches of external encrustation (A) and with arrows b–d locating B–D; B,D, fragment of outer calcium phosphate encrustation with holdfast of unknown organism; densely packed vertical euendoliths (D) become horizontal and widely spaced along the ray (to left and right in B); C, densely packed, short sections of *Scolecia* on the internal mould and crossing acicular shell structure. **E–I,** PMU 21439, internal mould of lateral ray replicating acicular microstructure of ray interior with longitudinal burrow infillings of *Scolecia*. Note incomplete calcium phosphate deposition within burrows and perpendicular sections (arrows in G) and rare branching. Deep pits in internal mould surface reflect diagenetic crystal growth on inner side of ray prior to calcium phosphate deposition. **J–L,** PMU 21440, details of Fig. 3A, with coccoids and *Scolecia* infilled borings on encrustation of upper surface of sclerite. Note impression of parallel microstructure laths and borings penetrating the shell (now a void) but generally not passing through to the internal mould surface (J). Scale bars: 5 μm (K,L); 20 μm (C,D,F,G,H); 30 μm (I,J);50 μm (B); 100 μm (A,E).

were assigned by Li (1997) to *Cunicularius* Green, Knoll & Swett, (1988), although Moore *et al.* (2019) suggested that they should be placed in the trace fossil *Scolecia* Radtke, 1991.

Tangled masses of short casts about 2–3 μm wide occur mainly on the surface of the internal mould but near vertical borings penetrated through the shell towards the outer surface (Figs. 4G,J, 6A–D,J,K). They tend to form dense groups in local patches, often near the suture between adjacent rays (Fig. 4G), but become more openly spaced and continuous in their length as they pass distally along the rays (Fig. 4A,E,H, and the left and right margins in Fig. 6B), and in *Nisusia* (Fig. 7A,D). Branching is rare, although threads with rounded ends may terminate next to other threads (Fig. 4H). *Cunicularius halleri* Green, Knoll & Swett, 1988 of Li (1997) has filaments of similar diameter. *Cunicularius idiametrus* Li, 1997 also occurs in dense masses, but has wider threads.

Endoconchia Runnegar in Bengtson *et al.*, 1990

As with *Cunicularius*, Moore *et al.* (2019) considered it appropriate to refer *Endoconchia* to the ichnotaxon *Scolecia*.

This second group of threads, preserved on the slender, recrystallised internal mould of a chancelloriid ray (Fig. 6E–I) and in the brachiopod *Nisusia* (Fig. 7B,D) has widely spaced, straight or slightly curved cord-like threads that are about 6 μm in diameter (Fig. 6E–I, 7D) with rounded terminations. As with *Cunicularius*, dense patches of threads occur locally (Fig. 7A). Branching is rare (Fig. 1C). The threads often have a slight beaded form and the boring may not be completely filled with calcium phosphate, creating a pelletoidal effect (Fig. 6H). The surface of the threads is finely ribbed parallel to the much coarser acicular recrystallisation of the underlying internal mould (Figs. 1C, 6G). Rare conical bodies penetrate into the

