

The integument of Cambrian chancelloriids

STEFAN BENGTON and XIANGUANG HOU



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Details of the body surface of the chancelloriid *Allonnia* from the Lower Cambrian Chengjiang biota in southwestern China elucidate the nature of these enigmatic organisms. Rhombically arranged elements, about $30 \times 60 \mu\text{m}$, are interpreted as representing imbricating platelets, the distal ends of which projected as spinules from the body surface. Comparisons with other chancelloriids suggest that the flexible integument was continuous with the aragonitic sclerites that sit on the surface like cactus spines, and that both were formed by an epidermal epithelium secreting a continuous exo- and endocuticle. In the sclerites, the exocuticle was mineralized; the unmineralized endocuticle and cellular extensions from the epithelium filled the interior of the sclerites. In the flexible integument the epithelium was overlain by endocuticle and unmineralized exocuticle. This structure of soft integument and sclerites is at variance with proposals of poriferan or ascidian affinity of chancelloriids but in accord with a coeloscleritophoran model.

Key words: Chancelloriidae, Coeloscleritophora, integument, sclerite, Cambrian, China.

Stefan Bengtson [stefan.bengtson@nrm.se], Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden;
Xianguang Hou [xghou@ynu.edu.cn], The Research Center for Chengjiang Biota, Yunnan University, Kunming 650091, China.

Introduction

Chancelloriids are Cambrian organisms characterized by a sacular body covered with spiny sclerites in a manner reminiscent of cacti. First described from the Burgess Shale by Walcott (1920), they were interpreted as heteractinid sponges. Chancelloriid sclerites were subsequently found to be common and characteristic fossils in earliest Cambrian to early Late Cambrian rocks. Most sclerites are composite and star-shaped; a few taxa have single-rayed sclerites, only occasionally grouped in twins (Bengtson *et al.* 1990). Each ray has a thin calcareous wall and an extensive inner cavity which communicates with the exterior through a basal pore; adjacent cavities in composite sclerites are separated by a double wall (Sdzuy 1969; Bengtson *et al.* 1990). The sclerite wall was probably aragonitic (James & Klappa 1983; Bengtson *et al.* 1990; Mehl 1996, 1998), with a significant component of structural organic matter (Butterfield & Nicholas 1996).

Walcott's interpretation of chancelloriids as sponges was accepted for more than 50 years (e.g., Laubenfels 1955; Sdzuy 1969; Finks 1970; Rigby 1976, 1978; Bergquist 1978; Mostler 1980, 1985) but was challenged by Goryansky (1973) and Bengtson & Missarzhevsky (1981). The latter argued that chancelloriid sclerites could not have been formed by sponge-type sclerocytes but show structural similarities with sclerites of certain other Cambrian problematic non-poriferan taxa constituting the monophyletic taxon Coeloscleritophora. The argument that chancelloriid sclerites were non-homologous with sponge spicules has been accepted by most subsequent workers (e.g., Grigoreva & Zhuravleva 1983; Rigby 1983, 1986; Vasileva 1985; Dzik 1986; Rozanov 1986; Beresi & Rigby 1994; Briggs *et al.* 1994; Mehl 1996, 1998; Chen & Zhou 1997; Li 1999). Butterfield (1995) and Butterfield & Nicholas (1996), however, supported the sponge model by homologizing chancelloriid sclerites with spongin fibres and, by implication, with sponge spicules.

Walcott's figures of Burgess Shale chancelloriids (e.g., Walcott 1920: pl. 88: 1c) clearly show the presence of a resistant integument between the sclerites. He interpreted this as representing a 'strong dermal layer', or 'a compact skin layer' (Walcott 1920: pp. 328–329). In fact, his recognition of this 'skin' was the cause for a misinterpretation of the Burgess chancelloriids. Walcott regarded all the varieties of spicular form and ray number to be the effect of differential burial of a single type of sclerite in the integument. This led him to assign all the Burgess chancelloriids to a single species, *Chancelloria eros* Walcott, 1920. A restudy of Walcott's material (Bengtson *et al.* 1990: pp. 45, 47) suggests that at least three genera – *Chancelloria* Walcott, 1920, *Allonnia*, Doré & Reid, 1965, and *Archiasterella* Sdzuy, 1969 – are represented and are characterized by distinctly different scleritomes.

Subsequent to Walcott's study, published mentions or illustrations of the intersclerite integument in well-preserved chancelloriids have implied a smooth, featureless surface (Rigby 1978: p. 1338; Bengtson *et al.* 1996; Chen *et al.* 1996: figs. 90–94; Mehl 1996: p. 379). Butterfield & Nicholas (1996: p. 896), however, found 'remnants of a relatively robust punctate integument' from chancelloriids in the the Mount Cap Formation in northwestern Canada, the 'punctae' being regularly disposed and about 200 µm across (N.J. Butterfield personal communication 1998). Chen & Zhou (1997: p. 29) reported an 'epidermis ... [with] polygonal divided pits and nodes about 0.15 mm in diameter', each node with an 'elongated, outwardly directed spine... about 0.12 mm long' in a specimen from the Chengjiang fauna in China.

