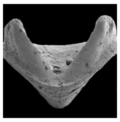
Shell tubules in *Cassitella* (Hyolitha) from the Cambrian (Series 2) of Greenland (Laurentia)

John S. Peel



Opercula of *Cassitella baculata* Malinky & Skovsted, 2004, originally described from the Bastion Formation (Cambrian Series 2) of North-East Greenland, are characterised by prominent protruding cardinalia on the inner surface of the thick shell that promote assignment to Hyolitha. Acid etching of phosphatised shells from the Bastion Formation and the equivalent Aftenstjernesø Formation of North Greenland has revealed that the seemingly massive shell is penetrated by abundant closely spaced tubules about 5 µm in diameter that may be preserved as pores on the interior surface, but not on the cardinalia. Diagenetic infilling of the tubules produced a characteristic columnar internal structure, with a suite of tubercles on the internal moulds that is also seen in helcionelloid molluscs and other contemporary small shelly fossils. The tubules represent extensions of epithelial tissue through the shell, seemingly to the organic periostracal layer, and likely contributed to rapid growth of the thick shell by enhancing transportation from the epithelium to shell production sites at the base of the periostracum. *Cassitella malinkyi* sp. nov. is described from the Bastion Formation of North-East Greenland. • Key words: Hyolitha, shell structure, Cambrian Series 2, Greenland, Laurentia.

Peel, J.S. 2025. Shell tubules in *Cassitella* (Hyolitha) from the Cambrian (Series 2) of Greenland (Laurentia). *Bulletin of Geosciences 100*(*X*), xxx–xxx (6 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received September 13, 2025; accepted in revised form October 31, 2025; published online November 30, 2025; issued Xxxxxxx XX, 2025.

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Cassitella baculata Malinky & Skovsted, 2004 is a robust, originally calcareous, cap-shaped, small shelly fossil first described from the Bastion Formation (Cambrian Series 2, Stage 4) of North-East Greenland (Fig. 1; Malinky & Skovsted 2004). It was described subsequently from the equivalent Forteau Formation of western Newfoundland (Skovsted & Peel 2007) and the Aftenstjernesø Formation of North Greenland (Peel 2021a); its distribution across North Greenland is extended herein (Fig. 2). In addition, *Cassitella malinkyi* sp. nov. is proposed for material from North-East Greenland that Skovsted (2006) left unassigned. Collectively, these records are derived from a small group of localities located on the eastern side of Laurentia just south of the equator in the Cambrian (Torsvik & Cocks 2016).

While not making a formal systematic assignment, Malinky & Skovsted (2004) and Skovsted (2006) noted that *Cassitella* resembles the operculum of hyolithid hyoliths (Class Hyolitha Marek, 1963), but the conical conch typical of hyoliths is not yet known in *Cassitella*. This is a common situation with phosphatised material derived from limestone samples using weak acids where specimens are often sorted into discrete size classes as a result of taphonomic processes and sample preparation. Opercula in such samples are often associated with juveniles or microconchs of similar size whereas the elongate conchs in life associations are several times longer than the diameter of the opercula. As noted by Peel & Gubanov (2022), comparison between assemblages of hyoliths preserved as macrofossils and those that are described as microfauna, such as the present one, is complicated by the size difference between the two preservational states.

The systematic position of hyoliths is debated. They have often been classified as problematic fossils (Bengtson *et al*. 1990), molluscs (Marek & Yochelson 1976, Malinky & Yochelson 2007) or as a separate phylum (Runnegar *et al*. 1975, Runnegar 1980). Moysiuk *et al*. (2017) considered them to be lophophorates, but Li *et al*. (2019) noted similarities in shell structure between hyoliths and molluscs.

Cassitella baculata is characterised by a pair of massive protuberances (Fig. 1), here referred to collectively as cardinalia, that are located on the lower surface of the operculum beneath the sub-marginal apex (summit; Fig. 1B). The lower margin is strongly convex in lateral view (Fig. 1A), suggesting that it fitted against the ventral extension of the conch margin into the shelf-like ligula characteristic of most hyolithid hyoliths.

All described opercula of *Cassitella baculata* consist of diagenetically phosphatised replicas and internal moulds recovered by digestion of limestone samples in weak acetic or formic acid. When well preserved, the

DOI 10.3140/bull.geosci.1951

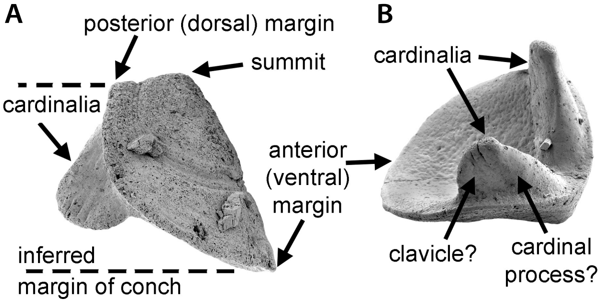

Figure 1. Terminology of the operculum of *Cassitella baculata* Malinky & Skovsted, 2004. A – lateral view. B – oblique postero-lateral view of inner surface.

external surface of these is seen to be ornamented by fine comarginal growth lines (Figs 1A; 3B, I), while the inner surface retains a finely mottled texture (Figs 1B, 3H). Despite the overall compact, massive appearance, phosphatisation in broken specimens of *Cassitella baculata* reveals an internal structure of closely spaced columns perpendicular to the internal mould (Figs 4E, F; 5A, C). The columns represent tubules, now infilled by diagenetic calcium phosphate, which passed through the calcareous shell, with the surrounding calcium carbonate having been removed by the preparation in acid. Their presence is commonly evidenced by the preservation of coarse tubercles on the central surface of phosphatised internal moulds (Fig. 4E).

Preserved surfaces of *Cassitella baculata* may reflect phosphatisation of the original shell layer and display fine details of pores (Fig. 6F, on the inner surface of the operculum) or a smooth organic periostracum on the exterior (Vendrasco *et al.* 2017, Oh *et al.* 2024). However, even if pores penetrated to the outer surface they may be obscured by a thin calcium phosphate diagenetic encrustation that typically has a microcrystalline texture perpendicular to the shell surface, although this encrustation may be difficult to delimit from the original shell (upper surface arrowed in Fig. 4F).

Holes and galleries in the shell wall may be an original structure (as are the tubules described herein) but they can also result from the activities of boring organisms both during life and post-mortally (Fig. 3B, J, M). The galleries produced by these euendoliths are often filled with diagenetic calcium phosphate in lower–middle Cambrian small shelly fossils and thus readily preserved (Runnegar 1985, Peel 2025). Striated borings in phosphatic shells result from ambient inclusion trails of non-organic origin (Yang *et al.* 2017; Peel 2025, fig. 3d, g).

This paper describes the closely spaced internal tubules of *Cassitella baculata* and discusses their function in life. Tubules are not unique to *Cassitella* amongst hyoliths, having been described from the Cambrian of China by Qian & Zhang (1985), and in *Tchuranitheca* Sysoev, 1968 and *Majatheca* Missarzhevsky, 1969 *in* Rozanov *et al.* (1969) from the Cambrian of Siberia by Kouchinsky (2000) and Kouchinsky *et al.* (2015a). Vendrasco *et al.* (2017) described tubules in *Cupitheca holocyclata* (Bengtson, 1990) *in* Bengtson *et al.* (1990) from the lower Cambrian of Australia.