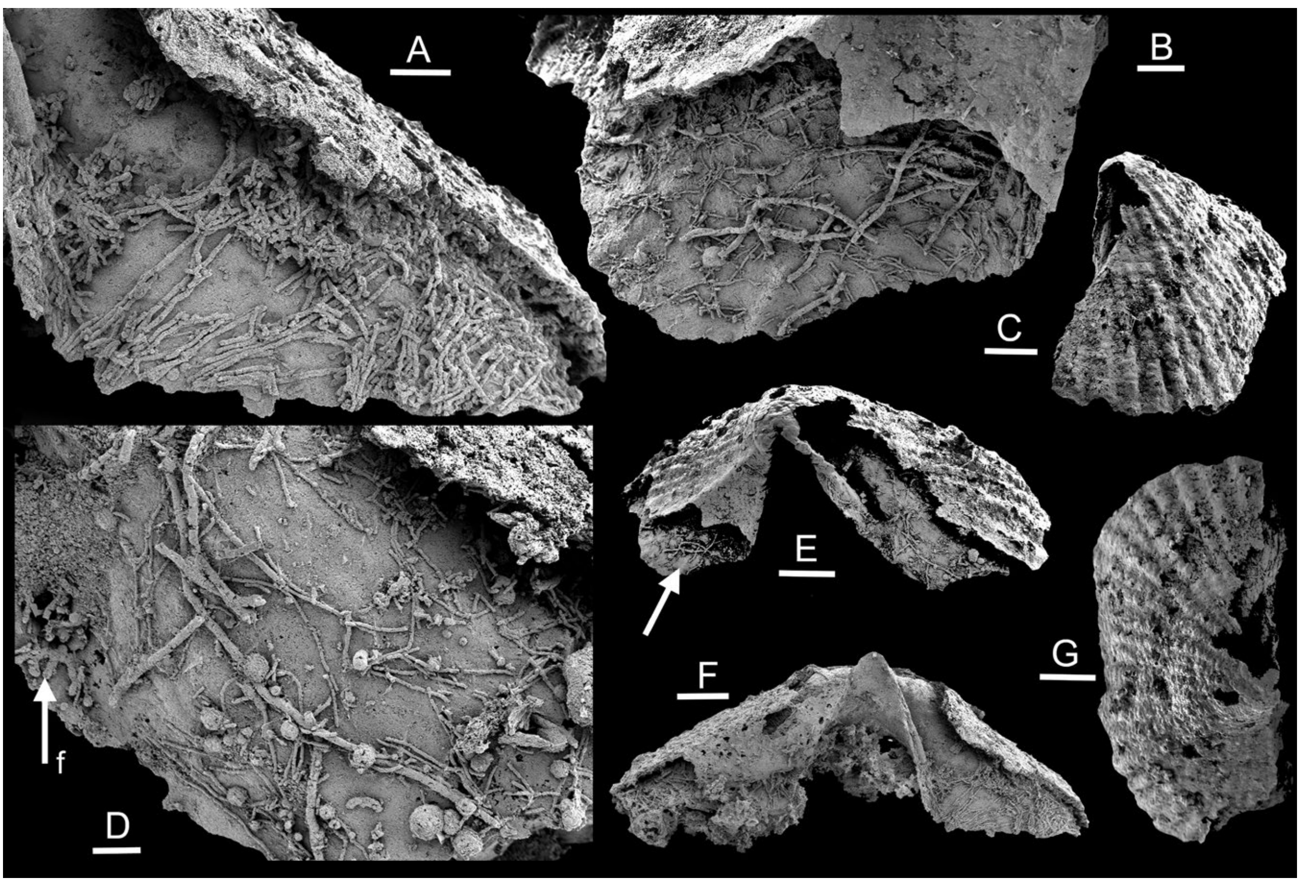

Fig. 7. Incompletely phosphatised valves of the calcareous rhynchonelliformean brachiopod *Nisusia* after decalcification in weak acetic acid, with euendolith assemblages preserved on the calcium phosphate encrustation of the valve interior. GGU sample 271718, Henson Gletscher Formation, Cambrian (Miaolingian Series, Wuliuan Stage), Løndal, Peary Land. **A,F,** PMU 21451 showing entangled mass of *Scolecia* passing vertically through the shell and becoming more linear and widely spaced. **B–E,G,** PMU 39665, showing exterior ribbing (C,G) with inner surface of calcium phosphate encrustation of inner surface (B,D) showing both the narrow and a wide forms of *Scolecia* threads, coccoids (some of which appear to be associated with the threads) and *Fascichnus* (arrow f in D). Scale bars: 30 μm (B–D); 50 μm (A); 200 μm (F); 300 μm (E).

shell (now a void above the internal mould) perpendicular to the threads (arrows in Fig. 6G). Coccoids appear to be associated with the threads in some cases (Fig. 7D) although most are not. Deep, smooth, pits on the *Chancelloria* internal mould represent diagenetic crystal growth on the shell interior prior to formation of the now phosphatised internal mould (Fig. 6I).

