

# Geopetal microbial threads (cryptoendoliths) within middle Cambrian brachiopods from North Greenland (Laurentia)

JOHN S. PEEL



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Cavities (crypts) formed postmortally within conjoined valves of acrotreoid brachiopods from the Fimbuldal Formation (Cambrian, Miaolingian Series) of North Greenland contain phosphate encrustations of microbial threads, probably fungi. The planar relationship between these cryptoendolithic masses and the sediment that partially fills the brachiopod interiors defines palaeohorizontal surfaces within geopetal structures. These surfaces parallel the commissural plane, indicating that the dead shells lay in a hydronamically stable position on or within the bottom sediment at the time the geopetals were formed.

**Keywords:** Cryptoendoliths, geopetals, Cambrian, Miaolingian Series, North Greenland, Laurentia.

John S. Peel, [[john.peel@pal.uu.se](mailto:john.peel@pal.uu.se)], Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, SE-75236 Uppsala, Sweden.

Residues of phosphatised small shelly fossils resulting from acid digestion of limestones from the Cambrian of North Greenland often display interaction between the host organisms (basibionts) and micro-organisms that lived on (epibionts) or within (endoliths) the skeletonised elements. Firm surfaces of the basibionts provided attachment sites akin to hardgrounds and other fast lithic surfaces for the holdfasts of numerous groups of epibionts, such as the minute holdfasts attaching threads of *Girvanella* Nicholson & Etheridge, 1878 to the epiphytacean *Orpikania* Peel, 2018 described by Peel (2018) from the middle Cambrian Ekspedition Bræ Formation (Fig. 1A, D), or vesicular epibionts attached to tomotiid sclerites from the Henson Gletscher Formation (Fig. 1B; Peel 2025a). Ring-shaped scars on the outer surface of organo-phosphatic valves of the brachiopod *Botsfordia* Matthew, 1891 from lower Cambrian strata of the basal Brønlund Fjord Group (Peel 2014) were likely produced by the attachment of the tubular cnidarian(?) *Hyolithellus* Billings, 1871.

Shells may be penetrated by euendoliths that are usually preserved as diagenetically infilled galleries on the surface of internal moulds (Fig. 1C, F, G; Peel 2024). In Greenland, borings of this kind have also been described from calcareous oolites from the Proterozoic and Cambrian (Green *et al.* 1988; Stockfors & Peel 2005a). Threads likely of fungal origin that were encrusted by calcium phosphate within cavities (cryptoendoliths) are known from several formations within the Ediacaran–Cambrian succession of North Greenland (Peel & Willman 2022), notably within the postmortal crypts of articulated shells of middle Cambrian linguliformean brachiopods (Fig. 1E; Stockfors & Peel 2005b; Peel & Willman 2022). However, similar postmortal crypts subsequently occupied by cryptoendolithic fungal threads may have been produced by diagenetic phosphatisation of soft-bodied organisms (Peel & Willman 2022; Willman & Peel 2024) or be a feature of the entombing lithology, such as sedimentary shelter structures.

The term ‘cryptoendolith’ was introduced by Golubic *et al.* (1981) as the collective name for organisms