Tubules are not confined to hyoliths, being a characteristic feature of helcionelloid molluscs such as *Anhuiconus microtuberus* Zhou & Xiao, 1984 and *Emargimantus tunuensis* (Peel & Skovsted, 2005) in the lower Cambrian of Greenland. Parkhaev (2006) described similar structures in *Auricullina* Vassiljeva, 1998 and *Daedalia* Parkhaev, 2001 *in* Gravestock *et al.* (2001) from the lower Cambrian of South Australia and reviewed other occurrences. Kouchinsky *et al.* (2017) discussed similar infilled tubules in *Barskovia hemisymmetrica* Golubev, 1976 from the lower Cambrian of Siberia. Vendrasco *et al.* (2004) described canal systems in the shell sclerites of Late Palaeozoic multiplacophorans, making comparisons with the extensive aesthetes canals of chitons (Fernandez *et al.* 2007, Vendrasco *et al.* 2008).

Vinther (2009) reported extensive canal systems within sclerites of *Sinosachites delicatus* (Jell, 1981) and in *Hippopharangites* Bengtson, 1990 *in* Bengtson *et al.* (1990) from the lower Cambrian of Australia. Pores were also described in the chancelloriid *Cambrothyra ampulliformis* Qian & Zhang, 1983 from the lower Cambrian of China by Moore *et al.* (2010). More widely spaced pores were described by Kouchinsky *et al.* (2010) and Skovsted *et al.* (2014) in *Tannuolina* Fonin & Smirnova, 1967 from Cambrian strata of the Siberian platform and Morocco, respectively. Setigerous and other internal tubular structures have been described in the shells of stem group brachiopods (Holmer *et al.* 2008; Skovsted *et al.* 2010, 2014; Kouchinsky *et al.* 2015b; Liang *et al.* 2020).

At first glance, the columnar structure preserved in etched, phosphatised specimens of *Cassitella baculata* may appear similar to the phosphatic pillar structures in the shells of acrotretid linguliformean brachiopods classically described by Williams & Holmer (1992) and recently revised by Zhang *et al.* (2024). However, structures in *Cassitella baculata* are tubular canals diagenetically infilled with phosphatic material rather than pillars of original shell material.

Geological background

Lower Cambrian sediments crop out in three main areas within the transarctic Franklinian Basin succession of northern Greenland (Higgins *et al.* 1991, Ineson & Peel 1997). In Inglefield Land and Daugaard-Jensen Land (Fig. 2D) inner shelf carbonates overlie transgressive siliciclastic sediments (Poulsen 1927, 1964; Palmer &

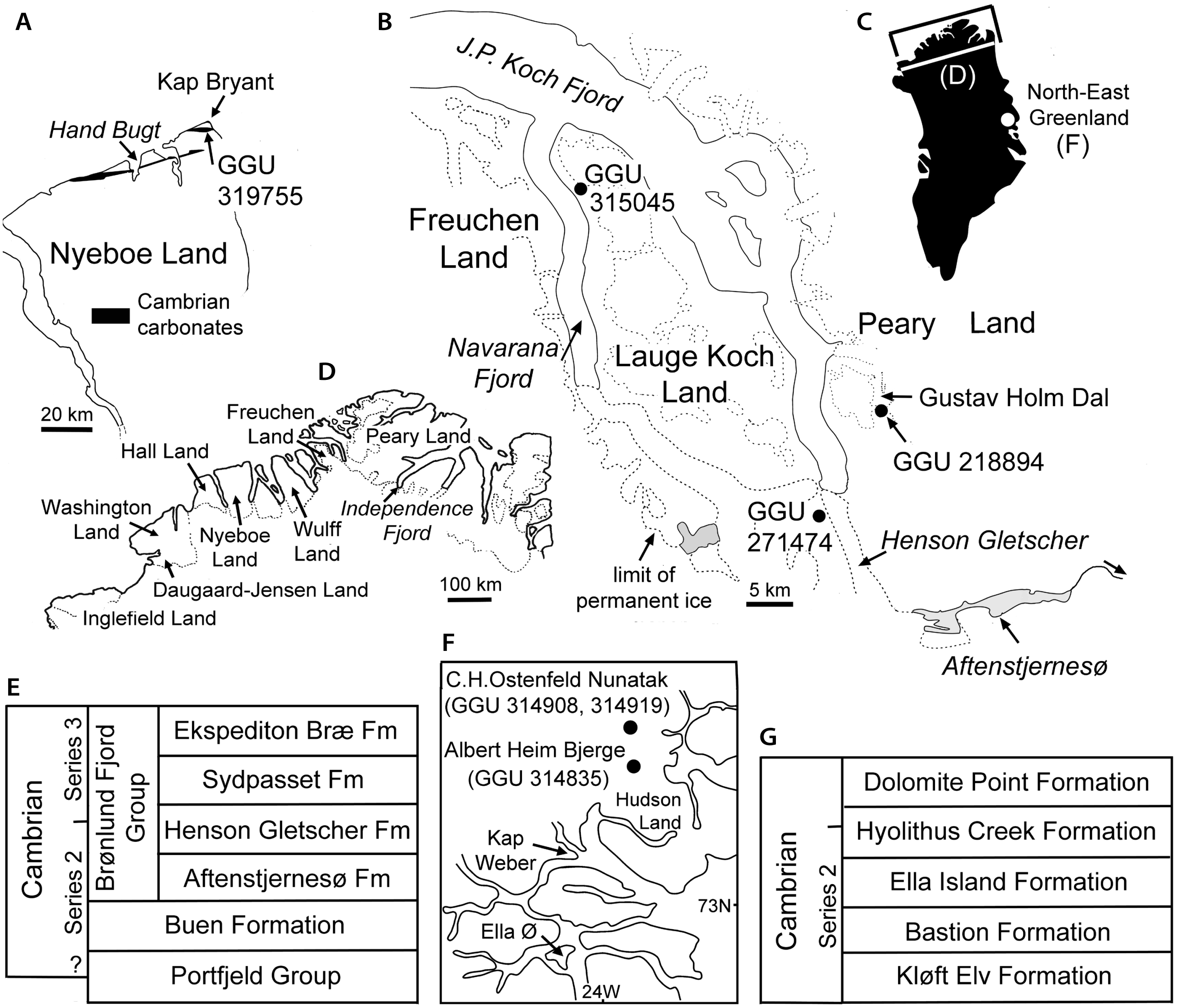

Figure 2. Derivation of samples, with overviews located in C and D. • A – Nyeboe Land. • B – Lauge Koch Land – western Peary Land. • E – Cambrian stratigraphy in southern Lauge Koch Land and western Peary Land. • F – collection localities at Albert Heim Bjerge and on C.H. Ostenfeld Nunatak in North-East Greenland. • G – Cambrian stratigraphy in North-East Greenland.

Peel 1981; Peel 2021b). Ediacaran–Cambrian carbonates of the Portfjeld Group (Willman *et al.* 2020, Ineson *et al.* 2024) are overlain by siliciclastic sediments of the Buen Formation (Fig. 2D, E; Ineson & Peel 1997, Peel & Willman 2018) in an eastern belt from southern Wulff Land to southern Peary Land. An overlying complex of shelf carbonates (Brønlund Fjord Group) progrades northward across the open shelf (Higgins *et al.* 1991, Ineson & Peel 1997). Along the northern coast, from northern Nyeboe Land to Peary Land (Fig. 2D), outer shelf and deep-water Cambrian sediments re-emerge from beneath Ordovician and Silurian strata as a result of middle Palaeozoic Ellesmerian orogenesis (Higgins *et al.*1991).

All material from North Greenland described herein was collected from the Aftenstjernesø Formation, the basal formation of the Brønlund Fjord Group. The formation is dominated by cliff-forming dolostone grainstones. It is 62 m thick in its type area in southern Lauge Koch Land (Fig. 2B, Ineson & Peel 1997) but reduced to just 18 m to the north in northern Lauge Koch Land (Peel 2021a). Fossils are generally restricted to the basal few metres (Member A) of nodular grainstones that are rich in glauconite, phosphorite bioclasts, pyrite, and phosphatised hardgrounds (Frykman 1980, Peel 2017), forming a condensed unit that accumulated in a sediment-starved outer ramp setting.