Runnegar in Bengtson *et al.* (1990) proposed *Endoconchia* to include two unbranching species from the lower Cambrian of South Australia that are similar to the Henson Gletscher Formation specimens, but one narrower (diameter 3 μm) and one wider (diameter 10 μm). Runnegar (1985, fig. 1E) noted spheroidal and terminal swellings in the narrow species (*Endoconchia angusta* Runnegar in Bengtson *et al.*, 1990) not seen in the Greenland material. Li (1997, pl. 3) described threads with similar swellings from China and speculated that *Endoconchia angusta* might be a synonym of *Cunicularius*. However, it is frequently branched and shows a much less tortuous thread pattern than the original definition of Green *et al.* (1988).

Fascichnus Radtke & Golubic, 2005

Radtke & Golubic (2005) referred borings made by *Hyella,* and by implication also *Eohyella*, to the ichnogenus *Fascichnus*. The calcium phosphate filled borings with radiating branches described in ooliths as *Eohyella* sp. (= *Fascichnus* isp.) by Stockfors & Peel (2005a; Fig. 1A) have not been observed in available chancelloriids from GGU sample 271718, but a single specimen is preserved on the encrustration of the interior surface of a valve of the brachiopod *Nisusia* (Fig. 7D, arrow f). The short branches have a slightly beaded form and are about 6 μm in diameter, which is less than most of the internal moulds described by Stockfors & Peel (2005a; Fig. 3B). A similar specimen was illustrated by Li (1997) from China.

Discussion

There is significant discussion in the literature concerning the occurrence of euendolith microborings and ambient inclusion trails resulting from mineral migration in Cambrian sediments (summary with full references by Yang *et al.* 2017). It is evident that both occur, and that they are often confused. Thus, descriptions of ridged open galleries in late middle Cambrian organophosphatic brachiopods from the Holm Dal Formation by Stockfors & Peel (2005b) are now known to be ambient inclusion trails and not euendolith borings, as originally described, although euendoliths do occur in the same samples. Ambient inclusion trails have not been recognised in the currently described calcareous chancelloriid sclerites and valves of the brachiopod *Nisusia*, but they are present in organophosphatic fossils from the same sample.

Moore *et al.* (2019) noted that calcium phosphate internal moulds of chancelloriid rays from the lower–middle Cambrian boundary region (Delamaran regional stage) of Nevada often preserved rounded threads (diameter 2–6 μm) that they interpreted as the casts of endolithic microborings. They also illustrated a coccoid sphere arising from such a thread (Moore *et al.* 2019, fig. 17L). As in the Greenland material, the unbranching threads are often oriented parallel to the long axes of the chancelloriid rays.

The assemblage of phosphatised euendolith borings described by Li (1997) from the early Cambrian Maidiping Formation of Sichuan, China, includes several taxa proposed by Green *et al.* (1988) from the Proterozoic Eleonore Bay Group of North-East Greenland. The Sichuan assemblage is closely similar in its composition to the middle Cambrian (Miaolingian Series, Wuliuan Stage) assemblage described here from the Henson Gletscher Formation, although the compact multi-sphered *Parenchymodiscus* Green, Knoll & Swett, 1988 described by Li (1997) has not been observed in the Henson Gletscher Formation.