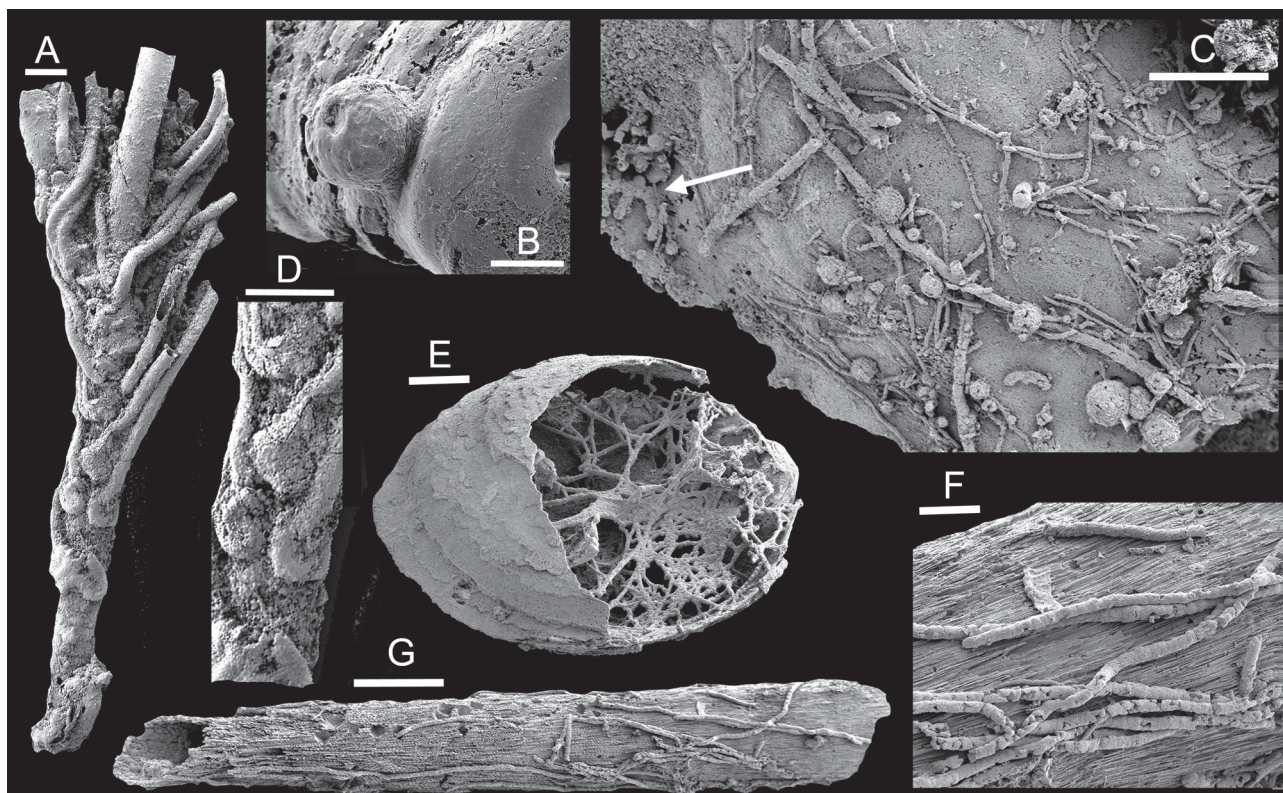
that occupied the cavities (crypts) within hard substrata in a nomenclature that also introduced 'euendolith' for borers into hard surfaces. Peel & Willman (2022, p. 247–249) reviewed the usage of these terms and additional terminologies employed by other authors. Epibionts, euendoliths and cryptoendoliths may be associated with living or dead hosts.

This paper develops the description first reported by Peel & Willman (2022) of a novel assemblage of cryptoendolithic threads, likely fungi, from the middle Cambrian Fimbuldal Formation (Miaolingian Series, Drumian Stage) of North Greenland (Fig. 2) that have been encrusted with diagenetic calcium phosphate. The phosphatised threads form planar surfaces and sheets within the articulated shells of acrotretoid

linguliformean brachiopods, delimiting geopetal (palaehorizontal) structures indicative of the orientation of the brachiopod shells at the time of their diagenetic phosphatisation.

## Materials and methods

All described specimens were recovered from limestone samples derived from the middle Cambrian (Miaolingian Series) Fimbuldal Formation within a belt of Lower Palaeozoic strata that crops out across North Greenland as part of the southern shelf succession of the transarctic Franklinian Basin (Higgins *et al.* 1991). The Cambrian stratigraphy of the Freuchen



**Fig. 1.** Cambrian epibionts and endoliths from North Greenland. **A, D:** *Girvanella lianiformis* Peel, 2018, PMU 31762 from GGU sample 315119, holotype, Ekspedition Bræ Formation (Cambrian, Miaolingian Series) attached with holdfasts to *Orpikania freucheni* Peel, 2018. Note that *Girvanella lianiformis* was inadvertently referred to as *Girvanella freucheni* n. sp. by Peel (2018, caption to fig. 2). **B:** Spherical epibiont attached to sclerite of tomotiid, PMU 18354 from GGU sample 482337, Henson Gletscher Formation (Cambrian, Miaolingian Series). **C:** Calcium phosphate encrustation of inner surface of the brachiopod *Nisusia* Walcott, 1905 with infilled endolithic borings of narrow and wide threads of *Scolecia* Radtke, 1991, coccoids (some of which appear to be associated with the threads) and *Fascichnus* Radtke & Golubic, 2005 (arrow); PMU 39665 from GGU sample 271718, Henson Gletscher Formation, (Cambrian, Miaolingian Series). **E:** Acrotretoid linguliformean brachiopod with threads of cryptoendoliths encrusted with calcium phosphate; PMU 38174 from GGU sample 315006, Fimbuldal Formation (Cambrian, Miaolingian Series). **F, G:** Phosphatised internal mould of chancelloriid lateral ray replicating acicular microstructure of ray interior with longitudinal endolithic burrow infillings of *Scolecia*; PMU 21439 from GGU sample 271718, Henson Gletscher Formation (Cambrian, Miaolingian Series). Scale bars: 20  $\mu\text{m}$  (F); 30  $\mu\text{m}$  (B,D); 50  $\mu\text{m}$  (C); 100  $\mu\text{m}$  (A,E,G).