Cambrian strata in North-East Greenland outcrop within the East Greenland Caledonides (Henriksen & Higgins 1976, Smith *et al.* 2004, Smith & Rasmussen 2008) and outcrops were described in detail by Cowie

& Adams (1957), Smith *et al.* (2004), Skovsted (2006) and Stouge *et al.* (2012). Cambrian strata occur in a number of discrete outcrops from Ella Ø in the south to C.H. Ostenfeld Nunatak to the north (Fig. 2F). Basal siliciclastic lower Cambrian sediments of the Kløft Elv and Bastion formations are overlain by platform carbonates of the Ella Island, Hyolithus Creek and Dolomite Point formations (Fig. 2G). The derivation of specimens of *Cassitella* from North-East Greenland was described by Malinky & Skovsted (2004) and Skovsted (2006), the latter documenting the extensive accompanying Cambrian Series 2, Stage 4 fauna. All currently described specimens from North-East Greenland are derived from thin limestone beds and nodules within the upper member of the Bastion Formation on C.H. Ostenfeld Nunatak and at Albert Heim Bjerge, Hudson Land (Fig. 2F).

Material and methods

Samples were collected during mapping and regional geology projects of Grønlands Geologiske Undersøgelse (GGU; Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. All samples are of early Cambrian age (Series 2) unless stated.

GGU sample 218894 was collected by Peter Frykman on 10th July 1979 from the Aftenstjernesø Formation, Member A, in Gustav Holm Dal, western Peary Land, North Greenland (Fig. 2B; 82° 22′ N, 39° 44′ W).

GGU sample 271474 was collected by J.S.P. on 25th June 1978 from the Aftenstjernesø Formation, Member A, in the type section of the formation (Ineson & Peel 1997) on the western side of Henson Gletscher in southern Lauge Koch Land, North Greenland (Fig. 2B; 82° 10′ N, 40° 24′ W).

GGU sample 314835 was collected by J.S.P. on 6th July 1988 from about 30 m above the base of the upper member (thickness about 91 m) of the Bastion Formation on the western side of Albert Heim Bjerge, Hudson Land, North-East Greenland (Fig. 2F; 73° 10′ N, 23° 40′ W; Malinky & Skovsted 2004, fig. 1; Skovsted 2006, fig. 1).

GGU samples 314908 and 314919 were collected by J.S.P. on 18th July 1988 from about the middle of the upper member of the Bastion Formation (thickness about 70 m) at the northern tip of C.H. Ostenfeld Nunatak, North-East Greenland (Fig. 2F; 73° 22′ N, 23° 40′ W; Malinky & Skovsted 2004, fig. 1; Skovsted 2006, fig. 1).

GGU sample 315045 was collected by J.S.P. on 7th July 1984 at about 60 cm above the base of Aftenstjernesø Formation on the east side of Navarana Fjord in northern Lauge Koch Land, North Greenland on the northern limb of the Navarana Fjord anticline (Fig. 2B; 82° 36′ N, 42° 18′ W). The diverse fauna from this sample was described by Peel (2021a).

GGU sample 319755 was collected by Anthony K. Higgins on 11th August 1985 from about 24.8 m above the base of the Aftenstjernesø Formation, south of Kap Bryant, northern Nyeboe Land, North Greenland (Fig. 2A; 82° 19′ N, 55° 17′ W).

All specimens were recovered from wet-sieved residues of limestone samples treated with weak acetic or formic acid. Selected specimens were studied by scanning electron microscopy (SEM) and images were assembled in Adobe Photoshop (Adobe Systems, San Jose, California, U.S.A.).

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

Systematic palaeontology

This published work and the nomenclatural acts it contains have been registered in Zoobank: *lsid:zoobank.org:pub:1A2F645B-D55D-4722-BC01-69301FEC047C.*

Phylum uncertain
Class Hyolitha Marek, 1963
Order Hyolithida? Sysoev, 1957
Family unknown

Genus *Cassitella* Malinky & Skovsted, 2004

Type species. – *Cassitella baculata* Malinky & Skovsted, 2004.

Diagnosis. – Sub-triangular to almost circular, convex operculum with the rounded apex displaced towards the higher side (interpreted as dorsal and posterior). Exterior with fine comarginal ribs and depressions. Interior with two prominent, widely diverging ridges (herein referred to collectively as the cardinalia) emanating from just within the sub-apical margin of shell. Terminations of the cardinalia free from the shell surface and sometimes divided into distinct lobes. Interior of the robust shell with a dense pattern of tubules (revised after Malinky & Skovsted 2004).

Remarks. – The unusual morphology of *Cassitella* makes this genus readily distinguishable from other cap-shaped Problematica described from the lower Cambrian. The

