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ABSTRACT

Phosphatized sclerites of *Chancelloria* and *Allonnia* are described from the Henson Gletscher Formation (Cambrian, Miaolingian Series, Wuliuan Stage) of North Greenland and the lower Cambrian of Siberia. They preserve diagenetic, unusually large, elongate crystals within the internal cavity (lumen) that maintain the imbricate lamellar structure of the original microstructure of the aragonitic sclerite wall.

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FINDS OF COMPLETE scleritomes of chancelloriids, in which the sessile sack-like body is studded with calcareous sclerites, are mainly restricted to shales in early–middle Cambrian Lagerstätten (Walcott 1920, Rigby 1978, Bengtson & Hou 2001, Janussen *et al.* 2002, Randell *et al.* 2005, Bengtson & Collins 2015, Cong *et al.* 2018, Yun *et al.* 2018, 2019, 2021a, Zhao *et al.* 2018, Peng *et al.* 2023). In contrast, the disarticulated hollow sclerites (coelosclerites of Bengtson & Collins 2015), may be abundant as phosphatic replicas or as internal moulds in residues from limestones that have been treated with weak acids to recover assemblages of Small Shelly Fossils (Bengtson *et al.* 1990, Moore *et al.* 2014, 2019, Yun *et al.* 2021b, Kouchinsky *et al.* 2011, 2022). Most chancelloriid sclerites have a rosette form with up to about ten radiating hollow rays, each with a basal foramen for the passage of soft tissues connecting with the main body mass (Bengtson & Hou 2001, Yun *et al.* 2021b, Fig. 1B–D, K). Numerous morphotaxa have been introduced at the level of genus and species for sclerite morphologies with different numbers (one or more) and combinations of rays (summarized by Moore *et al.* 2010, 2014, 2019). Complete scleritomes are usually dominated by a single sclerite morphotype, but small numbers of other morphotypes may

be present (Bengtson & Collins 2015). However, Moore *et al.* (2019) demonstrated that biological species can be recognized by the analysis of large assemblages of disarticulated spicules.

The phylogenetic position of chancelloriids is problematic (Bengtson & Collins 2015, Botting & Muir 2018, Cong *et al.* 2018). Bengtson & Missarzhevsky (1981) proposed Coeloscleritophora to unite chancelloriids with other Cambrian fossils, such as the halkieriids, showing a similar method of sclerite formation (Porter 2008), but other authors favour assignment of chancelloriids to the sponges, close to the protomonaxonids (Botting & Muir 2018, Cong *et al.* 2018).

The original aragonitic shell structure of chancelloriid sclerites has been recognized by several authors, and most recently summarized by Yun *et al.* (2021b), who discussed models for sclerite structure and formation. In this paper we describe unusual diagenesis in sclerites of *Chancelloria* and *Allonnia* Doré & Reid, 1965 from the middle Cambrian (Miaolingian Series, Wuliuan Stage) of North Greenland and Cambrian Series 2 in Siberia.

Materials and methods

Specimens were hand-picked from residues after digestion of limestone samples in 10% acetic acid. Following scanning electron microscopy, images were assembled in Adobe Photoshop CS4.

Derivation of the Greenland samples

Samples from North Greenland (Figs 1–4) were collected from the Henson Gletscher Formation in southern Lauge Koch Land and in Løndal, southern Peary Land (Ineson & Peel 1997, fig. 31, Geyer & Peel 2011, fig. 3, Peel & Kouchinsky 2022, figs 1, 2, Peel 2023, figs 1, 2), where the formation ranges in age from Cambrian Series 2 (Stage 4) to the Miaolingian Series (Wuliuan Stage).

GGU sample 271492 was collected by J.S.P. on 25 June 1978 from bioclastic limestone in the upper Henson Gletscher Formation at 56.5 m above the base of the formation (thickness 62 m) at the type locality in southern Lauge Koch Land (82°10'N, 40°24'W). GGU sample 271718 was collected by J.S.P. on 15 July 1978 from a thin-bedded bioclastic, dolomitic, limestone occurring about 1 m below the top of the Henson Gletscher Formation on the west side of Løndal (82°18'N, 37°00'W). Material of GGU samples 271492 and 271718 described here is derived from the Wuliuan Stage, *Ptychagnostus gibbus* Biozone (Robison 1984, Higgins *et al.* 1991, Ineson & Peel 1997, Geyer & Peel 2011). Clausen & Peel (2012), Peel (2021a,b, 2022a,b, 2023) and Peel & Kouchinsky (2022) described rich faunas in which helcionelloid molluscs are conspicuous.

Derivation of the Siberian samples

Sample 19/12.75 (Fig. 5E, F) was collected by A.K. from the upper part of the Erkeket Formation (Cambrian Stage 4, Botoman Regional Stage) along the Khorbusuonka River, Olenyok Uplift, northern Siberia (Kouchinsky *et al.* 2022, figs 1, 3; 71°28.8'N, 123°50.0'E).

Sample 6/66.2 (Fig. 5A–D) was collected by A.K. from the upper part of the Emyaksin Formation (Cambrian Stage 3, Atdabanian Regional Stage) on the right bank of the Bol'shaya Kuonamka River, 1.5 km downstream from the mouth of the Ulakhan-Tjulen Brook, on the eastern flanks of the Anabar uplift, northern Siberia (Kouchinsky 2000, fig. 1, Kouchinsky *et al.* 2015, fig. 34A; 70°43'N, 112°50'E).

Institutional abbreviations

GGU, Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. PMU, Palaeontological Collections, The Museum of Evolution, Uppsala University, Sweden. SMNH,

Swedish Museum of Natural History, Stockholm, Sweden.