We present a study of Chengjiang chancelloriids which preserve details of the flexible integument. The new data indicate that soft skin and sclerites were structurally, functionally and developmentally integrated in the chancelloriid integument. This has bearing on the biological nature of chancelloriids, in particular their contentious relationship with sponges.

Material and methods

There are six specimens on five slabs, three of which have been recovered as part and counterpart. All specimens belong to *Allonnia*, but to two species, *Allonnia prixothrix* sp. n. and *Allonnia* sp. They are preserved on bedding surfaces in soft mudstones from the lower part of the Yu'an shan Member of the Qiongzhusi Formation. *Allonnia*

phrixothrix sp. n. was collected from the Xiaolantian Section, Chengjiang, Yunnan, and *Allonnia* sp. from the Anshan Section at Haikou, Kunming (see Hou & Bergström 1997 and Luo *et al.* 1997 for locality information). The specimens are deposited at The Research Center for Chengjiang Biota, Yunnan University, Kunming (RCCBYU), under the numbers 10160–10164.

Fig. 2D and E were taken on Kodak Ectachrome with a Wild M400 photomicroscope; all other light photographs were taken with a Leaf Microlumina digital scanner with a Micro Nikkor 60 mm macro lens, at the highest resolution (3380 × 2700 pixels per frame). Two main methods of lighting were used: (1) Low-angled, directional light to bring out the surface topography (e.g., Fig. 1B). (2) High-angled, plane-polarized light in combination with a polarizing filter on the lens; these filters were set so as to extinguish direct reflected light in the manner of crossed nicols of a petrographic microscope (e.g., Fig. 1A; cf. Boyle 1992; Rayner 1992; Bengtson 2000). The effect is similar to that obtained by immersion of the specimen in a liquid, a technique unsuitable for the friable Chengjiang mudstone. Stereograms were taken with an angular difference of 8°. Figs. 5 and 7B–E were taken with a Philips XL30 scanning electron microscope (specimens coated with gold–palladium) in normal or BEI (backscattered electron image; Fig. 5B) mode. Chemical analyses were done with a Philips XL30 SEM equipped with an EDS (energy dispersive X-ray spectrometry) detector.

Terminology

The *integument* is here taken to include the complete outer skin of the animal. In our interpretation, the main constituents of the chancelloriid integument are a cellular *epidermis* and an extracellular *endocuticle* and *exocuticle*. The exocuticle is unmineralized in the *flexible* (*soft, inter-sclerite*) *integument* and mineralized (aragonitic) in the *sclerites*. The sclerites are composite, consisting of three *rays*. Each ray has its own mineralized wall and a *basal pore*, through which the unmineralized tissue in the interior of the ray is connected with the endocuticle and epidermis of the flexible integument. The exocuticle contains minute more-or-less rhombically arranged elements referred to as *platelets*, the distal parts of which protrude as *spinules*.

Taphonomy and preservation

Like most Chengjiang fossils, the chancelloriids are preserved in partial compression in yellow mudstones, and much of the tissue is enhanced by a reddish stain. RCCBYU 10160 (Figs. 1–4) is a slab with one complete and one partial specimen, both with substantial continuous portions of inter-sclerite tissue, marked by a reddish lamella. Sclerites are preserved in a bluish-white material, shown by EDS analyses to be rich in Si (56–57%) and Al (29–30%), with smaller amounts of K (8–9%), Fe (2–3%), and Ti (0.5–0.7%), suggesting a clay-mineral composition. It is almost identical in chemical composition to the surrounding yellow mudstone, which differs only in its somewhat higher content of Fe (5–8%). The sclerite material is consequently interpreted as a secondary clayey infilling of the internal cavities. Some infillings are solid and some have a thin streak of reddish material along the center. In most cases, however, the rays are crushed by compaction, with longitudinal fractures commonly developed, and appear



Fig. 1. *Allonnia phrixothrix* sp. n., holotype, part, RCCBYU 10160a. A. High-angled illumination, crossed nicols. B. Low-angled illumination from NW, plain light. Small frames (2A–C) show position of enlargements in Fig. 2A–C, respectively; large frame (4) shows position of enlargement in Fig. 4.

to have had a substantial part of the internal cavity unfilled by the clayey material. RCCBYU 10161 (Figs. 5, 7) is a small piece of integument, similar in preservation to RCCBYU 10160 but without exposed sclerites. RCCBYU 10162 (Fig. 8) is a large specimen with fragmentary sclerites and isolated patches of inter-sclerite integument. The sclerites are commonly represented by reddish internal moulds and are less compressed than those in RCCBYU 10160. All these are referred to *Allonnia phrixothrix* n.sp. RCCBYU 10163–10164 (Fig. 9), referred to as *Allonnia* sp., are large specimens with smooth inter-sclerite integument and scattered, fractured sclerites.

