



# Sclerite ray canals in the Cambrian coeloscleritophoran *Chancelloria* from North Greenland (Laurentia)

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## Abstract

A sclerite of *Chancelloria* from the Henson Gletscher Formation (Cambrian Stage 4) of North Greenland preserves phosphatised central ray canals within the sclerite rays, confirming the extension of epithelial tissue into the sclerite interior. The canals fill the basal foramina and extend as thin central tubes within the lumen towards the apex of the individual rays, developing longitudinal ridges distally. In general terms they resemble the robust central canal of *Sinosachites* (= *Thambetolepis*), although the leaf-like sclerites of this halkieriid develop an extensive pattern of lateral canals and tubules not seen in the conical rays of *Chancelloria*. This internal similarity between chancelloriid and halkieriid calcareous sclerites adds support to the notion that coeloscleritophores are a paraphyletic group in which parallel episodes of calcareous mineralisation of pre-bilaterian and bilaterian coeloscleritophoran stocks took place in the early Cambrian from a sclerotised but non-mineralised, chancelloriid-like, eumetazoan ancestor.

**Keywords** *Chancelloria* · Coelosclerite · Internal ray canals · Coeloscleritophoran · Cambrian stage 4 · North Greenland

## Introduction

Disarticulated, hollow, calcareous sclerites of chancelloriids are widely distributed and often abundant in the early–middle Cambrian (Fig. 1). Their phosphatised replicas or internal moulds of the internal cavity (lumen) occur frequently in residues from limestones that have been treated with weak acetic acid to recover assemblages of Small Shelly Fossils (Bengtson et al., 1990; Moore et al., 2010, 2014, 2019; Yun et al., 2021; Kouchinsky et al., 2011, 2022). In contrast, flattened, complete bag-like bodies of sessile chancelloriids, in which the outer organic integument is studded with aragonite sclerites (Bengtson & Collins, 2015; Yun et al., 2021), are mainly restricted to shales in early–middle Cambrian Lagerstätten such as the Burgess Shale and Chengjiang (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, 2021; Zhao

et al., 2018; Peng et al., 2023). With the exception of an upper opening (osculum), internal organs or other anatomical features have not been described.

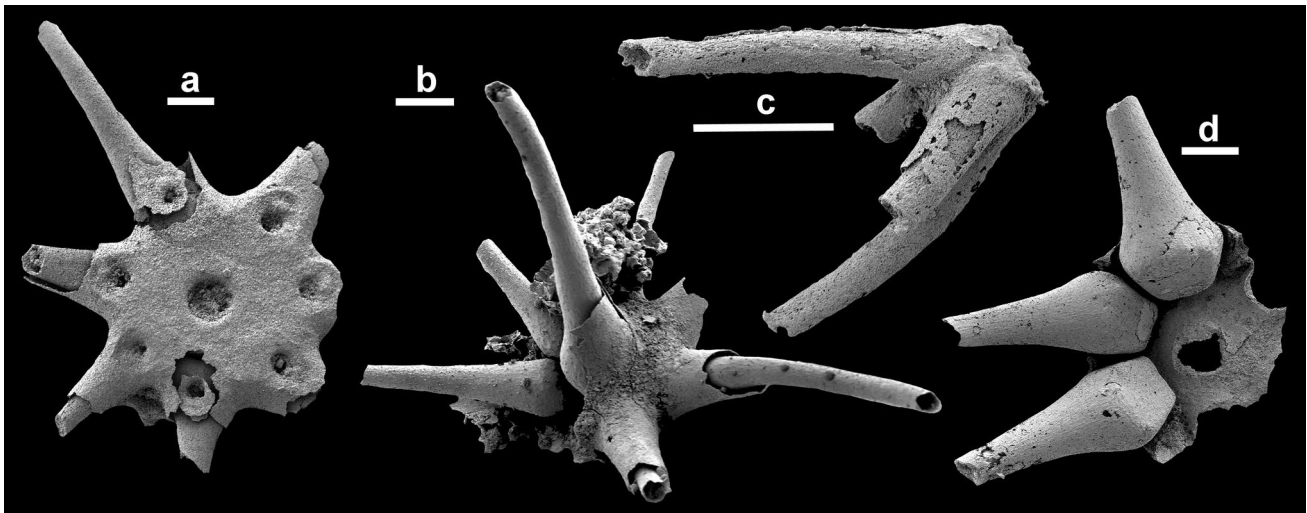
Most chancelloriid sclerites display a stellate form with up to eleven lateral rays arranged radially about a central ray, as in *Chancelloria* Walcott, 1920 (Fig. 1b), but others, often referred to *Allonnia* Doré & Reid, 1965, lack a central ray and develop 2–5 inclined lateral rays (Fig. 1c). A variety of taxa has been described at the level of genus and species for sclerite morphologies with different numbers (one or more) and combinations of rays (summarised by Moore et al., 2010, 2014, 2019).