Chancelloria sclerites

Of the approximately 20 sclerites of *Chancelloria* from each of GGU samples 271492 and 271718 from the Henson Gletscher Formation (Miaolingian Series, Wuliuan Stage) of North Greenland, two thirds display a formula of 6–1 (six radiating lateral rays and a single central ray on the upper surface) and one third show 7–1 (Fig. 1B). GGU sample 271718 also yielded three specimens with 5–1 rays (Fig. 1D). In almost all specimens the radial rays are coplanar; they have broken ray tips and are associated with internal moulds of numerous disarticulated rays. The internal cavity (lumen) of each ray connects to the soft tissues of the scleritome through a large foramen on the basal surface, although these may be partially covered by diagenetic encrustation (Fig. 1B, K). The radial rays are mainly of similar length, but a few specimens have one longer ray. After acid digestion, most articulated sclerites in the residues are preserved as phosphatized internal moulds of the internal cavity, with traces of external phosphatic encrustation deposited on the sclerite exterior (Fig. 1B, C, K).

Allonnia sclerites

Peel *et al.* (2016) assigned isolated chancelloriid sclerites from the Henson Gletscher Formation (latest Cambrian Stage 4) in Løndal, North Greenland with two, three or four slightly to moderately upturned rays, but no central ray, to *Allonnia* Doré & Reid, 1965. Additional rare specimens occur in GGU sample 271718 (Miaolingian Series, Wuliuan Stage), about 15 m higher in the same section, although the radial rays in most of these have only slight inclination (Fig. 2C). Only a few sclerites are available in each assemblage so it is uncertain if all the sclerites derive from species (or a single species) of *Allonnia* or just represent rare sclerites within scleritomes of other chancelloriids, as noted by Bengtson & Collins (2015) and Moore *et al.* (2014).

A four-rayed broken specimen from GGU 271492 can be compared to *Allonnia tetrathallis* Jiang in Luo *et al.*, 1982 (Fig. 2B, C), although the rays lack the swollen bases seen in specimens illustrated by Moore *et al.* (2014). Four steeply inclined broken rays are present in a specimen from GGU sample 271718 (Fig. 2E–G). A broken and heavily encrusted specimen from the same sample has six strongly inclined rays