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References

Babcock, L.E. 1994: Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton Formations (Middle Cambrian), North Greenland. Bulletin Grønlands Geologiske Undersøgelse 169, 79–127. http://dx.doi.org/10.34194/bullggu.v169.6727

Bengtson, S. 2005: Mineralized skeletons and early animal evolution, 101–124. In: Briggs, D.E.G (ed): Evolving form and function: fossils and development: proceedings of a symposium honoring Adolf Seilacher for his contributions to paleontology, in celebration of his 80th birthday. Peabody Museum of Natural History, New Haven. http://dx.doi.org/10.1017/s0016756806293051

Bengtson, S. & Collins, D. 2015: Chancelloriids of the Cambrian Burgess Shale: Palaeontologia Electronica 18.1.6A, 1–67. http://dx.doi.org/10.26879/498

Bengtson, S. & Hou, K. 2001: The integument of Cambrian chancelloriids. Acta Palaeontologica Polonica 46, 1–22.

Bengtson, S. & Missarzhevsky, V.V. 1981: Coeloscleritophora — a major group of enigmatic Cambrian metazoans, 19–21. In: Taylor, M.E. (ed.): Short papers from the Second International Symposium on the Cambrian System. US Geological Survey Open-File Report, 81-743, Denver. http://dx.doi.org/10.3133/ofr81743

Bengtson, S., Conway Morris, S., Cooper, B.J.,Jell, P.A. & Runnegar, B.N. 1990: Early Cambrian fossils from South Australia. Memoirs of the Association of Australasian Palaeontologists 9, 1–368.

Bengtson, S., Rasmussen, B., Ivarsson, M, Muhling, J., Broman, C., Marone, F., Stampanoni, M. & Bekker, A. 2017: Fungus-like mycelial fossils in 2.4-billion-year-old vesicular basalt. Nature Ecology & Evolution 1, 041, https://doi.org/10.1038/s41559-017-0141

Blaker, M.R. & Peel, J.S. 1997: Lower Cambrian trilobites from North Greenland. Meddelelser om Grønland, Geoscience 35, 1–145. https://doi.org/10.1017/s0016756898258432

Bornet, É. & Flahault, C. 1888: Note sur deux nouveaux genres d'algues perforantes. Journal de Botanique 2, 161–165.

Campbell, S.E. 1982: Precambrian endoliths discovered. Nature 299, 429–431. http://dx.doi.org/10.1038/299429a0

Clausen, S. & Peel, J.S. 2012: Middle Cambrian echinoderm remains from the Henson Gletcher Formation of North Greenland. GFF 134, 173–200. https://doi.org/10.1080/11035897.2012.721003

Geyer, G. & Peel, J.S. 2011: The Henson Gletscher Formation, North Greenland, and its bearing on the global Cambrian Series 2–Series 3 boundary. Bulletin of Geosciences 86, 465–534. https://doi.org/10.3140/bull.geosci.1252

Golubic, S., Friedmann, I. & Schneider, J., 1981, The lithobiontic ecological niche, with special reference to microorganisms: Journal of Sedimentary Petrology 51, 475–478. http://dx.doi.org/10.1306/212f7cb6-2b24-11d7-8648000102c1865d

Golubic, S., Perkins, R.D. & Lukas, K.J. 1975: Boring microorganisms and microborings in carbonate substrates, 229–259. In: Frey, R.W. (ed.), The study of trace fossils. Springer-Verlag. Berlin–Heidelberg–New York. http://dx.doi.org/10.1007/978-3-642-65923-2_12

Green, J.W., Knoll, A.H. & Swett, K. 1988: Microfossils from oolites and pisolites of the Upper Proterozoic Eleonore Bay Group, Central East Greenland. Journal of Paleontology 62, 835–852. http://dx.doi.org/10.1017/s0022336000030109

Higgins, A.K., Ineson, J.R., Peel, J.S., Surlyk, F. & Sønderholm, M. 1991: Lower Palaeozoic Franklinian Basin of North Greenland. Bulletin Grønlands Geologiske Undersøgelse 160, 71–139. https://doi.org/10.34194/bullggu.v160.6714