All chancelloriid rays are hollow within the aragonitic sclerite wall and consequently were termed coelosclerites by Bengtson and Collins (2015) on account of their inner cavity (lumen). They possess a basal foramen (Fig. 1a) for the passage of soft tissues connecting the internal cavity of the individual rays with the main body mass (Bengtson & Hou, 2001; Bengtson, 2005; Yun et al., 2021), but individual rays within the sclerite do not connect with each other (Fig. 1d). Complete chancelloriid specimens (scleritomes) are usually dominated by a single sclerite morphotype, although small numbers of other morphotypes may be present (Bengtson & Collins, 2015). However, analysis of large assemblages

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**Fig. 1** Morphology and preservation of phosphatised cancelloriid sclerites, GGU sample 271718, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage, Løndal, Peary Land, North Greenland. In all specimens, the gap between the outer surface and the internal moulds of the individual rays represents calcareous sclerite wall dissolved during preparation in weak acetic acid. **a** *Chan-*

*celloria* sp., PMU 19137, basal view showing foramina of central ray and seven broken lateral rays; **b** *Chancelloria* sp., PMU 21442, oblique view of upper surface with central ray and six lateral rays; **c** *Allonnia* sp., PMU 19138, oblique lateral view with four steeply inclined lateral rays; **d** *Chancelloria* sp., PMU 21442, internal moulds of three rays. Scale bars 100 µm (**a**, **b**, **d**), 200 µm (**c**)

of disarticulated sclerites may provide a foundation for the recognition of biological species (Moore et al., 2019).

The phylogenetic position of cancelloriids is problematic (Bengtson & Missarzhevsky, 1981; Bengtson & Hou, 2001; Janussen et al., 2002; Bengtson, 2005; Moore et al., 2014; Bengtson & Collins, 2015; Botting & Muir, 2018; Cong et al., 2018). Traditionally, they have been interpreted as problematic fossils (Rosén, 1919) or sponges (Walcott, 1920) but Goryansky (1973) pointed out that the sclerites were external rather than internal as in sponges. Bengtson & Missarzhevsky (1981) proposed Coeloscleritophora to unite cancelloriids with other Cambrian fossils, such as the halkieriids, which show a similar method of formation of the hollow sclerites (Bengtson & Hou, 2001; Bengtson, 2005; Porter, 2008; Bengtson & Collins, 2015). However, the dissimilarity in body plan between the sessile, bag-like cancelloriids and the motile halkieriids argues against a close relationship. Other authors have presented strong arguments favouring assignment of cancelloriids to the sponges, close to the ascosponges (Botting & Butterfield, 2005; Botting & Muir, 2018; Cong et al., 2018), but consensus has not been achieved. Cong (2023) noted that cancelloriids can be regarded as sponge-grade animals while displaying an epitheliozoan-grade integument derived from the epidermis.