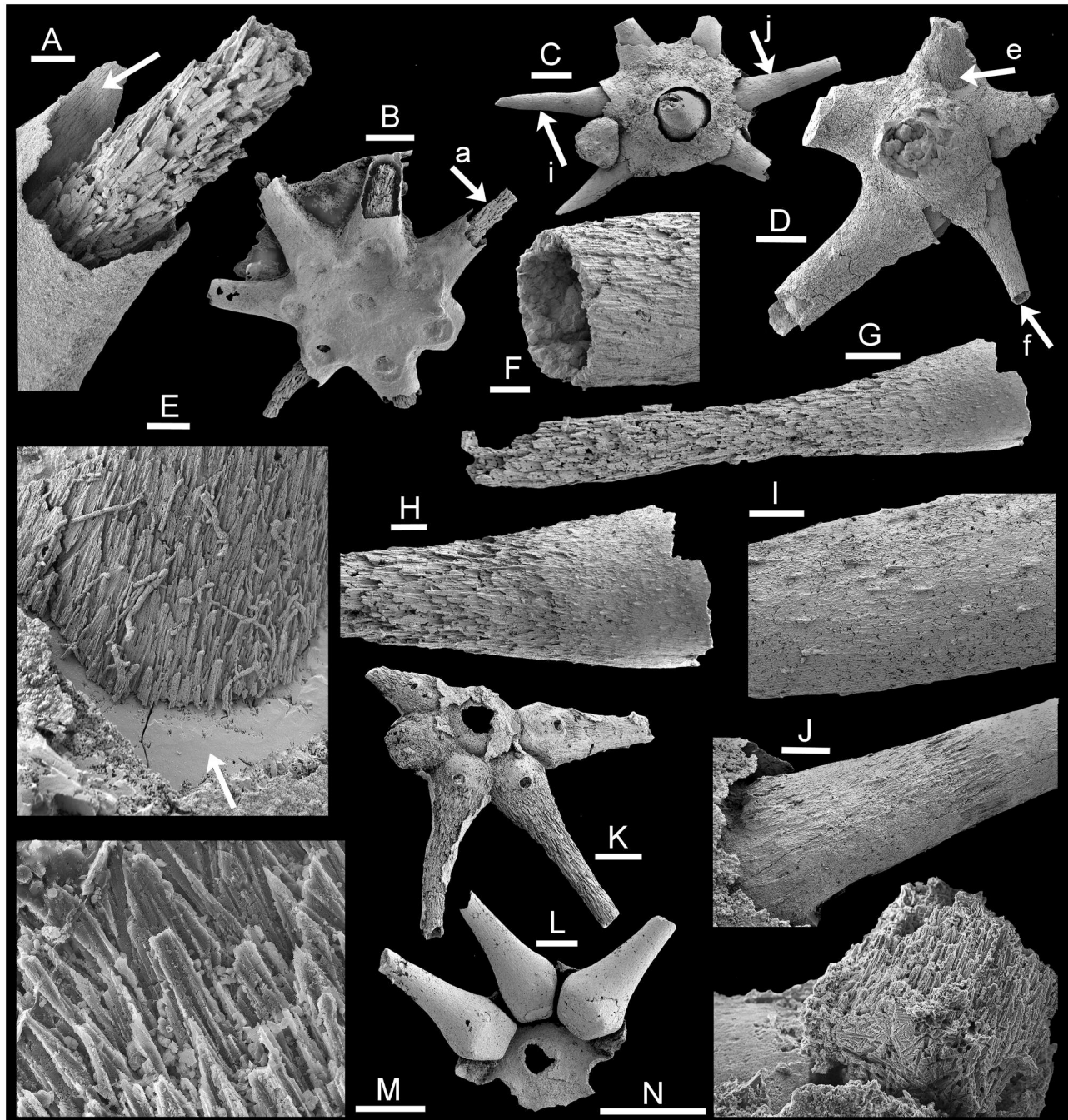


Fig. 1. Sclerites of *Chancelloria* sp. from the Henson Gletscher Formation (Cambrian, Miaolingian Series, Wuliuan Stage) of North Greenland. GGU sample 271718 unless stated. All specimens are broken, phosphatized sclerites and have been decalcified by preparation in weak acetic acid. **A, B**, PMU 21447 from GGU sample 271492. **B**, Basal view of sclerite showing phosphatized encrustation covering the foramina and large elongate crystals of the internal mould. **A**, Detail of broken ray (located by arrow **a** in **B**) shows outer layer of phosphatic encrustation with impression of fibrous texture of aragonitic outer shell (arrow; circumperipheral gap results from acid digestion) and coarsely crystalline core. **C, I, J**, PMU 21191, **C**, upper surface of internal mould partially encrusted by phosphate, with **I, J**, surface details of rays located by arrows in **C**. **D, E, F**, PMU 21192, **D**, upper surface of phosphatized internal mould with arrows locating **E** and **F**. **E**, Detail of infilled euendolith galleries on surface of coarsely crystalline internal mould with crystal of diagenetic quartz (arrow). **F**, termination of broken ray of internal mould showing blocky crystals within central void (dissolved diagenetic calcareous core). **G, H**, PMU 21193 from GGU sample 271492, phosphatized internal mould of broken ray, with detail (**H**). **K**, PMU 21444, basal view of coarsely crystalline rays with foramina. **L**, PMU 21194, upper surface of smooth internal moulds of three rays. **M**, PMU 21195, imbricated crystals. **N**, PMU 21195, irregular orientation of crystals at base of broken ray. Scale bars: 10 µm (**I**); 20 µm (**A, E, F, H**); 30 µm (**G, J**); 100 µm (**B, C, L, N**); 200 µm (**D, K**). (Images **M, N** by Michael J. Vendrasco).

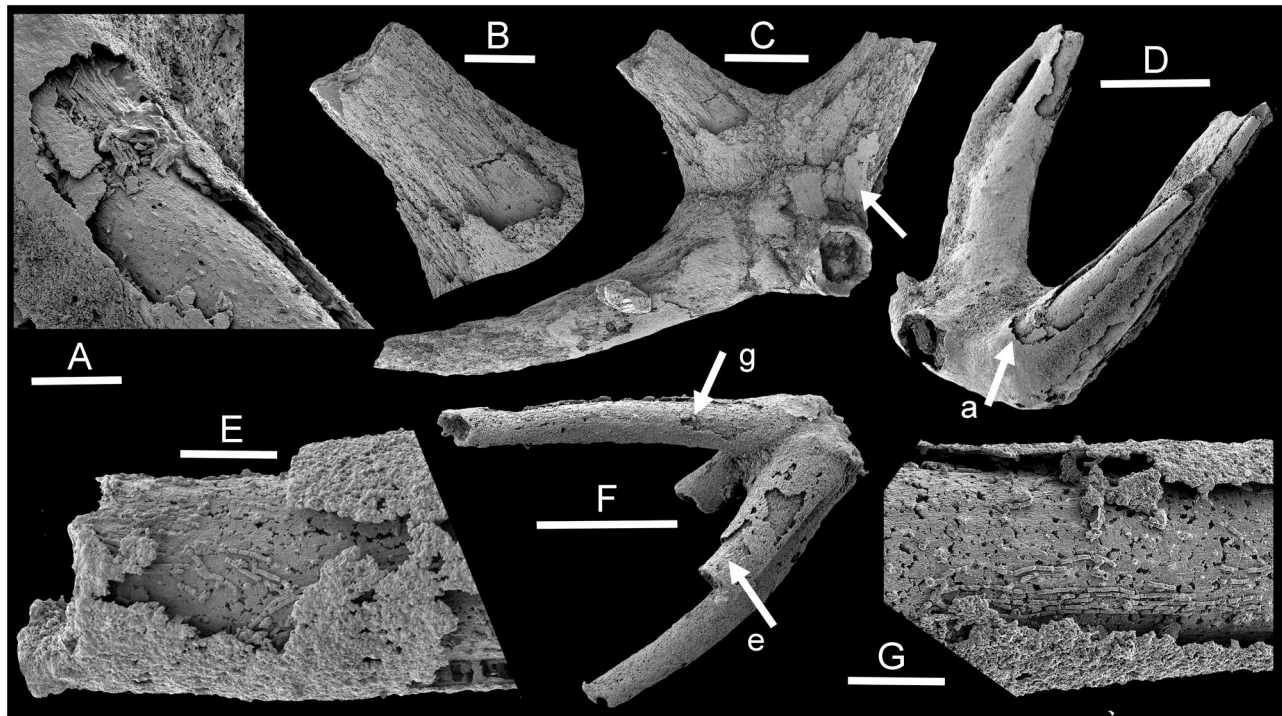


Fig. 2. Sclerites of *Allonnia*, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage, North Greenland. **A, D**, PMU 21196 from GGU sample 271492, encrusted internal mould of *Allonnia* sp. with detail of internal mould, fibrous shell (mainly dissolved) and encrusted layer. (A, located by arrow in D). **B, C**, PMU 21197 from GGU sample 271492, upper surface of exfoliated specimen showing fibrous shell (B) and patches of possible outer surface (C, arrow). **E–G**, PMU 21198 from GGU sample 271718, encrusted internal mould with detail of fibrous surface of internal mould and euendoliths (E, G, located by arrows in F). Scale bars: 30 μm (E, G); 50 μm (a); 100 μm (B); 200 μm (C, D, F).

arranged in three pairs, although one pair has been broken away (Fig. 2A, D); it is tentatively referred to *Allonnia*.