Land to Peary Land region (Fig. 2B) was described by Ineson et al. (1994) and Ineson & Peel (1997). The Fimbuldal Formation consists of an alternation of recessive, dark weathering, dolostone and dominant cliff-forming units of pale dolostone that attains a thickness of about 180 m at the type locality in Gustav Holm Dal, western Peary Land. (Fig. 2; Ineson & Peel 1997). Dark weathering limey dolostones near the middle of the formation yield abundant fossils, including agnostoids indicative of the *Ptychagnostus punctuosus* Biozone (Miaolingian Series, Drumian Stage; Robison 1984, Ineson & Peel 1997).

Peel (2021) described the rostroconch mollusc *Pseudomyona groenlandica* Peel, 2021 from GGU sample 315006 of the Fimbuldal Formation. GGU samples 218645 and 315006 have yielded grasping spines of the chaetognath *Fimbulispina laurentica* Peel, 2025b associated with a variety of small shelly fossils, including the protoconodonts *Gapparodus* Abaimova, 1978, *Phakelodus* Miller, 1984 and *Paibiconus?* Dong, 1983 (Peel 2025b).

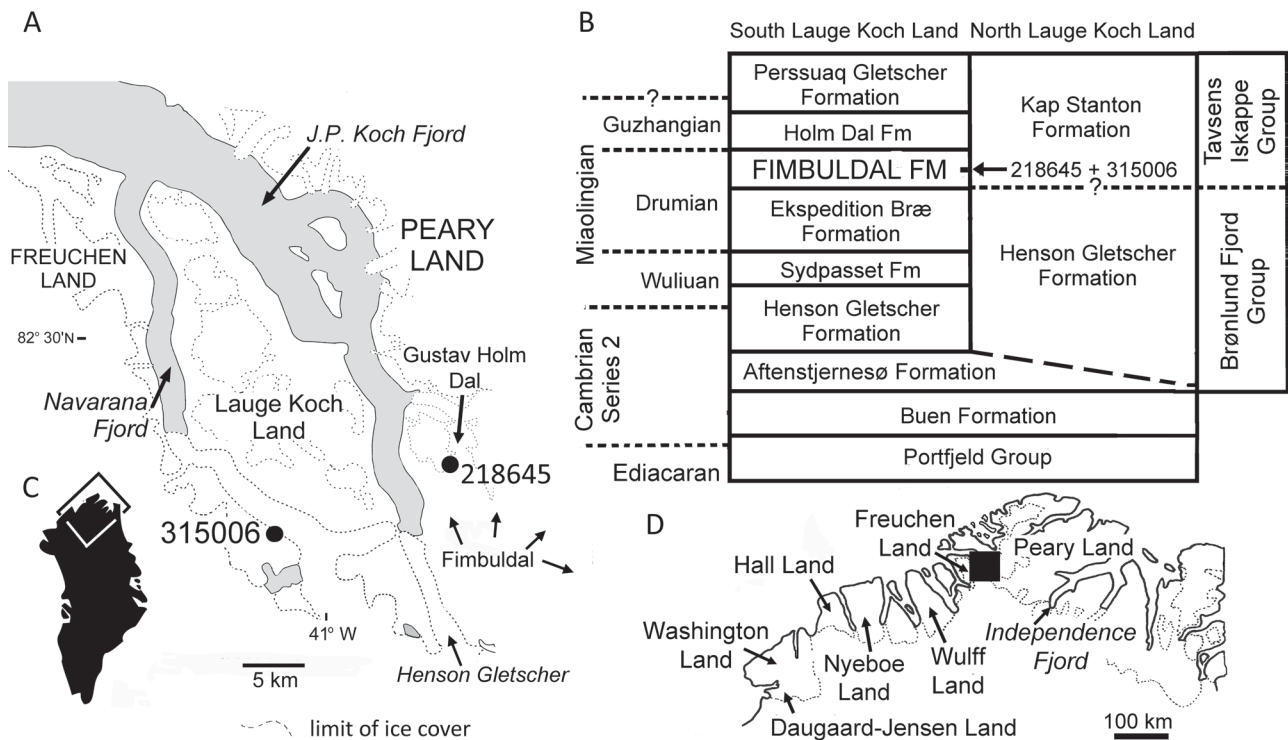
GGU sample 218645 was collected by J.R. Ineson on 7th July 1979 from the western side of Gustav Holm Dal, western Peary Land (Fig. 2A; 82°20.3'N, 39°45'W) from just above the middle of a unit of dark, bitumi-