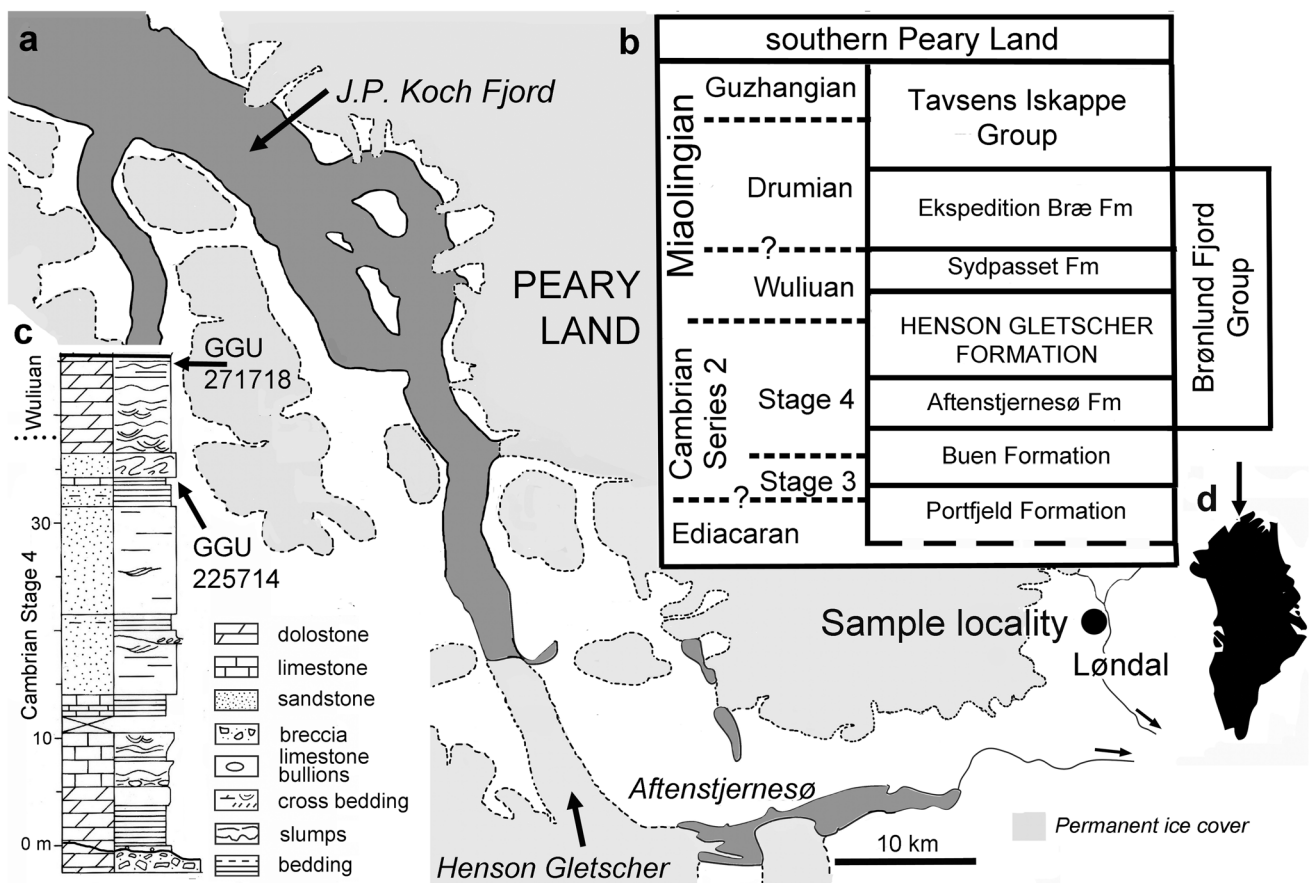
Shell structure indicates that cancelloriid sclerites were composed of aragonite (Bengtson et al., 1990; Kouchinsky, 2000; Bengtson & Hou, 2001; Bengtson, 2005; Porter, 2008; Moore et al., 2014, 2019; Bengtson & Collins, 2015; Yun et al., 2021, 2023), see also Peel & Kouchinsky (2024). Yun et al. (2021) discussed models for sclerite structure

and formation and agreed with Bengtson and Hou (2001), Bengtson (2005) and Bengtson & Collins (2015) that the calcified sclerite formed within a cuticular layer secreted by an epidermal epithelium that entered the central cavity (lumen) through the basal foramen. The present description of phosphatised internal canals with the lumina of a *Chancelloria* sclerite from North Greenland (Cambrian series 2, stage 4) supports this model.

## Materials and methods

PMU prefix indicates a specimen deposited in the palaeontological collections of the Museum of Evolution, Uppsala University, Uppsala, Sweden. GGU prefix indicates a sample collected by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark.

GGU sample 225714 was collected by J.S.P. on 15 July 1979 from the Henson Gletscher Formation (Cambrian Series 2, uppermost Stage 4, *Ovatoryctocara granulata* Assemblage) in Løndal (82°17.5'N, 37°03'W; Fig. 2a). The sample was collected about 12 m stratigraphically below the top of the formation (thickness 45 m) from a unit consisting of about 1 m of dark carbonates (Fig. 2c). This unit occurs just below the top of the prominent sandstone member that occurs in the middle of the formation and makes up about half of its total thickness (Higgins et al., 1991; Ineson & Peel, 1997). The diverse fauna of this interval was described



**Fig. 2** Derivation of samples. **a** Peary Land region, North Greenland, showing locality for GGU samples; **b** Cambrian stratigraphic nomenclature in southern Peary Land; **c** stratigraphic section through

the Henson Gletscher Formation showing location of GGU samples 225714 and 271718; **d** location of study area in Greenland (arrow)

by Blaker & Peel (1997), Geyer & Peel (2011) and Peel et al. (2016).