A single sclerite from GGU sample 271718 in which four slender and closely spaced rays rise perpendicular to the plane of the basal surface (Fig. 3A). The specimen compares closely to two specimens illustrated by Qian (1989, pl. 68, figs 1–4) from the Xinji Formation (Cambrian Series 2) of Henan Province, China. The sclerites in Qian's illustration are oriented with the basal surface uppermost, opposite to that seen here (Fig. 3A). The North Greenland specimen has an overall height of about 2 mm and a width of about 650 μm , while both of the Chinese specimens are about 1.1 mm in height, with the largest specimen attaining a basal width of about 500 μm . The four closely spaced rays are circular in cross-section and extend perpendicular to the basal surface. In basal view, the basal facets are equidimensional with a foramen varying in position from a central to almost marginal (Fig. 3A–D). In the Greenland specimen the rays narrow slightly from the basal facet but soon thereafter are initially of uniform width in lateral view before tapering slightly distally and curving inwards

(Fig. 3A). However, the tips are worn or broken and partially covered by mineralized sediment. The rays in the Xinji Formation specimens taper slightly throughout their length from their swollen base and meet distally.

In the North Greenland specimen, the rays are preserved as separate internal moulds with local preservation of patches of encrustation of the outer surface of the dissolved shell (Fig. 4B, with detail in Fig. 3E, G). The Xinji specimens also may be internal moulds, although the space between the rays is filled with matrix.

Qian (1989, p. 244) assigned the Xinji Formation specimens to an un-named species of *Archicladium* Qian & Xiao, 1984, originally described from the early Cambrian Yurtus Formation of Xinjiang, China, as a heteractinidan sponge (Qian & Xiao 1984), but this differs in having a prominent stub extending in the opposite direction from the group of parallel rays. This opposing ray is absent in the Xinji specimens where the basal facets carry a prominent foramen, as in the North Greenland specimen. Parkhaev & Demidenko (2010, p. 1116) listed the Xinji specimens as *Onychia quadrocornuformis* Ding & Li in Ding