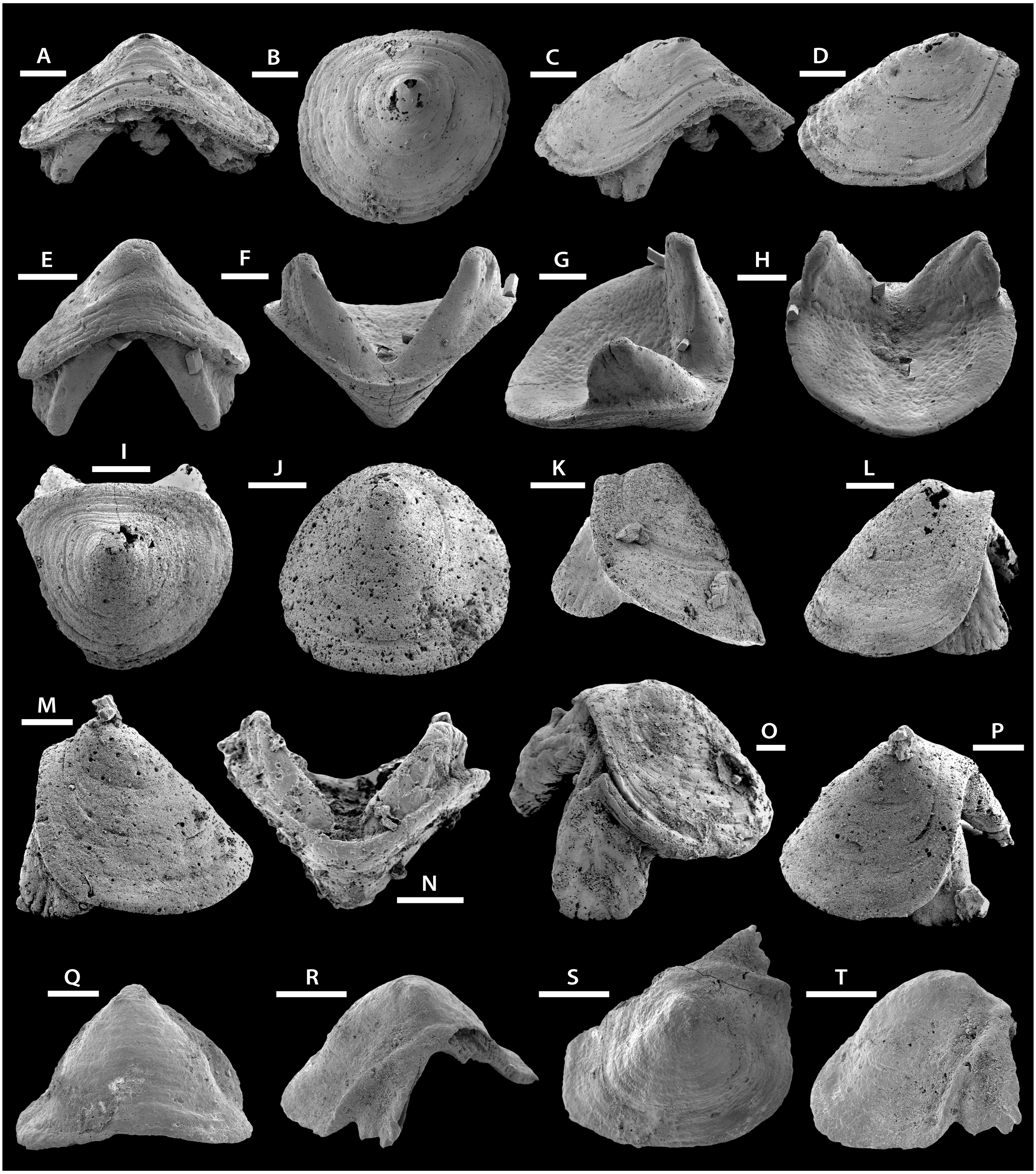

Figure 3. *Cassitella* Malinky & Skovsted, 2004, Cambrian Series 2, Greenland. • A–P – *Cassitella baculata* Malinky & Skovsted, 2004. Specimens from GGU sample 315045, Aftenstjernesø Formation, northern Lauge Koch Land, unless stated. A–D – MGUH 27130 from GGU sample 314835, holotype, Bastion Formation, Albert Heim Bjerge, external surface in posterior (A), plan (B), postero-lateral (C) and lateral (D) views. E – PMU 36938, posterior view. F–H – PMU 36937, interior in posterior (F), oblique lateral (G) and plan (H) views. I, L – PMU 36940 in oblique posterior plan (I) and lateral (L) views. J – PMU 36939, oblique plan view. K – PMU 36941, lateral view. M, P – PMU 17851 from GGU sample 218894, Aftenstjernesø Formation, Gustav Holm Dal, lateral (M) and postero-lateral (P) views. N – Specimen from GGU sample 271474, Aftenstjernesø Formation, southern Lauge Koch Land, posterior view. Lost after imaging. O – PMU 17852 from GGU sample 218894, Aftenstjernesø Formation, Gustav Holm Dal, postero-lateral view. • Q–T – *Cassitella malinkyi* sp. nov., MGUH 27616 from GGU sample 314908, holotype, Bastion Formation, C.H. Ostenfeld Nunatak, North-East Greenland, in anterior (Q), oblique posterior (R), plan (S) and lateral (T) views. Scale bars: 100 µm (O); 200 m (A–L, M, N, P–T).

prominent, diagnostic, cardinalia on the inner surface of *Cassitella* are suggestive of the clavicles ordinarily seen among hyoliths, but clearly defined cardinal processes have not been recognised. However, the cardinalia often show incipient differentiation of a robust posterior protruberance from a more slender, lobed, anterior ridge that may permit tentative interpretation as cardinal processes and clavicles (Fig. 1B).

Cassitella resembles the problematic (aculiferan?) molluscs *Ocruranus* Liu, 1979 and *Eohalobia* Jiang, 1982 *in* Luo *et al*. (1982) from the Meishucunian of South China in terms of its thick shell and cap-shaped form (Qian & Bengtson 1989, Vendrasco *et al*. 2009). Shells refered to *Ocruranus* by Peel & Skovsted (2005) occur together with C*assitella* in the Bastion Formation and also in the Aftenstjernesø Formation (Peel 2021a) but they lack the massive cardinalia on the inner surface characteristic of *Cassitella*.

Cassitella baculata **Malinky & Skovsted, 2004**
Figures 3A–P, 4–6

- 2004 *Cassitella baculata*; Malinky & Skovsted, p. 574, fig. 15.
- 2007 *Cassitella baculata*. – Skovsted & Peel, p. 741, fig. 5m, n.
- 2021a *Cassitella baculata*. – Peel, p. 15, fig. 10.

Holotype. – MGUH 27130, a phosphatised shell from GGU sample 314835, Bastion Formation, Albert Heim Bjerge, North-East Greenland; Cambrian Series 2.

Figured material. – In addition to the holotype (Fig. 3A–D), PMU 17853–PMU 17856, PMU 17859 and PMU 17860 from GGU sample 314835, Bastion Formation of Albert Heim Bjerge, North-East Greenland. PMU 17857 from GGU sample 314919, Bastion Formation of C.H. Ostenfeld Nunatak, North-East Greenland.

PMU 36937–36941 from GGU sample 315045, Aftenstjernesø Formation, northern Lauge Koch Land, North Greenland. PMU 17851 and PMU 17852, Aftenstjernesø Formation, Gustav Holm Dal, North Greenland. PMU 17858 from GGU sample 319755, Aftenstjernesø Formation, northern Nyeboe Land, North Greenland. The original specimen of Figure 3N from GGU sample 271474, Aftenstjernesø Formation, southern Lauge Koch Land, was lost after imaging and is not assigned a museum number.

Additional material. – Paratypes MGUH 27131–27135 from GGU sample 314835 from the upper Bastion Formation of Albert Heim Bjerge were illustrated by Malinky & Skovsted (2004). Malinky & Skovsted (2004) reported more than 170 specimens from the upper Bastion Formation of Albert Heim Bjerge and C.H. Ostenfeld Nunatak, North-East Greenland (Fig. 2F, G) and most of this material was deposited by Christian Skovsted in the Swedish Natural History Museum (Naturhistoriska Riksmuseet), Stockholm. Skovsted & Peel (2007) recorded 14 specimens from the Forteau Formation of western Newfoundland. Peel (2021a) noted seven specimens from the Aftenstjernesø Formation of northern Lauge Koch Land (GGU sample 315045). *Cassitella baculata* is common in the Aftenstjernesø Formation of Gustav Holm Dal (GGU sample 218894) but also occurs infrequently in samples from southern Lauge Koch Land and in northern Nyeboe Land (Fig. 2A, B).

Description. – Slightly curved, robust, cap-shaped shell varying from sub-circular to sub-triangular in plan view, with the rounded apex (summit) located at about one third of the distance from the sub-apical margin (interpreted as dorsal and posterior; Fig. 1A) to the supra-apical margin (ventral and anterior). Height varying from about half (Malinky & Skovsted 2004, fig. 15c) to slightly less than the total length (Fig. 3K, L). Supra-apical surface flat to shallowly convex in lateral view (Fig. 3K–M); sub-apical surface varying from shallowly concave to shallowly convex. Sub-apical margin broadly sinuate (Fig. 3A, E, P) such that the apertural margin in lateral view is strongly convex between the posterior and anterior margins (Fig. 3D, K, M).

Inner surface with two prominent and widely diverging protruberances (here referred to collectively as cardinalia) on the internal surface that rise abruptly from just within the posterior/dorsal margin of the shell. In posterior view, near the margin (Fig. 3E, F), the cardinalia are peg-like, broad and rounded, but they decrease in height and become narrower, often with longitudinal furrows and lobes, as they extend along the lateral areas of the operculum (Fig. 3G). Their length, in posterior view, may approach the height of the upper surface (Fig. 3A–F, K, L).

The shell is massively thickened, up to about 0.4 mm, but the cardinalia may be twice or more this thickness at their posterior margin (Fig. 3A, F). Internal shell structure with closely spaced tubules, diameter about 5 µm, mainly oriented perpendicular to the shell surface and opening through pores on the operculum interior. The external surface is ornamented with fine comarginal growth lines and grooves that may become more strongly expressed on the sub-apical surface (Fig. 3C, D). The inner surface is finely dimpled (Fig. 3G, H). Conch unknown.