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 (Miaolingian Series, Wuliuan Stage) on the west side of Løndal, just to the north of GGU sample 225714 (82°18'N, 37°00'W; Fig. 2c). Other elements of this richly fossiliferous assemblage were described by Clausen & Peel (2012), Peel & Kouchinsky (2022, 2024) and Peel (2023).

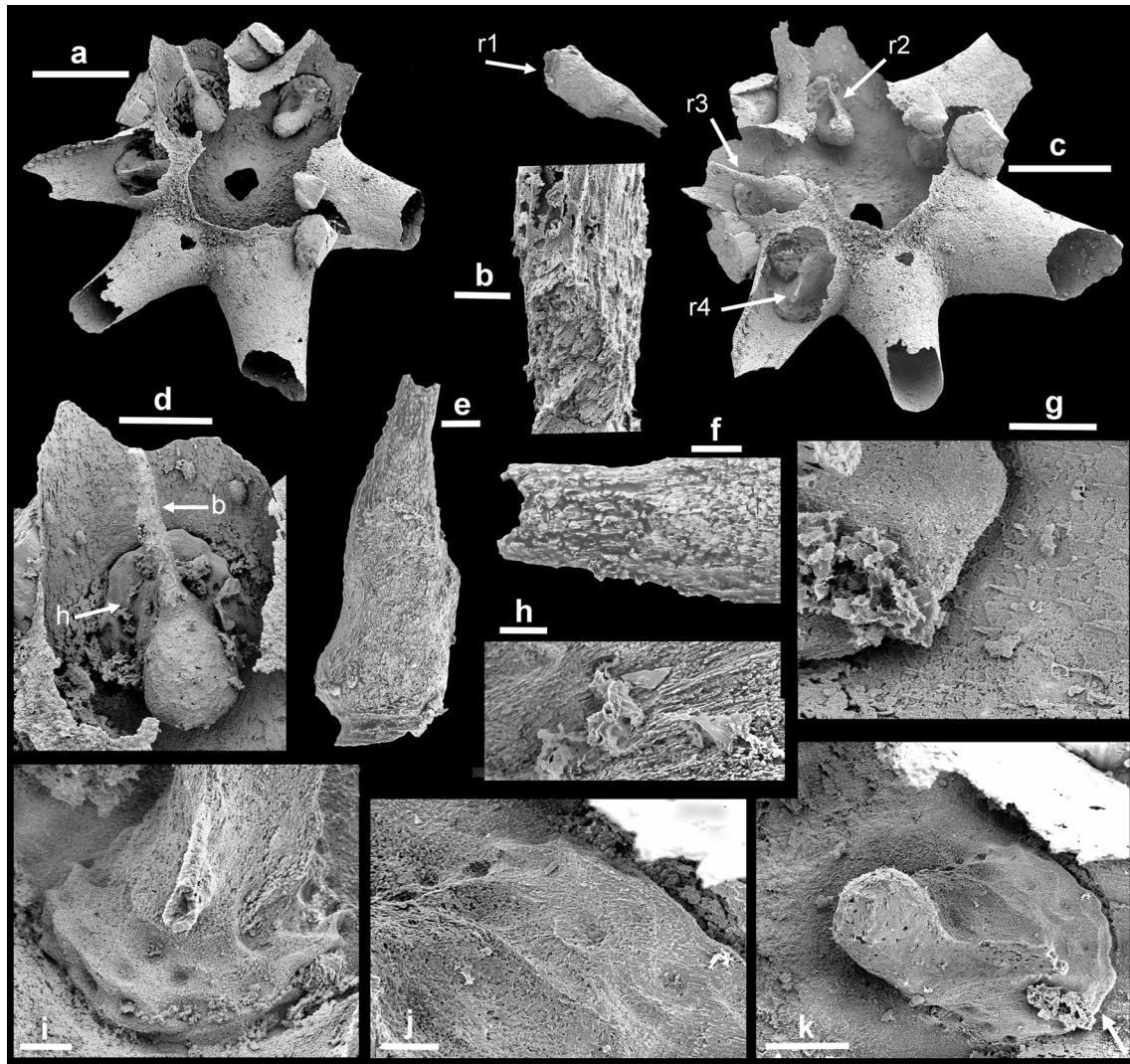
Selected specimens were gold-coated prior to scanning electron microscopy (SEM), using a Zeiss Supra 35VP scanning electron microscope operating at 5 kv; images were assembled using Adobe Photoshop CS4.