nous limestones forming the recessive middle unit of the Fimbuldal Formation in its type section (Ineson & Peel, 1997, figs 44, 45); Cambrian, Miaolingian Series, Drumian Stage. I collected GGU sample 315006 on 27th June 1984 from dark, recessive limestone forming the middle part of the Fimbuldal Formation on the south-west side of the glacier feeding into Navarana Fjord, Freuchen Land (Fig. 2A; 82°16.7'N, 41°20'W).

The phosphatised specimens were picked from sieved residues after digestion of limestone samples in 10% acetic acid. Images were prepared using a Zeiss Supra 35VP scanning electron microscope (SEM; Zeiss, Oberkochen, Germany) operating at 5 kV and then assembled in Adobe Photoshop 7 (Adobe Systems, San Jose, California, U.S.A.).

## Encrusted microbial threads

Linguliformean brachiopods are the most conspicuous fossils in the examined residues of GGU samples 218645 and 315006 from the Fimbuldal Formation. With the exception of the acrotretoids, most of the brachiopods are preserved as isolated valves without traces of commensal organisms. They attain a maxi-



**Fig. 2.** A: Collection localities, located by black rectangle in D. B: Stratigraphic nomenclature and derivation of samples. C, D: Toponymic map of North Greenland (D), located by rectangle in C.

mum observed size of about 1.5 mm, although this size may have been influenced by taphonomic processes and the preparation technique. Acrotretoids are generally preserved as conjoined valves that also lack traces of commensals when complete. However, in specimens apparently broken during preparation, the inner void left after the dissolution of the calcareous matrix during preparation often reveals complex masses of anastomosing threads preserved in spherulitic calcium phosphate that conveys a beaded, botryoidal appearance (Figs 1E, 3, 4). The tangled threads are usually arranged in an irregular sub-radial pattern within the shell interior, with oblique to orthogonal junctions with its inner surface (Fig. 1E). However, the specimens described herein differ in the organisation of the threads into a well defined layer that is approximately parallel to the commissural plane separating the ventral and dorsal valves (Figs. 3, 4).

Specimen 1 shows this preserved layer through a hole in the dorsal valve (Fig. 4G). In specimen 2 (Fig. 3A, B, D), most of the ventral valve has been broken away to reveal a sheet of closely packed threads extending across the entire inner surface at the commissural plane; the pedicle opening is indicated by arrows in Figure 3D. In both of these specimens the upper surface of the sheet is generally flat without upwards projecting phosphatised threads and spaces between the closely packed threads are mainly closed by phosphate deposition. The dorsal valve has been almost entirely broken away in the partly crushed specimen 3 (Fig. 3E) in which the threads are mainly disposed in an irregular planar structure.

Specimen 4 displays the interior of a ventral valve with an open planar network of threads extending from the broken pedicle opening (Fig. 3C, arrowed). This specimen may have separated from the dorsal(?) valve during deposition or, less likely, during preparation.

Specimen 5 (Fig. 4A–F, in which the ventral valve with pedicle is located uppermost in the illustration) preserves the posterior portion of an articulated shell that has been broken transversely, perpendicular to the commissure. It displays two planar masses of threads, the more extensive of which is located at the commissure, with a few threads extending downwards (as illustrated) to join the inner surface of the dorsal valve. A smaller second sheet of threads lies parallel to the first sheet but is restricted to the central area of the ventral valve.

Encrusted threads are mainly of relatively uniform thickness within each specimen, although some thinner threads occur at the margins of the planar masses in specimens 4 and 5 (Figs 3C, 4C). The uniformity may suggest some limiting factor on the degree of encrustation (diameter of the threads) but it can not be

demonstrated that encrustation occurred simultaneously in the described specimens.