Remarks. – The strong convexity of the margins in lateral view (Fig. 3K–M, P) indicates equivalent concave lateral margins in the conch aperture, and an operculum with an oblique contact with the conch (Fig. 1A). This degree of curvature is characteristic of hyolithid hyoliths, which characteristically display a well-developed ligula, often with an amblygonal aperture, as an anterior extension of

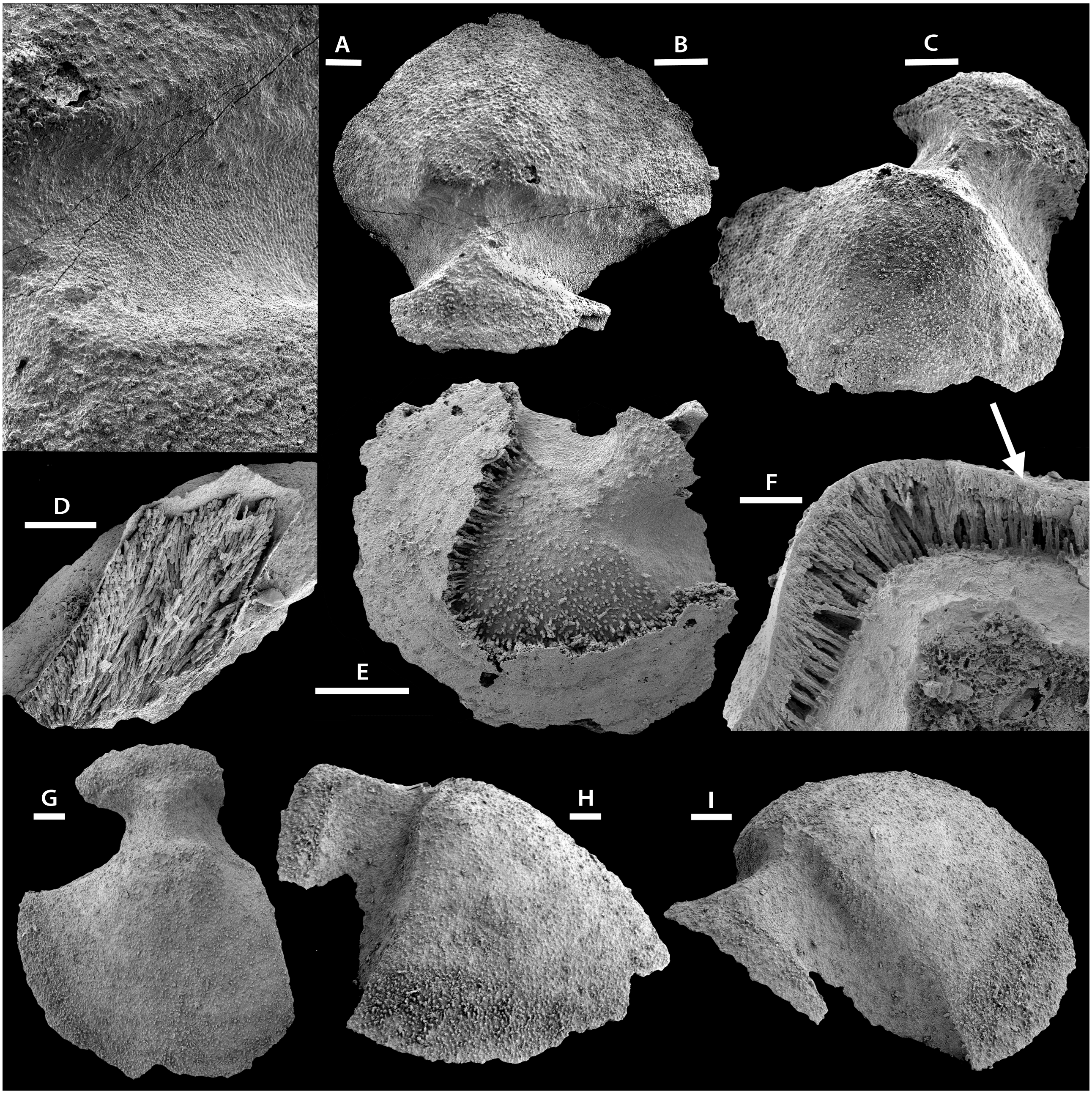

Figure 4. *Cassitella baculata* Malinky & Skovsted, 2004. Bastion Formation, North-East Greenland. A–F – GGU sample 314835, Albert Heim Bjerge; A–C – PMU 17853, internal mould with channels corresponding to the robust clavicles; B – oblique plan view, with detail of sculpture in A; C – oblique anterior view; D – PMU 17854, internal structure of broken clavicle; E – PMU 17855, external view of exfoliated specimen showing infilled tubules between the internal mould and the outer shell surface; F – PMU 17856, infilled tubules in shell wall. Note thin outer layer (arrow). G–I – GGU sample 314919, C.H. Ostenfeld Nunatak, PMU 17857, internal mould in plan (G) and oblique lateral (H, I) views. Scale bars: 50 µm (A); 100 µm (F–I); 200 µm (B–E).

the ventral surface of the conch (Malinky & Berg-Madsen 1999, text-fig. 2). The aperture in orthothecid hyoliths is usually coplanar.

The tendency for the cardinalia to become narrower and lobed or furrowed anteriorly may suggest incipient differentiation of clavicles from the more prominent cardinal processes (Figs 1B, 3E–H).

Cassitella malinkyi sp. nov.

Figure 3Q–T

2006 *Cassitella* sp. – Skovsted, p. 1104, fig. 10.24–10.27.

Holotype. – MGUH 27616 from GGU sample 314908 (Fig. 3Q–T).

Type horizon and locality. – Bastion Formation, C.H. Ostenfeld Nunatak, North-East Greenland.

Additional material. – Skovsted (2006) reported 11 additional specimens from the Bastion Formation at Albert Heim Bjerge and on C.H. Ostenfeld Nunatak, North-East Greenland.

Etymology. – In memory of John M. Malinky (1955–2025), in recognition of his life-long research concerning hyoliths.

Diagnosis. – Species of *Cassitella* in which the sub-apical surface is bounded by an upturned posterior/dorsal margin. Cardinalia blade-like, becoming longitudinally lobed distally.

Description. – Slightly curved, robust, cap-shaped, sub-circular to sub-quadrangular shell in plan view; apex (summit) located at slightly less than one third of the distance from the sub-apical margin (interpreted as dorsal and posterior; Fig. 1A) to the supra-apical margin (ventral and anterior). Height and total length about equal (Fig. 3S, T). Supra-apical surface shallowly convex in lateral view (Fig. 3T); sub-apical surface shallowly concave, upturned at the margin, which is broadly sinuate in posterior view (Fig. 3R). Apertural margin in lateral view is overall strongly convex, sub-angular, between the anterior and posterior margins (Fig. 3T) but concave in the posterior segment, where the protruding cardinalia are conspicuous (Fig. 3R, T).

Inner surface with prominent cardinalia consisting of two widely diverging ridges of uniform thickness on the internal surface that rise abruptly from just within the posterior/dorsal margin of the shell. The cardinalia are longitudinally furrowed (Fig. 3R). The shell and the cardinalia at their posterior margin are of similar thickness (Fig. 3R). The outer surface is ornamented with fine comarginal growth lines.

Remarks. – The operculum of *Cassitella malinkyi* differs from *Cassitella baculata* in its upturned posterior/dorsal margin, which clearly delimits the internal area of the operculum area with protruding cardinalia from the upper surface. In this respect, *Cassitella malinkyi* resembles *Protomicrocornus triplicensis* Pan, Skovsted, Sun & Li, 2019 from the Xinji Formation (Cambrian Series 2, upper Stage 3 to lower Stage 4) of North China (Pan *et al.* 2019). However, the swollen, protruding median dorsal area of the operculum of the latter produces convex lateral areas in contrast to the shallowly concave margins of *Cassitella malinkyi* in lateral view. In *Cassitella malinkyi* the cardinal area on the inner surface is much less inflated than in *Protomicrocornus*; it also lacks the folds on the ventral margin of the operculum characteristic of *Protomicrocornus triplicensis*.