### Central ray canals

The specimen of *Chancelloria* from GGU sample 225714 establishes the extension of epithelial tissue into the internal cavity of the rays initially proposed by Bengtson & Hou (2001). Well-developed internal moulds of phosphatised

central ray canals extend from the basal foramina through the lumina towards the tip of each ray (Figs. 3 and 4c and d). The canals lie centrally within the lumina and therefore would be located axially within the internal moulds of the entire lumina that are one of the most common preservational forms of chancelloriids (Fig. 1d). However, phosphatisation within the lumina is often restricted just to the inner surface of the sclerite wall, such that a broad cavity is left within the internal mould of each ray after specimens have been treated with acetic acid, removing calcium carbonate (Fig. 1b). This cavity is purely a diagenetic phenomenon and not equivalent to the phosphatised central ray canal described herein (Fig. 3a, c, d). Peel & Kouchinsky (2024) described diagenetic phosphatisation on the inner surface of the sclerite wall within the lumina of chancelloriids from the lower Cambrian of Siberia and the middle Cambrian (Miaolingian Series, Wuliuan Stage) of North Greenland, but this material retained no trace of the central ray canals described herein.

The described sclerite (Figs. 3 and 4) consists of a thin, broken, outer wall, which may be interpreted as the



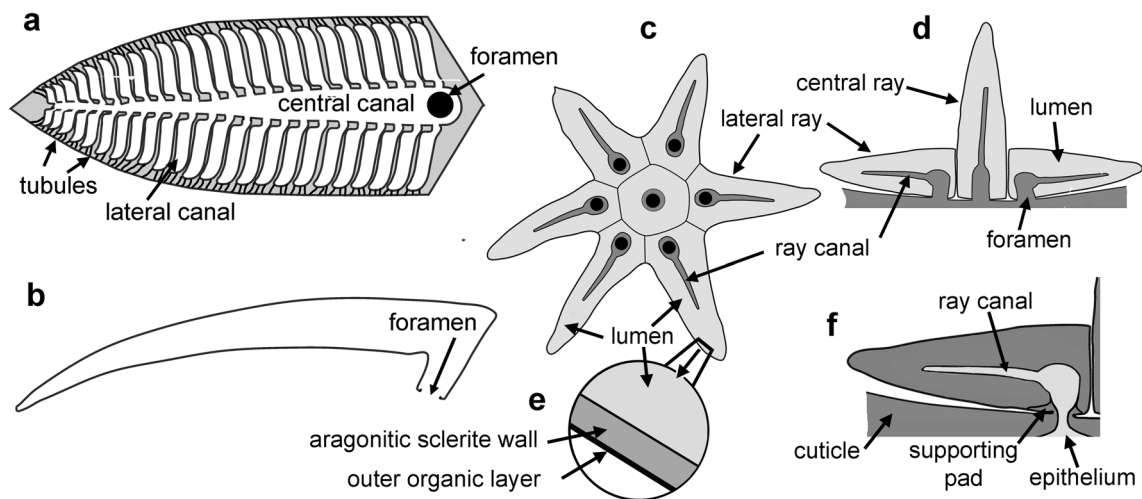
**Fig. 3** *Chancelloria* sp., phosphatised outer surface and internal moulds of axial canals (central ray canals) within the rays of the dissolved sclerite. PMU 28790 from GGU sample 225714, Henson Gletscher Formation, Cambrian Stage 4, Løndal, Peary Land, North Greenland. **a, c** Upper surface with central ray broken away and six broken lateral rays; r1–r4, internal moulds of the central ray canals with the mould of the central ray canal (r1) displaced from the sclerite (**c**); **b, d, h** internal mould of central ray canal r3 (**d**) with longi-

tudinally ridged distal termination (**b**, located in **d** by arrow **b**) and fibrous texture of supporting pad (**h**, located in **d** by arrow **h**); **e, f** internal mould of central ray canal r1 with longitudinally ridged tip (**f**); **g, j, k** internal mould of central ray canal r2 with detail of shell microstructure (**g**, located by arrow in **k**) and supporting pad (**j**); **i** central ray canal r4 showing depressions and ridges in the supporting pad. Scale bars 5  $\mu\text{m}$  (**b, h**); 10  $\mu\text{m}$  (**f, g, i, j**); 20  $\mu\text{m}$  (**e**); 30  $\mu\text{m}$  (**k**); 40  $\mu\text{m}$  (**d**); and 100  $\mu\text{m}$  (**a, c**)