Ineson, J.R. & Peel, J.S. 1997: Cambrian shelf stratigraphy of North Greenland. Geology of Greenland Survey Bulletin 173, 1–120. https://doi.org/10.34194/ggub.v173.5024

Kouchinsky, A., Alexander, R., Bengtson, S., Bowyer, F., Clausen, S., Holmer, L.E., Kolesnikov, K.A., Korovnikov, I.V., Pavlov, V., Skovsted, C.B., Ushatinskaya, G., Wood, R. & Zhuravlev, A.Y. 2022: Early–middle Cambrian stratigraphy and faunas from northern Siberia. Acta Palaeontologica Polonica 67, 341–464. http://dx.doi.org/10.4202/app.00930.2021

Larsen, N.H. 1989: Algae from the Lower Palaeozoic Strata of North Greenland. Geological Survey of Greenland Open File Series 89/3, 23 pp.

Li, G. 1997: Early Cambrian phosphate-replicated endolithic algae from Emei, Sichuan. south-west China. Bulletin of National Museum of Natural History 10, 193–216.

MacIntyre, I.G., Reid, R.P. 1978: Micritization. In: Middleton, G.V., Church, M.J., Coniglio, M., Hardie, L.A., & Longstaffe, F.J. (eds): Encyclopedia of Sediments and Sedimentary Rocks. Encyclopedia of Earth Sciences Series. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-3609-5_136

Moore, J.L., G. Li & Porter, S.M. 2014: Chancelloriid sclerites from the Lower Cambrian (Meishucunian) of eastern Yunnan, China, and the early history of the group. *Palaeontology* 57, 833–878. https://doi.org/10.1111/pala.12090

Moore, J.L., Porter, S.M. Webster, M. & Maloof, A.C. 2019: Chancelloriid sclerites from the Dyeran–Delamaran ('lower–middle' Cambrian) boundary interval of the Pioche–Caliente region, Nevada, USA. Papers in Palaeontology 7, 565–623. https://doi.org/:10.1002/spp2.1274

Peel, J.S. 2021a: Ontogeny, morphology and pedicle attachment of stenothecoids from the middle Cambrian of North Greenland (Laurentia). Bulletin of Geosciences 96, 381–399. https://doi.org/10.3140/bull.geosci.1839

Peel, J.S. 2021b**:** In-place operculum demonstrates that the middle Cambrian *Protowenella* is a hyolith and not a mollusc. Alcheringa 45, 385–394. http://dx.doi.org/10.1080/03115518.2021.2004225

Peel, J.S. 2022a: A priapulid larva from the middle Cambrian (Wuliuan Stage) of North Greenland (Laurentia). Bulletin of Geosciences 97, 445–452. https://doi.org//10.3140/bull.geosci.1865

Peel, J.S. 2022b: The oldest tongue worm: a stem-group pentastomid arthropod from the middle Cambrian (Wuliuan Stage) of North Greenland (Laurentia). GFF 144, 97–105. https://doi.org//10.1080/11035897.2022.2064543

Peel, J.S. 2023: A phosphatised fossil Lagerstätte from the middle Cambrian (Wuliuan Stage) of North Greenland (Laurentia). Bulletin of the Geological Society of Denmark 72, 101–122. https://doi.org/10.37570/bgsd-2022-72-03

Peel, J.S. in press: Sclerite ray canals in the Cambrian coeloscleritophoran *Chancelloria* from North Greenland (Laurentia). PalZ.