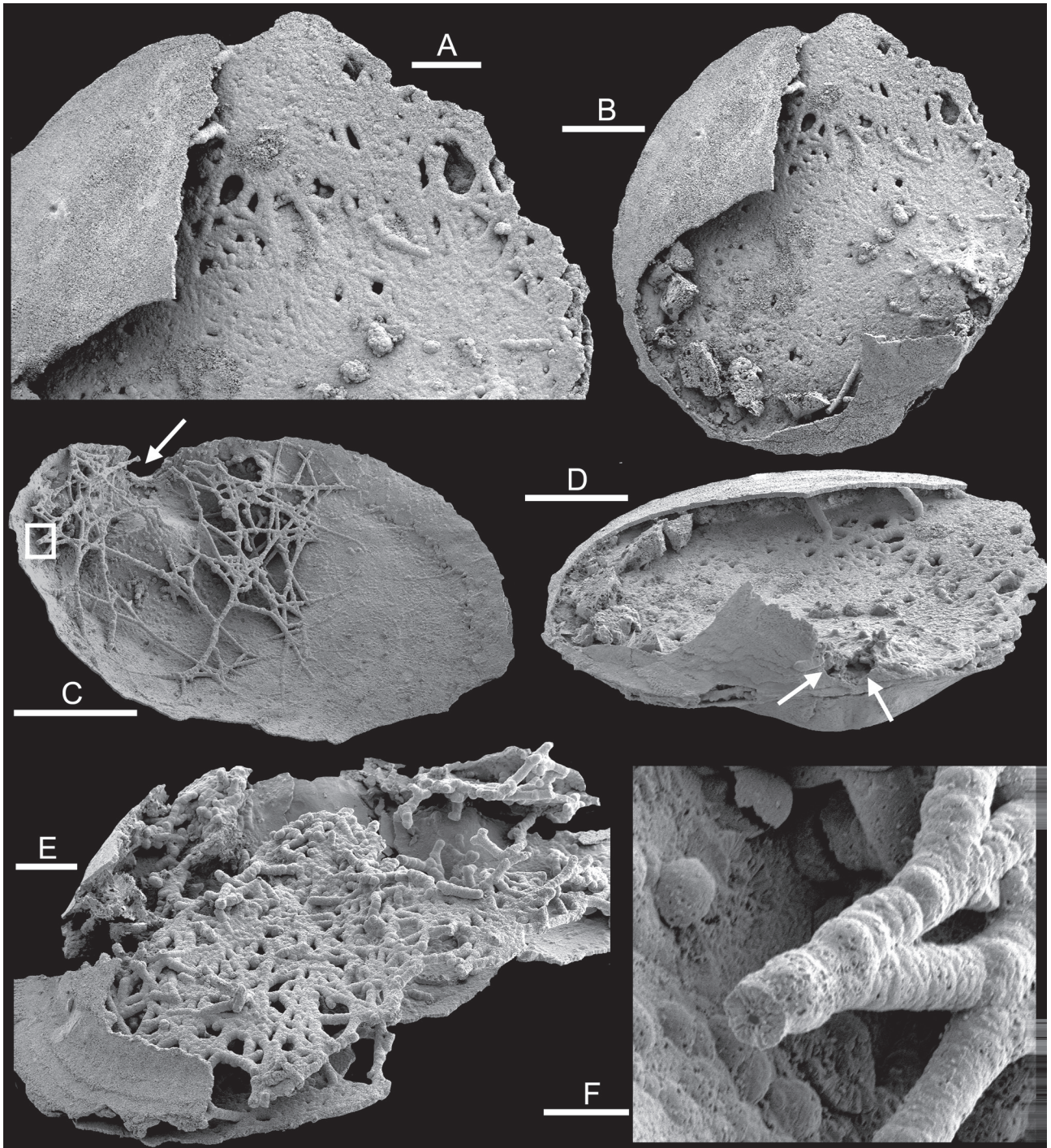
A cross-section of a broken phosphatised thread (Fig. 3F) has a diameter of about 8  $\mu\text{m}$  with encrusting crystals of calcium phosphate radiating from an axial cavity of about 1  $\mu\text{m}$  in diameter that represents the original fungal thread. Similar axial cavities are often visible in broken threads, for example in Figure 4D (insert) where the radial crystal coating is partially entombed within a diagenetically formed layer of orthogonal calcium phosphate crystals on the inner surface of the valve. As preserved, terminations of most threads are rounded and the axial cavities are not visible (Figs 3E, 4C). It is not possible to determine if these rounded terminations represent natural or broken ends of the original fungal threads, or both, due to the subsequent diagenetic phosphatisation.

While the network of the mineralised threads in specimen 4 (Fig. 3C) suggests frequent branching of the original fungal threads, numerous cross-over relationships are evident in denser thread masses (Figs 3E, 4C). Given the great thickness of the spherulitic encrustation relative to the axial cavities representing the original fungal threads (Figs 3F, 4D with inset), it is likely that individual phosphatised threads may contain several original fungal threads.