phosphatised outer surface of the sclerite or a calcium phosphate encrustation of that surface. All diagenetic calcareous material that filled the originally hollow sclerite has been dissolved during preparation. Patches of the outer surface of the sclerite wall, as preserved, display a faint meandering pattern of short ribs and wrinkles similar to that illustrated by Moore et al. (2019, fig. 18A–D), which they interpreted as the outermost surface of the sclerite. Yun et al. (2021) recently reviewed the function of the organic outermost layer of the sclerite (Fig. 4e) that is not observed in the present material. The distal parts of the six radiating lateral

rays have been broken away. The central ray is completely absent but the presence of the open foramen placed centrally on the basal surface of the sclerite confirms its presence (Fig. 3a, c).

Phosphatised internal moulds of central ray canals are preserved in four rays (Fig. 3c, r1–r4) but the internal mould from the central ray (r1) became detached during the mounting of the specimen on the SEM stub and it is now located to the side the sclerite (Fig. 3c, r1). This detached internal mould is slightly curved in lateral view (Fig. 3e) with a broken tip. A flattened lateral facet on the concave side suggests



**Fig. 4** Canal structure in *Sinosachites* and *Chancelloria*. **a** Schematic drawing of the internal mould of the lower surface of a sclerite of *Sinosachites* and longitudinal section (**b**), redrawn from Vinther (2009); **c–e** schematic drawings of the *Chancelloria* sclerite showing

relationship of central ray canals to the underlying foramina, which are shown as black circles in (**c**), with detail of sclerite wall (**e**); **f** schematic longitudinal reconstruction of lateral ray in *Chancelloria*

that the central ray was also slightly curved. The jagged broken basal margin of the internal mould corresponds to the central hole in the basal surface of the sclerite (Fig. 3a). A constriction just above the base of the internal mould was formed by the shell margin of the foramen, after which the mould increases in width as the canal enters the internal cavity (lumen) of the sclerite. The subcylindrical lower part of the internal mould narrows distally to a tube, the diameter of which is about one third of the basal diameter of the mould. It is broken distally, and its tubular form indicates a calcareous core that dissolved during specimen preparation.

Near its base, the outer surface of the internal mould consists of grains and fine fibres, possibly originally acicular aragonite crystals that are phosphatised; they are oriented crudely parallel to the length of the mould. Medially, the fibres become transverse, but this may reflect incomplete phosphatisation of the internal mould. Distally, the fibres increase in size and form a fabric of longitudinal ridges (Fig. 3b, f). The ridges may reflect wrinkling due to compaction of the canal wall. However, morphologically similar longitudinal ridges on the phosphatised siphuncle of Permian ammonoids described by Tanabe et al. (2000) were interpreted as epithelial folds, suggesting that the ridges in *Chancelloria* reflect the internal structure of the canal wall.

Phosphatised internal moulds r2–r4 are placed medially within lateral rays, with the corresponding area in the three remaining rays obscured by preserved sclerite wall (Fig. 3a, c). In contrast to the central ray, which rises vertically from the foramen, the internal moulds of the lateral rays extend along the length of the rays, perpendicular to the plane of the foramen (Fig. 3a, c, d). Each ray canal consists of a basal oval structure about 6  $\mu\text{m}$  long that extends as a

slightly tapering rod, broken at its tip, along the centre of the ray towards its apex. The rod is circular with a diameter of about 10  $\mu\text{m}$  in the best preserved example (ray r3 in Fig. 3c, shown in detail in Fig. 3d) and no doubt forms the internal mould of a tubular canal. Longitudinal ridges on its surface near the broken extremity are about 1  $\mu\text{m}$  wide and 3  $\mu\text{m}$  apart, with an inner, obliquely transverse, fibrous structure likely representing infill (Fig. 3b). The rod is laterally compressed in the two other preserved ray canals, appearing hollow due to the dissolution of diagenetic carbonate (r2 and r4 in Fig. 3c, shown in detail in Fig. 3i, k, respectively).