Cassitella baculata: internal structures of operculum

Internal moulds of the operculum of *Cassitella baculata* from North-East Greenland display a deep, transverse, saddle-shaped channel with a U-shaped profile corresponding to the prominent cardinalia that rise from the internal surface on each lateral area (Fig. 4B, C, E). This channel is clearly differentiated in terms of sculpture impressed on the internal mould from the main area of the internal surface of the operculum. Within the central part of the transverse channel ornament consists of closely spaced fine tubercles (about 3 μm in diameter with rounded upper surfaces) that may be arranged into discontinuous ridges (Fig. 4A). Towards the acute angular transition with the posterior and anterior area of the internal mould this dense, fine pattern passes into a more open pattern of coarser tubercles that are 5–8 μm in diameter with irregular upper surfaces. An exfoliated specimen from the same sample demonstrates that these coarser tubercles represent the base of columns that rise from the surface of the internal mould towards the thin outer surface of the specimen (Fig. 4E). It is evident that these phosphatised columns represent the diagenetic infilling of tubules within the original calcareous shell that is now represented by the void surrounding the columns, resulting from dissolution of the carbonate during the acid preparation technique.

The infilled tubules are cylindrical with a granular or fibrous texture, usually unbranched through most of their length and generally perpendicular to both the surface of the internal mould and the mineralized thin outer surface of the operculum (Fig. 4E). However, well-preserved fractured surfaces may show branching towards the outer surface (Fig. 4F).

The outermost external surface of the operculum retains growth ornamentation in comarginal bands that step down towards the margin (Fig. 3A–E). There is no indication that tubules passed through this etched, thinly phosphatised layer, an observation in accord with descriptions by Vendrasco *et al.* (2017) in conchs of the Cambrian hyolith *Cupitheca holocyclata* (Bengtson, 1990) *in* Bengtson *et al.* (1990) and the helcionelloid *Nomgoliella sinistrivolubilis* Missarzhevsky, 1981 from the Cambrian of Mongolia (Li *et al.* 2024).

A broken and exfoliated internal mould from North Greenland (GGU sample 319755; Fig. 5) shows a similar disposition of the transverse channel representing the cardinalia, near the posterior margin, and the dominant, shallowly convex supra-apical surface (Fig. 5B). Sculpture on the surface of the central area of the internal mould matches that seen on the specimens from North-East Greenland (Fig. 4A–C, E), although the columns in the North Greenland specimen frequently arise from a pattern of anastamosing, discontinuous ridges on the internal

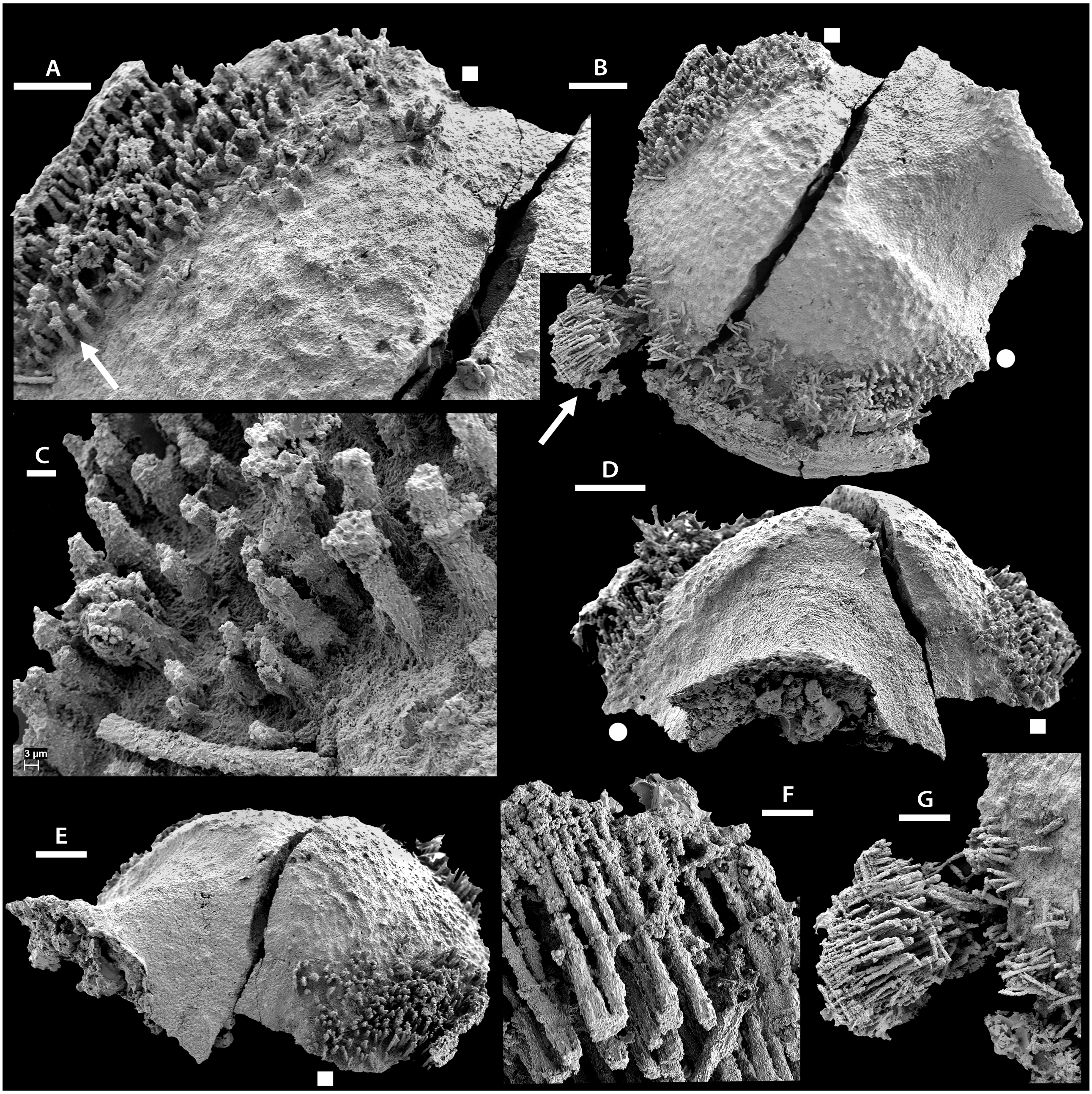

Figure 5. *Cassitella baculata* Malinky & Skovsted, 2004, PMU 17858 from GGU sample 319755, Aftenstjernesø Formation, northern Nyeboe Land, broken, phosphatised internal mould with infilled tubules. White squares and white circles locate equivalent points in images, respectively. A – arrow locates detail of infilled tubules (C). B – plan view, enlarged in A; arrow locates detail of detached clump of tubules at the anterior margin (F, G). C – detail of infilled tubules (arrow in A). D – posterior view. E – postero-lateral view. F, G – detached clump of infilled tubules (arrow in B) with detail in F. Scale bars: 5 µm (C); 20 µm (F); 50 µm (A, G); 100 µm (B, D, E).

mould that seemingly correspond to channels in the inner surface of the operculum shell (Fig. 5A). A fibrous surface texture is preserved between these ridges.

Individual columns in the central area are about 5 µm in diameter, with 10 µm interspaces, and up to 100 µm long (Fig. 5A, C, F, G); they may be crossed by traces of laminae paralleling the outer surface of the operculum (Fig. 5F). Many columns display a longitudinal pattern of needles or short fibres and the spaces between the tubules also have a fibrous structure (Fig. 5C, F). The columns taper towards the external surface and may branch (Fig. 5F, G). Most of the supra-apical surface of the operculum has these phosphate-infilled tubules arranged perpendicular to the external and inner surfaces of the operculum in cross-section (Fig. 6A, D). One or more shell layers separated by thin laminae may be present

(Fig. 6D); tubules often penetrate the overlying lamina but may regroup into different spacing patterns and thicknesses in the new layer.