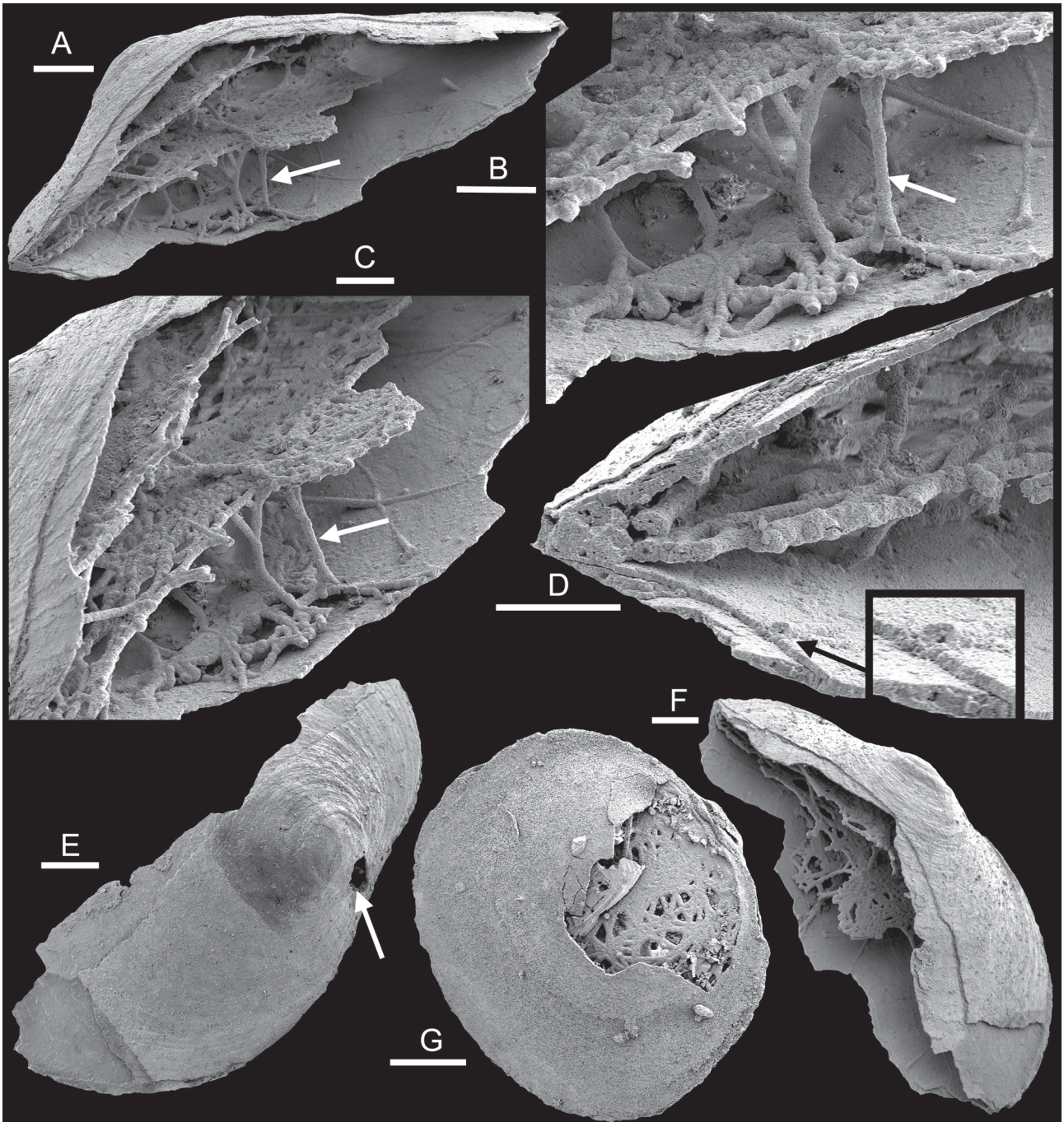
Mineralised threads joining the main planar sheet to the dorsal valve in specimen 5 display a single phosphatised thread medially, but diverge into bundles of diverging phosphatised threads at both ends (Fig. 4B). Rather than representing branching fungal threads, it appears that the original individual fungal threads twisted together for mutual support as they traversed the crypt between the main sheet and the dorsum, later becoming encrusted into a single phosphatised thread. Twisting together of much thicker threads (diameter 60–80  $\mu\text{m}$ ) for mutual support was described in *Girovella pituutaq* Peel, 2018 from the Ekspedition Bræ Formation in southern Freuchen Land by Peel (2018, fig. 2A).