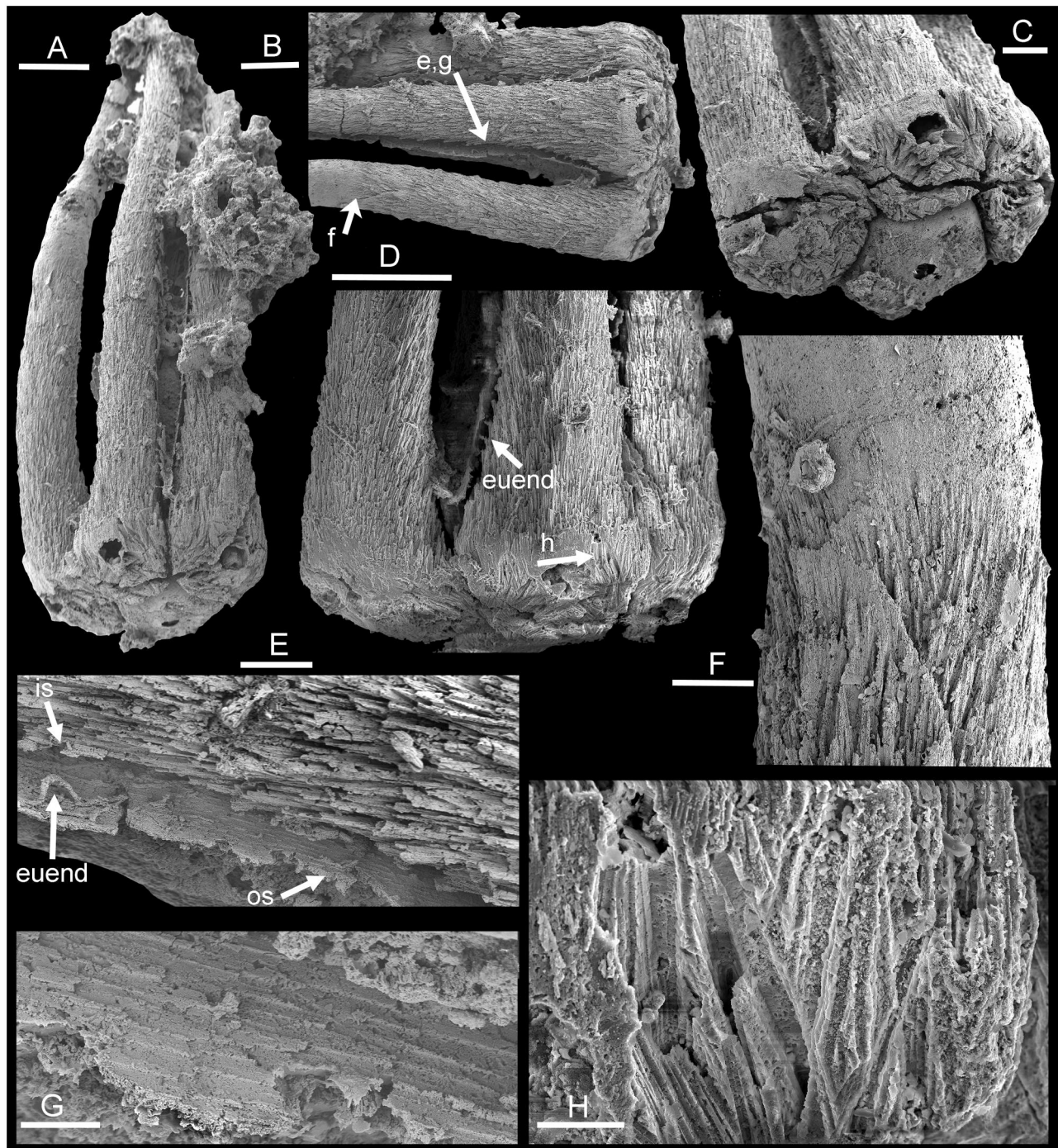


Fig. 3. Sclerite of *Allonnia quadrocornuformis* Ding & Li in Ding *et al.* 1992, PMU 21199 from GGU sample 271718, internal mould, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage, North Greenland. **A**, lateral view. **B**, lateral view showing location of E, F and G. **C**, oblique basal view showing crystals radiating from foramina (see also A and D). **D**, lateral view showing phosphatized infillings of euendoliths (arrow euend) crossing the cavity of the dissolved shell, and location of H. **E**, **G**, external mould of shell wall (located in B) with ridges; is, inner shell surface; os, outer shell surface; euend, infilled euendolith. **F**, detail of transition (located in B) from imbricating ridged lamellae to smooth tip of ray. **H**, detail of crystals (located in D). Scale bars: 10 µm (G); 20 µm (H); 50 µm (E, F); 100 µm (C); 200 µm (A, B, D). (Images D, H by Michael J. Vendrasco).

et al. 1992, which they re-combined to *Allonnia* Doré & Reid, 1965, and the North Greenland specimen is placed here. *Onychia* Jiang in Luo *et al.*, 1982 is a homonym of *Onychia* Lesueur, 1821 and several other

authors listed by Qian & Bengtson (1989) and Moore *et al.* (2014). *Chancelloria irregularis* (Qian, 1989) from the Zhujiqing Formation of Yunnan, China, as illustrated by Moore *et al.* (2014, fig. 7), is similar in

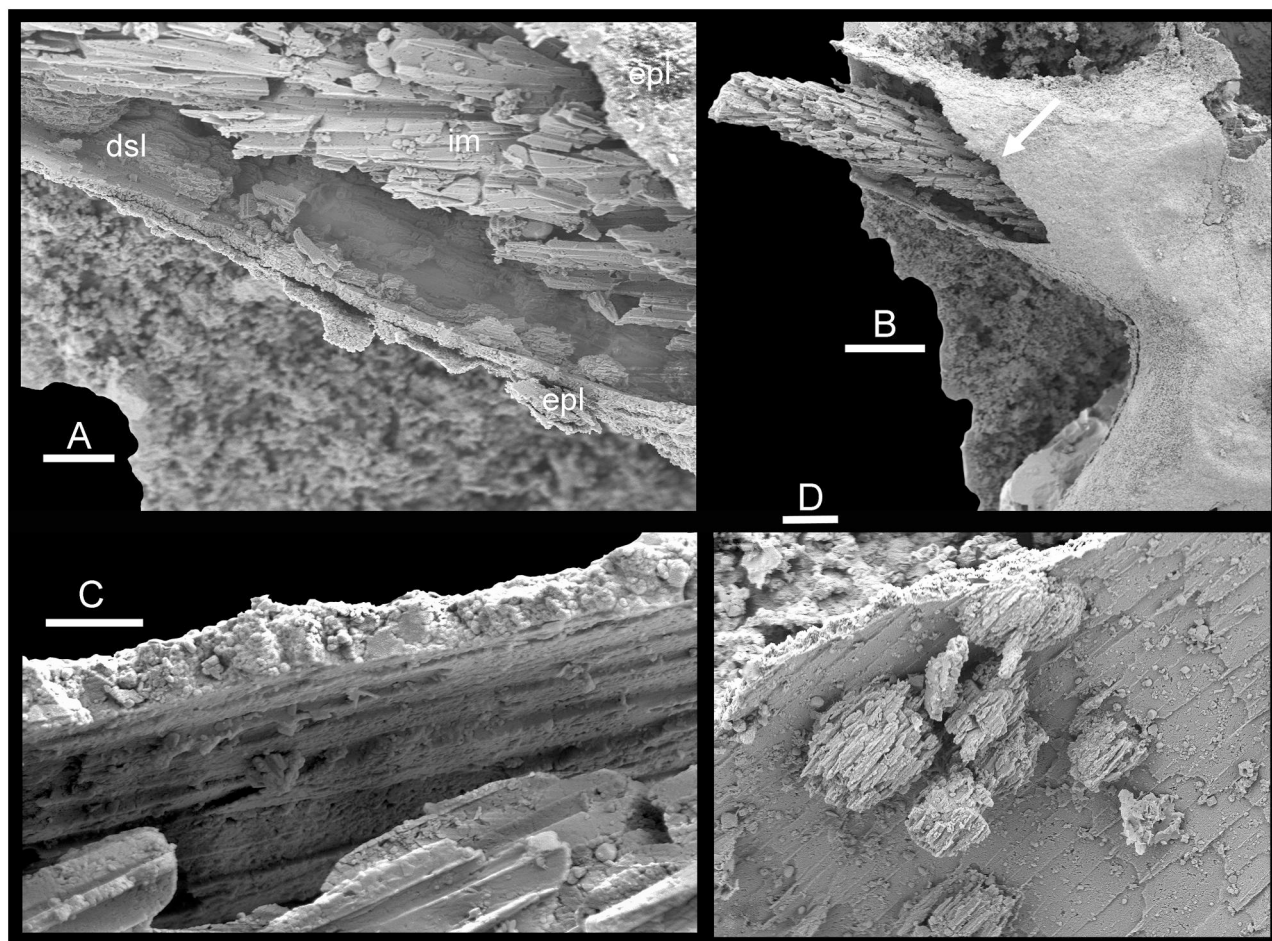


Fig. 4. Sclerite of *Chancelloria* sp. from the Henson Gletscher Formation (Cambrian, Miaolingian Series, Wuliuan Stage) of North Greenland, PMU 21447 from GGU sample 271492. Details of specimen illustrated in Fig. 1A, B, decalcified by preparation in weak acetic acid. **A**, detail of ray (located by arrow in B) showing coarsely crystalline internal mould (im), gap after the dissolved shell layer (dsl) and the encrusted outer phosphatized layer (epl). **B**, basal view of sclerite showing phosphatized encrustation covering the foramina, the coarsely crystalline internal mould and the circumperipheral gap representing the dissolved shell. **C**, cross-section of the encrusted outer phosphatized layer showing crystallites oriented perpendicular to the shell surface. **D**, impression of outer surface of the shell showing microstructure of imbricate laths and infilled galleries of euendoliths (see also Peel 2024). Scale bars: 3 μm (C); 5 μm (D); 10 μm (a); 50 μm (B).

possessing parallel lateral rays, but differs from *Allonnia quadricornuiformis* in also possessing a prominent central ray.