The basal oval structures are located over the foramen in each ray (Figs. 3c, d and 4c, d). Each lies on a phosphatised mass (supporting pad) that supports the basal part of the ray in the specimen, as currently preserved (Fig. 3c), covering and extending beyond the margins of the underlying foramen (Fig. 3d). A slight gap between the base of this mass and the inner surface of the phosphatised encrustation of the sclerite wall indicates the thickness of the now dissolved calcareous wall (Fig. 3g, k). The inner surface of the phosphatised sclerite wall displays pointed crystal laths (width about 1  $\mu\text{m}$ ) that are elongated along the length of the ray (Fig. 3g). The supporting pad forming the base of each lateral ray canal internal mould displays an irregular dimpled structure of depressions about 10  $\mu\text{m}$  in diameter and ridges (Fig. 3i, j), while the surface is composed of fine acicular crystals about 0.5  $\mu\text{m}$  wide (Fig. 3h).

Butterfield and Nicholas (1990, fig. 5.1, 5.5, 5.7; see also Harvey & Butterfield, 2011, fig. 4e) illustrated a central core within radial rays in organic-walled sclerites of chancellorids from the Mount Cap Formation (Miaolingian Series, Wuliuan Stage) of Northwest Canada, but considered that

they were a taphonomic feature. Bengtson & Hou (2001, fig. 12) and Bengtson (2005, fig. 6) suggested that the cores represented a cellular extension from the secreting epidermis, an opinion accepted by Yun et al. (2021, fig. 4F). One figured sclerite illustrated by Butterfield and Nicholas (1990, fig. 5.1) from the Mount Cap Formation has four lateral rays but no central ray; it may be referable to *Allonnia*. A clearly visible dark oval structure extending into a distal rod lies within one ray and is closely comparable to the phosphatised canal ray described here in the Greenland specimen (Fig. 3d). However, in the present specimen of *Chancelloria*, the basal part of the central ray canal completely fills the foramen whereas reconstructions by Bengtson (2005); Bengtson & Collins (2015) and Yun et al. (2021) recognised just a thin canal passing through the basal foramen into the central cavity (lumen) of individual chancelloriid rays.

Bengtson & Hou (2001) and Bengtson (2005) considered the biomineralised sclerite wall to be part of an exocuticle that was equivalent to the outer part of the intersclerite integument and contained calcareous platelets. The exocuticle was underlain by an endocuticle that passed through the basal foramina, filling most of the lumina of the sclerite rays, but a narrow central canal extended from the epithelia into the lumen. Yun et al. (2021, fig. 4F) proposed that the aragonitic sclerites and the outer surface of the integument were covered by an organic layer forming a template for biomineralisation, although acknowledging that mineralisation likely took place from within the lumen. The Greenland specimen demonstrates that the basal foramina are completely occupied by phosphatisation associated with the ray canals. The supporting pads in the three lateral rays (r2–r4) may have formed by the mineralisation of degraded internal tissue, but their dimpled surface is possibly a reflection of cellular structure from the underlying endocuticle that entered a short distance into the lumen rather than a diagenetic artifact. Phosphatisation delimits the central ray canal, and likely represents the interface between the cuticle within each ray and the epithelial tissues within the canal (Fig. 4f), but epithelial tissues may have extended beyond this canal as it is now preserved. Thus, the precise distribution of cuticular and epithelial tissues within the main part of the lumen of each sclerite ray is uncertain.

Bengtson & Hou (2001), Bengtson (2005), Bengtson & Collins (2015) and Yun et al. (2021) restored sclerites in close contact with the underlying cuticle, but Randell et al. (2005) described elevation of sclerites on a short, broad stalk encompassing the area of the foramina.

Preservation of the internal moulds of the central ray canals suggests that postmortal decay of the epithelial tissues and subsequent mineralisation of the canals took place prior to the decay of the cuticle, but this is not unlikely given the more robust function of the latter as the fundament of the sclerites. Evidence of diagenetic phosphatisation on the

inner sclerite wall is lacking, with the distinct gap between the phosphatised supporting pads of the ray canals and the inner wall, as preserved, indicating the dissolution of a thin layer of calcareous shell material during preparation. The sclerite wall in other illustrated chancelloriids from acid residues (Fig. 1a, b) is similarly represented by a gap between diagenetic mineralisation within the lumen and encrustation on the outer surface of the sclerite (see also Yun et al., 2021, fig. 1H).