## Geopetal structures

Geopetal cavities provide one of the most well known and useful ‘way-up’ criteria in sedimentary rocks. Gravitational settling of fine mud filling the lower part of cavities in rocks or fossils may establish an upper surface that defines a horizontal surface (‘palaeohorizontal’) at the time of formation. Most commonly in fossils, geopetals consist of a lower mass of sediment overlain by crystalline spar that filled the original upper part (the crypt) of the cavity (Playford & Cockbain 1972). Crypts within thrombolitic dolostones illustrated by Ineson & Peel (1997, fig. 12C) from the



**Fig. 3.** Phosphatised threads of cryptoendoliths within acrotretoid brachiopods from GGU Sample 315006, Fimbuldal Formation (Cambrian, Miaolingian Series) of North Greenland. **A, B, D:** Specimen 2, PMU 33488, view of planar mat of phosphatised cryptoendoliths through broken ventral valve, with pedicle opening arrowed in D. **C, F:** Specimen 4, PMU 38176, internal view of ventral valve (C) with pedicle opening (arrow) and detail of spherulitic phosphatisation around axial cavity in broken thread (F, located by square in C). **E:** Specimen 3, PMU 33489, mat of phosphatised threads, with dorsal(?) valve almost entirely broken away. Scale bars: 10  $\mu\text{m}$  (F); 100  $\mu\text{m}$  (A,E); 200  $\mu\text{m}$  (B–D).



**Fig. 4.** Phosphatised threads of cryptoendoliths within acrotreoid brachiopods, Fimbuldal Formation (Cambrian, Miaolingian Series) of North Greenland. **A–F:** Specimen 5, PMU 38177 from GGU sample 218645, transversely broken specimen with anterior broken away; ventral valve uppermost with pedicle opening near posterior margin visible in E (arrow). Conjoined valves show two planar mats of phosphatised cryptoendoliths, with phosphatised threads extending orthogonally from the more extensive mat, which lies in the commissural plane, towards the inner surface of the dorsal valve (arrows in A–C). Inset (D) shows broken thread with spherulitic phosphatisation around axial cavity partly submerged within layer of diagenetic phosphatisation on the interior of the dorsal valve. **G:** Specimen 1, PMU 38175 from GGU sample 315006, planar mat of phosphatised cryptoendoliths visible through hole in the dorsal valve. Scale bars: 50 µm (B–D); 100 µm (A,E,F); 200 µm (G).

Aftenstjernesø Formation are lined with arborescent microbial structures surrounded by fibrous calcareous cement. In the present material from the Fimbuldal Formation, the crystalline calcareous infilling of the crypt in conjoined acrotretoid shells has been removed during the digestion of the fossil samples in weak acids to reveal diagenetic phosphatic encrustations of original fungal threads.

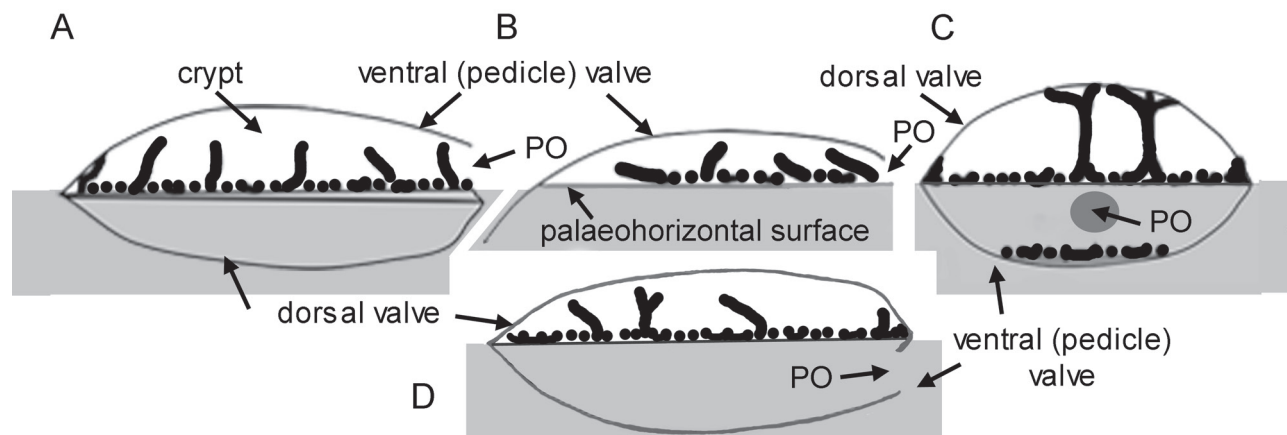
*Description.* The flat surface of the mass of phosphatised threads in specimens 1 and 2 indicates the limiting effect of an original sedimentary infill now preserved as a void following dissolution by acid during preparation. The interior of the conjoined specimens thus represents a geopetal structure in which the original fungal threads grew into a crypt overlying partial sedimentary fill that formed a substrate, the latter fill now preserved as a preservational void. In both specimens as illustrated (Fig. 3A, B, D, 4G), the void representing sediment lies uppermost, indicating that the specimens are inverted.