Chancelloriid shell structure

All specimens of *Chancelloria* and *Allonnia* described here have been affected by diagenesis, principally phosphatization, and by dissolution of calcium carbonate during preparation. Casts of euendolith borings are often preserved on internal moulds (Fig. 2E–G; Peel 2024).

Outer encrusted layer

The outer layer of chancelloriid sclerites in the present material from North Greenland often consists of

an encrustation of phosphorite (Figs 1B, 4B) in which elongate prismatic crystallites are oriented perpendicular to the surface (Fig. 4C). The layer is frequently broken away to reveal the underlying internal moulds of the rays, from which it is separated by a gap representing the dissolved calcareous shell (Figs 1A, B, D, 4B). The encrusted layer may be of relatively uniform thickness on the distal parts of the rays, with a relatively smooth outer surface and a thickness of about 3 μm (Figs 1A, B, 4C), but most commonly it is thicker with an uneven outer surface, particularly around the junction between the rays (Figs 1C, D, 2D). The inner surface retains an impression of the underlying, but now dissolved shell. It is often smooth but may show a structure of fine fibres, horizontal needles or laths reflecting the upper surface of the shell layer (Figs 3E, G, 4C, D). The encrusted

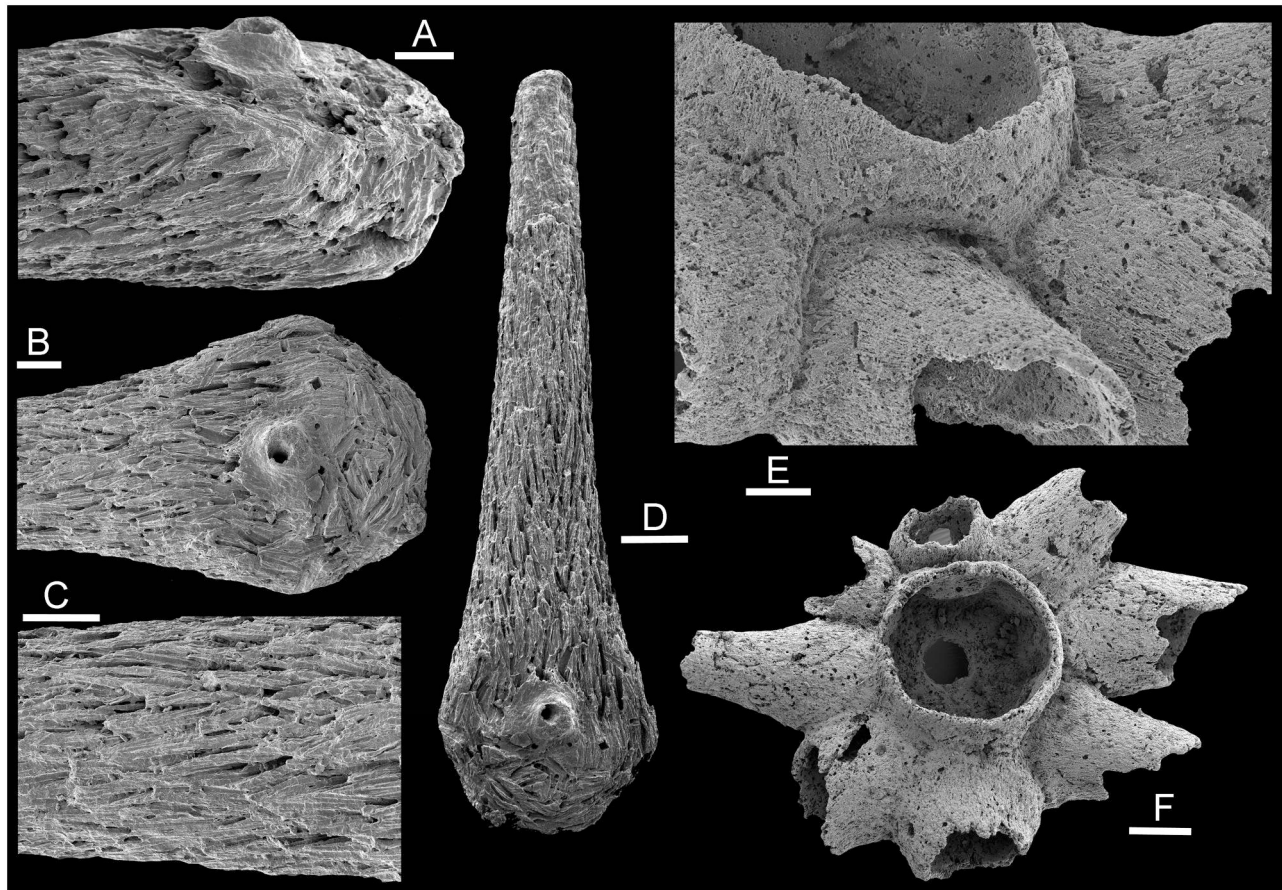


Fig. 5. *Chancelloria* sp. from Siberia. A–D, SMNH X3416, from sample 6/66.2, calcium phosphatic internal mould of a distal ray with imprints of diagenetic large elongate crystals from the inner surface of the now dissolved sclerite wall, Emyaksin Formation, Cambrian Stage 3, Atdabanian Regional Stage, Northern Siberia (Kouchinsky 2000, fig. 1; Kouchinsky *et al.* 2015, fig. 34A). E, F, SMNH X11100, from sample 19/12.75, phosphatized articulated sclerite with broken off rays, showing original microstructural fibres of the wall replicated by calcium phosphate, detail in F. Erkeket Formation, Cambrian Stage 4, Botoman Regional Stage, Northern Siberia (Kouchinsky *et al.* 2022, fig. 36S). Scale bars: 50 μ m (A–C, E); 100 μ m (D, F).

layer often covers the sutures between individual rays (Fig. 1B), although Bengtson & Hou (2001) noted that these may be obscured also in specimens even without encrustation. It often extends across the foramina on the sclerite base (Figs 1B, 4B) and the broken ends of individual rays (Fig. 2E), demonstrating its diagenetic origin.