Peel, J.S. & Kouchinsky, A. 2022: Middle Cambrian (Miaolingian Series, Wuliuan Stage) molluscs and mollusc-like microfossils from North Greenland (Laurentia). Bulletin of

the Geological Society of Denmark 70, 69–104. https://doi.org/10.37570/bgsd-2022-70-06
Peel, J.S. & Kouchinsky, A. in press: Unusual diagenesis of Cambrian chancelloriids from Greenland and Siberia. Alcheringa
Peel, J.S., Streng, M., Geyer, G., Kouchinsky, A. & Skovsted, C.B. 2016: *Ovatoryctocara granulata* assemblage (Cambrian Series 2–Series 3 boundary) of Løndal, North Greenland. Australasian Palaeontological Memoirs 49, 241–282.
Radtke, G. 1991: Die mikroendolithischen Spurenfossilien im Alt-Tertiär West-Europas und ihre palökologische Bedeutung. Courier Forschungsinstítut Senckenberg 138, 1–185.
Radtke, G., & Golubic, S. 2005: Microborings in mollusk shells, Bay of Safaga, Egypt: Morphometry and ichnology. Facies 51,125–141. http://dx.doi.org/10.1007/s10347-005-0016-02
Randell, R.D., Lieberman, B.S., Hasiotis, T. & Pope, M.C. 2005: New chancelloriids from the Early Cambrian Sekwi Formation with a comment on chancelloriid affinities. Journal of Paleontology 79, 987–996. http://dx.doi.org/10.1666/0022-3360(2005)079[0987:ncftec]2.0.co;2
Runnegar, B. 1985: Early Cambrian endolithic algae. Alcheringa 9, 179–182. http://dx.doi.org/10.1080/03115518508618966
Schmidt, H. 1992: Mikrobohrspuren ausgewählter Faziesbereiche der tethyalen und germanischen Trias (Beschreibung, Vergleich und bathymetrische Interpretation). Frankfurter Geowissenschaften Arbeiten A 12, 1–228.
Stockfors, M. & Peel, J.S. 2005a: Endolithic Cyanobacteria from the Middle Cambrian of North Greenland. GFF 127, 179–185. http://dx.doi.org/10.1080/11035890501273179
Stockfors, M. & Peel, J.S. 2005b: Euendoliths and cryptoendoliths within late Middle Cambrian brachiopod shells from North Greenland. GFF 127, 187–194. http://dx.doi.org/10.1080/11035890501273187
Walcott, C.D. 1905: Cambrian Brachiopoda with descriptions of new genera and species. Proceedings of the United States National Museum 28, 227–337. http://dx.doi.org/10.5479/si.00963801.1395.227
Walcott, C.D. 1920: Cambrian geology and paleontology IV. 6. Middle Cambrian Spongiae. Smithsonian Miscellaneous Collections 67, 261–364.
Wisshak M. 2012. Microbioerosion, 213–243, In: Knaust D. & Bromley R.G. (eds) Trace Fossils as Indicators of Sedimentary Environments. Elsevier, Amsterdam. https://doi.org/10.1016/B978-0-444-53813-0.00008-3
Wisshak, M., Seuss, B. & Nützel, A. 2008: Evolutionary implications of an exceptionally preserved Carboniferous microboring assemblage in the Buckhorn Asphalt lagerstätte (Oklahoma, USA), 21–54, In: Wisshak, M., Tapanila, L. (eds) Current Developments in Bioerosion. Springer Berlin–Heibedlberg–New York. https://doi.org/10.1007/978-3-540-77598-0_2
Yang, X.-G., Han, J., Wang, X., Schiffbauer, J. D., Uesugi , K., Sasaki , O. &% Komiya, T. 2017: Euendoliths versus ambient inclusion trails from early Cambrian Kuanchuanpu Formation, South China. Palaeogeography, Palaeoclimatology, Palaeoecology 476, 147–157. http://dx.doi.org/10.1016/j.palaeo.2017.03.028
Yun, H., Zhang, X., Brock, G.A., Li, L. & Li, G. 2021: Biomineralization of the Cambrian chancelloriids. Geology 49, 623–628. https://doi.org/10.1130/G48428.1
Zhang, Y. & Golubic, S., 1987: Endolithic microfossils (Cyanophyta) from early Proterozoic stromatolites, Hebei, China. Acta Micropalaeontologica Sinica 4, 1–12.