## Chancelloriid relationships

The establishment of the concept Coeloscleritophora by Bengtson & Missarzhevsky (1981) was motivated by the structure of the sclerites in which each ray possessed a separate thin aragonite sclerite wall deposited around an inner cavity that was connected to the epithelia through a basal foramen. The problem of unifying the great range in morphology which extends from radially organised chancelloriids with multi-rayed, stellate sclerites to bilaterians with thatches of closely overlapping sclerites was clearly apparent, and prompted Bengtson & Conway Morris (1984) to suggest that the chancelloriids were derived from bilaterian coeloscleritophores by the adoption of a sessile mode of life. In reviewing hypotheses concerning the interpretation of chancelloriids, Bengtson & Collins (2015) concluded that sclerite structure likely was not a synapomorphy of a monophyletic clade Coeloscleritophora if account was taken to interpretations of the halkieriids as possible molluscs (Vinther & Nielsen, 2005; Vinther, 2009; Vinther et al., 2017; Peel, 2020) or other lophotrochozoans (Bengtson & Conway Morris, 1984; Conway Morris & Peel, 1990). However, in contrast, the shell structure studies of Porter (2004, 2008) and Bengtson (2005) made convergent evolution of the distinctive sclerites unlikely (Bengtson & Collins, 2015). As an alternative, Bengtson (2005) suggested that the sclerites were plesiomorphic for Eumetazoa, a theme developed by Bengtson & Collins (2015) and Yun et al. (2021), and that coeloscleritophorans are paraphyletic. It was proposed that parallel episodes of calcareous mineralisation in pre-bilaterian and bilaterian coeloscleritophoran stocks took place in calcium ion rich Cambrian seas from a sclerotised, but non-mineralised, chancelloriid-like, eumetazoan ancestor.

Comparison of the internal ray canal structure in individual rays of *Chancelloria* from North Greenland with that present in some halkieriids supports their equivalence, and accordingly the paraphyletic interpretation of Coeloscleritophora advanced by Bengtson (2005) and Bengtson & Collins (2015). Some elongate sclerites of *Australohalkieria* Porter, 2004 from the middle Cambrian (Miaolingian Series) of the Georgina Basin in Australia develop a central canal in the distal part of the sclerites (Porter, 2004). However, this is

much more robust than the slender central canal seen in rays of *Chancelloria* and may be better viewed as a longitudinal partitioning of the sclerite interior.

Vinther (2009) described an elaborate canal system developed within mineralised sclerites of *Sinosachites* (= *Thambetolepis*) *delicatus* (Jell, 1981) from the early Cambrian of South Australia (Jell, 1981; Bengtson et al., 1990; Fig. 4a, b). A prominent central ray canal extends from the foramen to the sclerite tip in *Sinosachites*. This is much more robust than the corresponding ray canals in *Chancelloria* (Fig. 4c, d), no doubt reflecting its connection with the extensive system of lateral canals in *Sinosachites*. The lateral canals extend from the central canal to the lateral margins of the sclerite where series of tubules passing through the sclerite wall permit interaction with the environment, and likely also participated in the formation of the sclerite wall (Fig. 4a). Lateral rays and tubules are not known in *Chancelloria*, where the individual rays are conical in form and sclerites are not in close contact with each other but dispersed on the integument. In contrast, sclerites of *Sinosachites* are thin and leaf-like (Fig. 4a, b), a difference reflecting the tightly overlapping nature of the individual sclerites forming a thatched/shingled dorsal pattern in the scleritome in similar fashion to juxtaposition of sclerites developed in *Halkeria* (Conway Morris & Peel, 1990).

It is likely that the lateral canals and tubules in *Sinosachites*, and the shell pores in halkieriids such as *Hippopharangites* Bengtson in Bengtson et al., 1990 (Vinther, 2009), were developed in response to their thatched/shingled sclerite morphologies and patterns resulting from their motile life habit to perform sensory functions that were undertaken by the intersclerite integument in *Chancelloria*.

## Conclusions

The presence of phosphatised central ray canals within individual rays of a sclerite of *Chancelloria* from the Henson Gletscher Formation (Cambrian Stage 4) of North Greenland confirms the extension of epithelial tissues into the sclerite interior. The canals extended as thin central tubes from the basal lumina towards the apex of the individual rays. They resemble the robust central canal of the halkieriid *Sinosachites*, adding support to the notion that coeloscleritophores are a paraphyletic group in which parallel episodes of calcareous mineralisation of pre-bilaterian and bilaterian coeloscleritophoran stocks took place in the early Cambrian.

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## Declarations

**Conflict of interest** The author has no competing interests to declare.

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