In specimen 3, the upper surface of the thread mass as illustrated is more irregular than in specimens 1 and 2, with phosphatised threads rising up from the commissural plane (Fig. 3E). While a geopetal structure is seemingly present, determination of ‘way-up-ness’ is uncertain.

Specimen 4 differs from other illustrated specimens in being a disarticulated valve with an open meshwork of threads mainly radiating across the internal

surface from the pedicle opening (arrow in Fig. 3C) in the posterior part of the shell. The planar upper surface of the meshwork as viewed suggests contact with an overlying original substrate (now dissolved) that dominated the antero-lateral areas of the shell, indicating an inverted geopetal in the specimen as illustrated (Fig. 3C). The isolated ventral valve may have become separated from the dorsal valve during sample preparation, but it seems more likely that the geopetal formed as a shelter structure beneath a single valve (Fig. 5B). Similar shelter structures formed by isolated convex brachiopod shell were described by Peel (2017, fig. 4A) from the Holm Dal Formation in Gustav Holm Dal (Fig. 2).

Specimen 5 retains two planar meshworks in the ventral valve of which the smaller is restricted to median area of the valve (uppermost in Fig. 4A); the larger meshwork occurs in the commissural plane. The smooth upper (as illustrated) surface of both meshworks suggests contact with infilling sediment while phosphatised threads extending orthogonally from the lower surface (as illustrated) of the larger meshwork towards the dorsal valve confirm the presence of a crypt. Thus, the specimen as illustrated preserves an inverted geopetal. Specimen 5 differs from other described specimens in displaying evidence of two episodes of geopetal formation (Fig. 5C). However, no inferences are made concerning the time of formation of the geopetal structures in the described specimens relative to each other.



**Fig. 5.** Schematic sketches of geopetal structures in acrotretoid brachiopods from the Fimbuldal Formation (Cambrian, Miaolingian Series) of North Greenland. Encrusted fungal threads (black) are located in crypts above sediment infill (grey), the junction between the two defining a palaeohorizontal surface; PO, pedicle opening. **A, D:** Specimens with conjoined valves in lateral view, with crypt located in ventral valve (A) and dorsal valve (D). **B:** Isolated ventral valve in lateral view, with crypt developed as shelter structure. **C:** Schematic sketch of specimen 5 with conjoined valves in transverse section showing two episodes of mat development. The later, more extensive mat formed in a crypt within the dorsal valve, with threads extending orthogonally to the valve interior.

*Time of formation.* The position in life of the described brachiopod specimens is not known since brachiopods with pedicles show no consistently preferred shell orientation. They may be attached to a variety of substrates, lithological or organic, and many taxa occurred in tiered communities (Zhang *et al.* 2007, 2010; Wang *et al.* 2012; Topper *et al.* 2017). It cannot be assumed that the so-called ventral valve was located in a ventral position or at a similar inclination in different taxa during life, or even in life assemblages of individuals of the same species. Brachiopod shells often remain conjoined after transport and redeposition, rendering them prone to postmortal fungal infestation of crypts and the formation of geopetal structures in sedimentary settings far removed from those they occupied during life. Dead shells may show orientations consistent with their hydronamic properties.

The crypt in specimen 4 formed in a shelter structure beneath the disarticulated ventral valve lying in its stable 'convex side up' orientation following transport and deposition (Figs 3C, 5B). Geopetals in the other specimens show a planar contact (palaeohorizontal surface) between the crypt with phosphatised fungal threads and the underlying sedimentary fill that acted as a substrate and which is parallel with the commissure between the conjoined valves. As illustrated, specimens 1, 2 and 5 are inverted, with the crypt occupying the ventral valve (specimen 1, Fig. 4G) or the dorsal valve (specimens 2 and 5; Figs 3A, B, D, 4A–F). However, it is obvious that this inversion only reflects their arbitrary mounting as isolated specimens on the SEM stubs.

It is clear that all specimens were originally oriented in the sediment with the crypt uppermost, within either the dorsal or the ventral valve (Fig. 5), although it is possible that shells were later inverted during redeposition that followed full mineralogical filling of the geopetal. Irrespective of either the ventral or dorsal valve being uppermost, the coincidence of the palaeohorizontal median plane of the geopetals with the commissure indicates that the described specimens lay in a stable position within the sediment or on the sea floor.

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