Specimens broken through the basal portion of the cardinalia display a distinct frondose pattern with point of origin below the summit (Fig. 6B, C). Due to breakage, the three-dimensional disposition of the phosphatised threads forming this pattern within the peg-like cardinalia as they extend towards the inner surface is not well known, but they appear to radiate towards the surface of the cardinalia. Usually, a single frond is present in each of the cardinalia, originating near the midline of the operculum at its posterior/dorsal end, beneath the summit, and with its axis extending laterally parallel to the inner surface of the operculum (Fig. 6C). One specimen shows subdivision into two parallel fronds distally (Fig. 4D). The threads within each frond vary from round to lath-like in cross-section and curve away from the axis of the frond to meet the thin outer wall of the cardinalia obliquely, often branching as they approach the wall (Fig. 6B, C, F) and joining laterally with other threads (Fig. 6G). They are mainly preserved as bundles of sub-parallel fibres that are continuous through much of the length of the individual tubules (Fig. 6F–H). In this respect, they differ from the fibrous texture seen on the tubules of the main areas of the shell (Fig. 5). Some threads appear to preserve a hollow core, but most are solid, as confirmed by the general absence or rarity of the large tubercles representing infilled tubules on moulds of the cardinalia (Fig. 4A–C, F). The open pores in Figure 6F, J (arrows) are clearly related to tubules associated with an earlier surface of the interior of the operculum rather than the bundles of threads within the cardinalia.

Remarks

Vendrasco *et al*. (2017) described closely packed tubules upto 10 μm in diameter in the hyolith *Cupitheca holocyclata* from the lower Cambrian of Australia (Bengtson *et al*. 1990, Skovsted *et al*. 2016, Sun *et al*. 2020) that were interpreted as connecting to a continuous periostracum. While the diagenetic infill of many of these tubules was solid, others retained a hollow core, suggesting that the original canals were lined, although this could be a diagenetic phenomenon.

Tubule systems described by Li *et al*. (2024) in the helically coiled helcionelloid *Nomgoliella sinistrivolubilis* Missarzhevsky, 1981 from the Bayangol Formation (Cambrian, Fortunian) of Mongolia comprise a closely spaced pattern of tubules about 10 μm in diameter that lie within the calcareous shell perpendicular to a thin layer interpreted as phosphatised periostracum. As in *Cassitella baculata*, the tubules were interpreted as canals within the shell and their diagenetic infilling also forms tubercles on the internal mould. The phosphatised infilling of the tubules in *Nomgoliella sinistrivolubilis* illustrated by Li *et al*. (2024, figs 2c, 4a–d) displays a prominent transverse lamination in contrast with the longitudinal fibrous fabric seen in *Cassitella baculata* (Figs 5C, F; 6G), but both structures were illustrated in allathecid? hyoliths illustrated by Kouchinsky (2000) from the early Cambrian of Siberia.

Discussion

The tubercles on the mould of the central areas of the inner surface of the operculum in the present material of *Cassitella* indicate the presence of tubules with open pores (Fig. 4E). These pores are visible on the interior of the operculum where the phosphatised original shell surface is retained (Fig. 6F, J). This outer surface on the interior of the operculum with preserved pores (Fig. 6C, right side) contrasts markedly with the etched, broken surface where phosphatised, infilled tubules are visible as columns (white) surrounded by cavities (dark) after dissolution of the calcareous shell material and loss of the outer shell surface (Fig. 6C, left side; arrow in 6K). It has not been demonstrated that pores penetrated to the outer surface of the sclerite exterior, which supports the notion that the tubercles were mainly engaged in transporting replenishment of organic material to the inner levels of the periostracum to support its defensive functions and to the outermost shell (Vendrasco *et al*. 2017).

The general absence of prominent tubercles on the internal mould of the cardinalia (the broad transverse channel on the operculum internal mould; Fig. 4A–C) suggests that replenishing material did not pass into the shell through the cardinalia directly from the epithelium of the operculum interior. It is likely that the fibrous fronds represent a distribution system of organic material into the cardinalia from the area beneath the summit, rather than from the cardinalia towards the area beneath the summit. Differences in morphology of the two suites of fibrous columnar structures and in the sculpture of their respective areas on the internal mould (Fig. 4A, E) support their different functions. In essence, however, both suites of columns disperse nutrients to growing areas of the shell but the internal cardinalia obviously lack the periostracum that protects the outer surface of the operculum.

Tubules are a conspicuous feature of chiton (Polyplacophora) sclerites where the outer (dorsal) shell layer (tegmentum) is penetrated by bundles of microaesthetes that originate from aesthetes canals passing through the sclerite (Schwabe 2010, Li *et al*. 2015, Ampuero *et al*. 2024). Epoxy casts of the aesthetes system were described with excellent illustrations by Fernandez *et al*. (2007)