While the encrustation is clearly diagenetic, it should not be assumed that the layer represents just a single diagenetic event. A specimen from GGU sample 271492 preserves a very thin, irregular phosphatized layer that is separated from the previously discussed encrusted layer by a gap suggestive of dissolved calcareous material (Fig. 4A, B).

Shell layer and internal mould

Encrustation of the outer surface is lacking in a phosphatized specimen of *Allonnia* from GGU sample

271492 from the Henson Gletscher Formation in North Greenland (Fig. 2B, C) and a Siberian specimen of *Chancelloria* from the Erkeket Formation with the result that sutures are visible in the broken specimen (Figs 2C, 5F). A fine fibrous texture is preserved in the shell outer layer (Figs 2B, 5E), also seen in a *Chancelloria* specimen from GGU sample 271718 (Fig. 1N). The fibres are parallel to the length of the individual rays but usually show a more irregular, radiating pattern on the base of the rays around the foramen (Fig. 1N). The calcareous shell of most chancelloriid sclerites in the North Greenland material is usually represented by a circumperipheral gap between the outer encrusted layer and the underlying phosphatized interior as a result of dissolution of calcium carbonate during sample preparation (Figs 1A, B, 2E–G). Occasionally, the gap contains diagenetic blocky quartz overlying acicular crystals of the internal mould (Fig. 1E, arrow). In this specimen, the

innermost part of the spar layer was penetrated by euendolith galleries, as indicated by the phosphatized infilling of these galleries that lie irregularly across the acicular structure of the underlying internal mould.

In the North Greenland material, the lower surface of the overlying encrusting layer may preserve fine ridges and grooves (Figs 1A, 2E, F) or imbricated laths (Fig. 4D) as an impression of the texture of the outer surface of the sclerite. In *Allonnia quadrocornuformis* (Fig. 3), coarse ridges about 3 µm apart and intervening fine ridges are elongated parallel to the length of the rays (Fig. 3E, G). They lie on thin, irregular, imbricated lamellae (distance between successive crests about 10–20 µm), the edges of which step down towards the base of the ray (Fig. 3E, G). The ridges reflect grooves between fibres on the surface of the counterpart sclerite exterior, which lie on imbricate lamellae that step down towards the apex of each ray. The slope of the surfaces of the lamellae on the shell outer surface thus corresponds to the slope of the axes of the large, elongate crystals forming the interior of the sclerite (Fig. 3D) that in this specimen directly underlie the shell layer (Fig. 3E, arrow is).

A schematic section through a halkieriid sclerite by Porter (2008, text-fig. 1) shows projecting acicular fibres on the inner surface of the sclerite wall. These fibres within the shell wall are imbricated such that they step down towards the basal surface on the inner surface of the shell but towards the apex on the outer surface.

Internal moulds of *Chancelloria* sclerites or disarticulated rays in acetic acid residues from Cambrian Series 2 – Miaolingian Series are often smooth, without texture, and preserved in glauconite or phosphorite. The current material from the Henson Gletscher Formation (Wuliuan Stage) preserves a variety of surface textures. The surface of smooth internal moulds frequently preserves fine surface texture (Fig. 1C, I, J), typically fine, discontinuous ridges that lie parallel to the length of the ray and form a fibrous texture. However, this background pattern on the internal mould may be broken by short segments of projecting coarser spines or rods, about 0.05 µm in thickness, that vary in length from about 2–10 µm and lie at a low angle to the fibres (Fig. 1I). A similar feature, but composed of bunches of fine acicular crystals, was illustrated by Moore *et al.* (2019, fig. 19D) on an internal mould of *Archiasterella* sp. from the Pioche Formation. Yun *et al.* (2021a) illustrated the same texture on pyritized sclerites of *Allonnia* from the Guojiaba Formation of Shaanxi Province, China. These coarse segments of spines are parallel to the

background fibres but they are inclined such that only their tips emerge from the fibrous surface of the internal mould, forming a knobby pattern (Fig. 1C, I).

The spines on the internal mould correspond to depressions in the under surface of the shell layer, likely formed by hollows between the overlapping acicular fibres or by dissolution of projecting aragonite crystals, but before diagenetic infilling by phosphatization.

Internal moulds of other rays in the same sclerite (Fig. 1C, J) clearly demonstrate the occurrence of the projecting coarser ribs, which are inclined inwards towards the base of the ray in thin lamellae that overlie more distal parts of the ray surface.

Other sclerites show the degradation of the initial smooth surface as the coarse ribs emerge as ribbed lamellae that form a distinct imbrication, stepping down towards the apex of the rays (Fig. 1G, H). Ultimately, the lamellae become less uniform as the spinose elements develop distally into coarse, separate, ridged, imbricated megacrystals or crystal laths. In some specimens only the megacrystals are preserved, showing an irregular pattern around the foramen at the base of the rays similar to that seen in the fibres of the shell layer (Fig. 1N), before becoming parallel to the ray along its length (Figs 3A, C, 5A–D). In general, the surface texture of the internal mould of the ray is transformed from a compact surface with fine striations and the protruberant tips of coarser ribs (right in Fig. 1G, H) to a coarsely crystalline, imbricated, pattern of separated, spinose, ridged laths and laminae (left in Fig. 1G, H) with passage towards the tip of the ray.

The differences in the texture of the outer surface of the internal mould have become visible through the dissolution of calcium carbonate during preparation, although some of this likely represents a late diagenetic carbonate infill between the diagenetically formed large elongate crystals. The location of euendolith galleries and infillings around the interface between shell and internal mould suggests a pause in diagenetic history now coincident with the phosphatization front (Figs 1E, 2E, G). Euendolith galleries penetrating the outer surface of the shell layer (Fig. 4D) may have formed at a different time.

Growth of most of the large elongate crystals probably represents diagenetic growth into the developing void between degrading endocuticle and the sclerite shell (exocuticle) since crystals in the latter (now a gap) and the underlying large elongate crystals share a common orientation, with each crystal lamella being

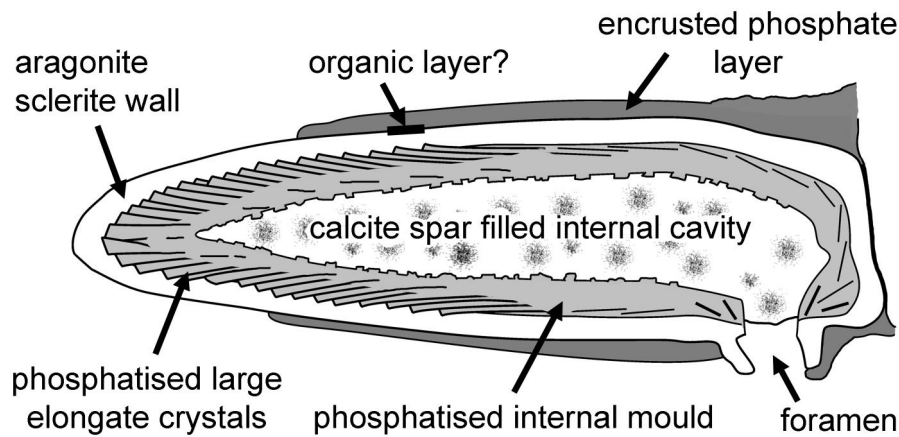


Fig. 6. Schematic section through a ray of *Chancelloria*. In most currently described material, the aragonite sclerite wall and the calcite spar filled internal cavity have been dissolved during sample preservation.

formed underneath the preceding one, in the direction from the basal foramen towards the apex of the ray. Spherulitic crystal growth from the inner shell walls into the central cavity is not present.

The zone of phosphatized, large elongate crystals may fill the internal cavity of the rays distally (Fig. 1A) but generally it surrounds a hollow core resulting from dissolution of calcareous material likely representing the latest diagenetic infill (Figs 1D, F, 6). Its inner surface is covered with equidimensional phosphate crystals (diameter 3–5 μm) quite unlike the elongate crystals forming the overlying laths and lamellae (Fig. 1F).

Discussion

Moore *et al.* (2019) and Yun *et al.* (2021b) described chancelloriid sclerites in which the outer layer was characterized by wrinkles and fine tubercles. Yun *et al.* (2021b) interpreted this as a non-biomineralized layer that was continuous with the outer surface of the integument occurring between sclerites in the scleritome and served as a template for mineralization of the aragonitic sclerite, following Kocot *et al.* (2016) and Gilbert *et al.* (2019). The studies of crystal nanostructure by the later authors potentially enable discrimination between biologically controlled mineralization and diagenetic crystal growth, but such a layer is not certainly recognized beneath the outer, diagenetic encrustation in the present material. Where visible, the lower surface of the encrustation usually reflects the lath-like, ridged or fibrous structure of the shell layer (Figs 3E, G, 4D). The upper surface of small patches of smooth phosphatized shell carry a finely papillate texture, lying above the fibrous shell in a specimen of *Allonnia* (Fig. 2C, arrow), that could

reflect an original outer organic layer or just a smooth surface to the sclerite shell.

Fine papillation has been observed on some *Chancelloria* specimens (Figs 1B, 4B) but even in this illustrated specimen the diagenetic origin of this layer is demonstrated by it covering the basal foramina. In general, the outer surface has a hackly or crudely spherulitic appearance reflecting the terminations of the diagenetic crystallites (Figs 1C, 2E, G).

If present, an outer non-biomineralized layer may have degraded rapidly prior to the diagenetic encrustation by phosphatic material, as demonstrated by the general absence of periostraca in Palaeozoic fossil molluscs. In a recent study of Cambrian helcionelloids and rostroconchs from North Greenland and Australia, Oh *et al.* (2024) described preferential preservation of structures associated with an organic periostracum, summarizing previous observations by Gubanov *et al.* (2004), Vendrasco *et al.* (2011) and Peel (2021b).

Yun *et al.* (2021b) agreed with Bengtson & Hou (2001) and Bengtson (2005) that the chancelloriid sclerites were likely mineralized from the cuticle (endocuticle) that filled the interior cavity of the sclerites. This is suggested by the continued similarity in orientation and stacking of the early diagenetic imbricated large, elongate crystals to that seen in the much finer fibrous growth of the original shell. Additionally, the integration of the sclerites into the epithelium is strengthened by the description of the central ray canal system within sclerites by Bengtson & Hou (2001) and Bengtson (2005), based on non-mineralized chancelloriid specimens from the Mount Cap Formation (Mialongian Series) of Canada originally described by Butterfield & Nicholas (1996).

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Samples from North Greenland were collected during the North Greenland Project (1978–1980), a regional mapping programme of Grønlands Geologiske Undersøgelse (GGU, Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark. Michael J. Vendrasco kindly made available his SEM images of specimens from GGU sample 271718. Comments from Anette Högström are gratefully acknowledged.

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