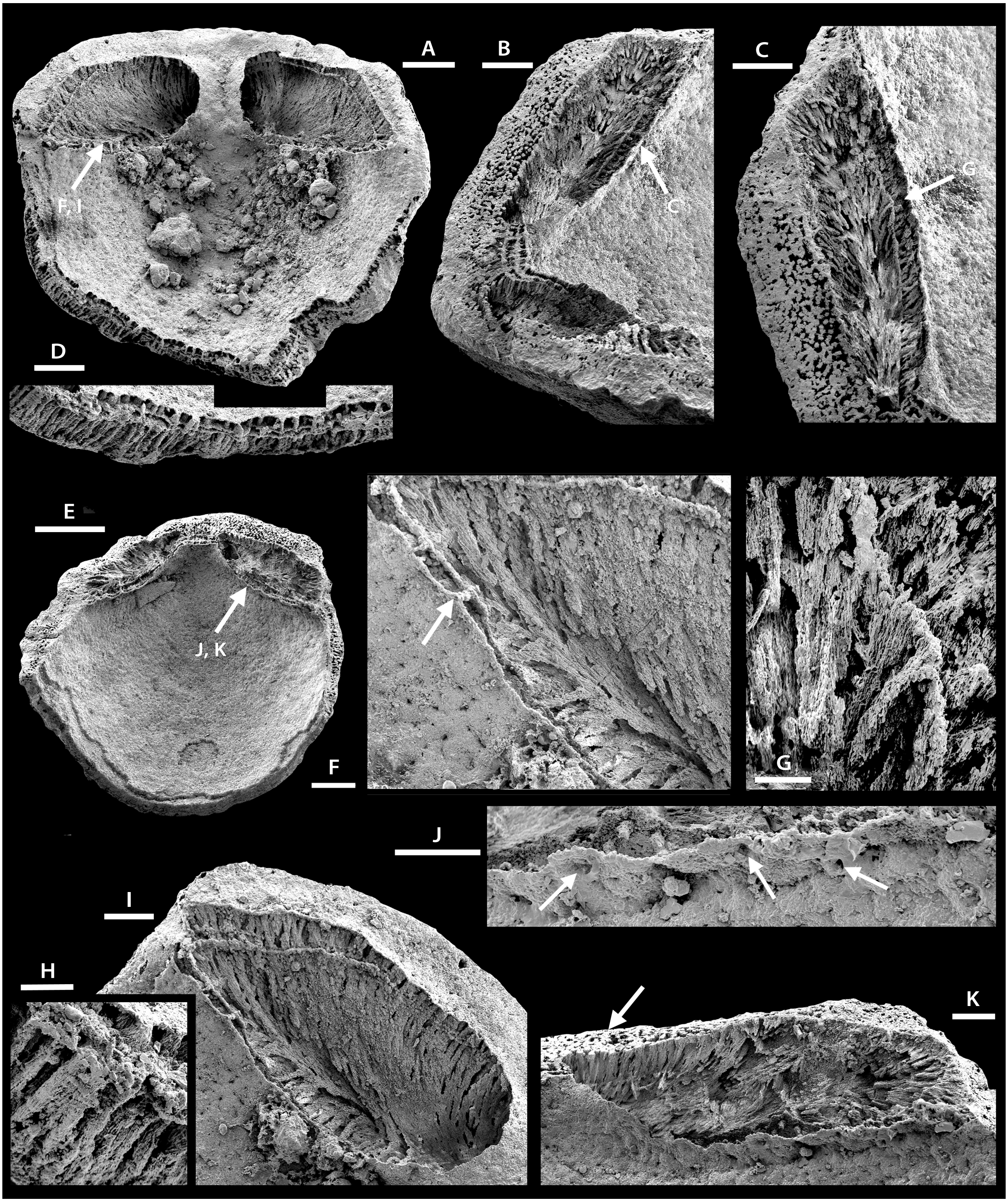

Figure 6. *Cassitella baculata* Malinky & Skovsted, 2004. GGU sample 314835, Bastion Formation, Albert Heim Bjerge, North-East Greenland. Interior views of broken phosphatised opercula after decalcification. A, D, F, H, I – PMU 17859; A – overview, showing sites of broken-away cardinalia with details of broken lower margin (D, H); F, I – details of left site (arrows in A) showing extended fibrous structure of cardinalia threads and pores on inner surface of operculum; arrow in F locates a tubule extending from an earlier growth surface to the latest surface. B, C, G, E, J, K – PMU 17860; B, E – overviews, showing sites of broken-away cardinalia; C – enlarged in C; G – detail of fibrous threads, located in C; J – pores (arrows) in the outer surface of the operculum interior (located in E); K – oblique view of C with porous inner surface of operculum (bottom) and expanding bundles of threads terminating at the exfoliated surface (arrow). Scale bars: 30 µm (G, H); 50 µm (F); 100 µm (D, I, J, K); 200 µm (A–C); 500 µm E.

and Vendrasco *et al*. (2008), while Ampuero *et al*. (2024) employed synchrotron imaging. The microaesthetes often have a light sensitive function but the variety of cell types present within the aesthete tissues (Fischer 1988) suggests that aesthetes canals perform a variety of sensory and transport functions (Vendrasco *et al*. 2008, Ampuero *et al*. 2024). The aethetes canals are often perpendicular near the sclerite outer surface (orthogonal) but become horizontal at lower levels (Fernandez *et al.* 2007, Vendrasco *et al*. 2008, Ampuero *et al*. 2024). Individual canals in the distal bundles of microaesthetes vary from about 1–5 µm in diameter whereas channels in the aesthetes canal system may attain a diameter of 50 µm. By comparison, the tubules in *Cassitella baculata* are about 5 µm in diameter (Fig. 5C, F).

Records of aesthetes canals in fossil chitons extend back to the Carboniferous (Hoare *et al*. 1983, Vendrasco & Runnegar 2004) but occurrences of pores attributed to possible aesthetes in Ordovician and Silurian material were discussed by Vendrasco & Runnegar (2004). Sclerites of the lower Cambrian *Qaleruaqia* Peel, 2020 from North Greenland, the oldest described palaeoloricate, preserve pores that Peel (2020) compared to aesthetes, but canals are not preserved. In contrast to the aesthetes of chitons, it has not been established that the tubules of *Cassitella baculata* passed through the outer surface of the dorsal sclerite exterior, although they may be visible on exfoliated surfaces (Fig. 6C). As in *Cupitheca holocyclata* and *Nomgoliella sinistrivolubilis*, the tubules likely terminated at the periostracum (Vendrasco *et al*. 2017, Li *et al*. 2024).

Following Reindl & Haszprunar (1996), Li *et al*. (2024) noted that shell tubules in general have been considered to serve a variety of biological functions such as sensory perception (including photoreception), respiration, the transport of ions and molecular compounds, mineralisation, constructional support, shell repair and protection against boring euendolithic organisms. It is likely that different functions and combinations of functions applied in different tubule-bearing taxa (Reindl & Haszprunar 1996) and even in different zones of single taxa. Thus, the advanced light sensitive aesthetes of chitons probably developed on a pre-existing system of tubules that initially had another function. Vendrasco *et al*. (2017) noted that microaesthetes were not recognised in *Cupitheca* although swelling of some tubules at their distal extremity is reminiscent of the bundles of microaesthetes in chitons. Tubules in *Cassitella bacculata* may show a similar feature, with distal branching (Fig. 4F), but there is no preserved evidence of a photoreceptive function.

Li *et al*. (2024) particularly focussed on a suggestion noted by Reindl & Haszprunar (1996) that tubules may have had a defensive function as a deterrent to boring by euendolithic cyanobacteria that penetrate the calcareous shell in search of domiciles and sustenance (Golubic *et al*. 1975, Runnegar 1985, Radtke & Golubic 2005, Stockfors & Peel 2005, Wisshak *et al*. 2008, Peel 2024). As such, in the present context they might form an element within the universal Cambrian Explosion defensive strategy of shell and periostracum development. While euendolith galleries avoid tubules, as might be expected given their mode of life as borers in hard shell rather than soft tissues, it seems likely that just this protective role is an ancillary benefit of the widespread tubules rather than a primary function. Euendolithic cyanobacteria are widely distributed in Cambrian fossils but do not approach the intensity or activity levels displayed by Mesozoic and present day biodegradation and micritisation processes.

As witnessed by the frequent iteration of calcium carbonate shells in the geological record, the production of inorganic calcareous shell material is metabolically less costly than the organic component (Palmer 1983, 1992), although the balance may be influenced by perturbations in sea water chemistry (*e.g.* Spalding *et al*. 2017). The tubules of *Cassitella baculata* do not increase the organic content of the shell material *per se* as they serve as canals with epithelial tissues that passed through the shell, connecting the epithelium to the shell-producing inner periostracum (Checa 2000, Vendrasco *et al*. 2017). When abundant, as in *Cassitella baculata* (Figs 4E, F; 5A), the tubules offer a reduction in the mass of calcium carbonate forming the shell. Together with enhancing contact between the epithelium and the inner shell-forming layer of the periostracum, this may be a significant contribution to the rapid formation of thick, defensive, calcareous shells.

Conclusions

Cassitella malinkyi sp. nov. is described from the Bastion Formation (Cambrian Series 2) in North-East Greenland.

Etching in weak acetic acid of phosphatised specimens from Cambrian Series 2 in North and North-East Greenland reveals that the originally robust calcareous operculum of *Cassitella baculata* Malinky & Skovsted, 2004 is penetrated by numerous closely spaced tubules that are about 5 µm in diameter and often with 10 µm interspaces. The tubules open as pores on the interior surface but seemingly do not penetrate the outer surface; they were likely filled with epithelial tisue. Similar tubules have been described in numerous other invertebrates and likely served a variety of functions. In *Cassitella*, the abundance of tubules offers an energy efficient reduction in the mass of calcium carbonate in the operculum. In connecting the epithelium with the shell-producing, inner periostracum, the tubules contribute to the replenishment of the periostracum and the rapid formation of thick, defensive, calcareous shells.

Acknowledgements

Christian B. Skovsted kindly provided raw SEM images of some of the illustrated specimens from the Bastion Formation of North-East Greenland. Cecilia Larsson and Timothy Topper facilitated examination and loan of specimens from North-East Greenland deposited by Christian Skovsted in the Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm, Sweden. Martin Valent (Prague), an anonymous reviewer and journal editorial staff are acknowledged for comments concerning the submitted manuscript.

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