The reddish lamella marking the soft tissue is frequently folded and can be traced at several levels in the mudstone (e.g., Fig. 4). In *Allonnia phrixothrix* the surface texture is apparent as a fine relief, often enhanced by the concentration of the reddish substance in the lower or higher parts (depending on which surface is viewed) of the relief, contrasting with the surrounding yellow rock. Fig. 5A shows an SEM picture of a por-

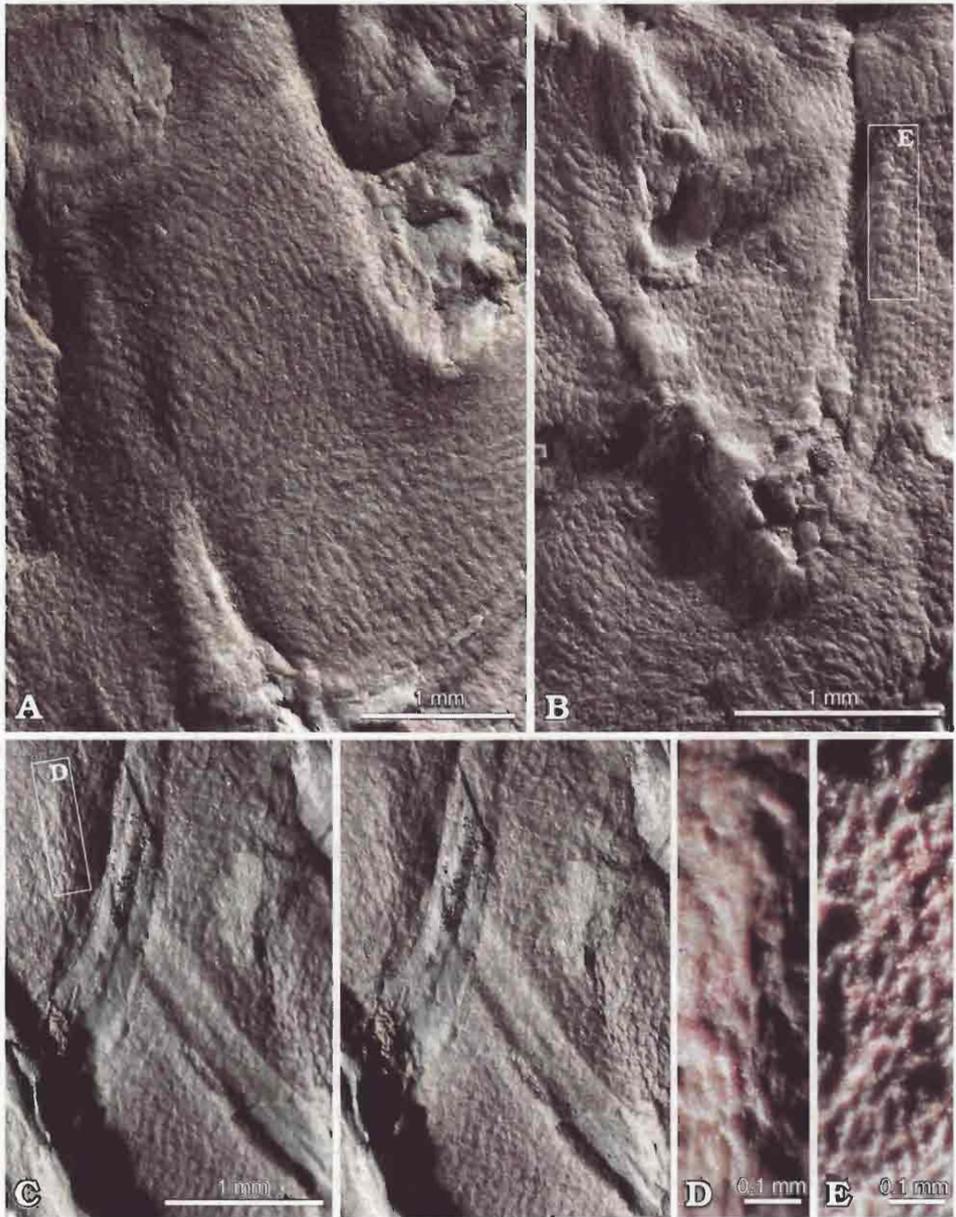


Fig. 2. *Allonnia phrixothrix* sp. n., holotype, part, RCCBYU 10160a. **A, B.** Low-angled illumination from NE, plain light. Frame in B indicates position of E. **C.** Stereo photograph; low-angled illumination from SW, plain light; frame indicates position of D. **D.** Detail of C. **E.** Detail of B.

tion of the tissue pictured in Fig. 7B. The **reddish substance** is here concentrated in the lower portions of the relief, and a backscattered electron image (Fig. 5B) picks out these areas as light (indicating high atomic weights) patches. EDS analyses of the same patches show the reddish areas to be considerably enriched in iron oxides (up to 43%

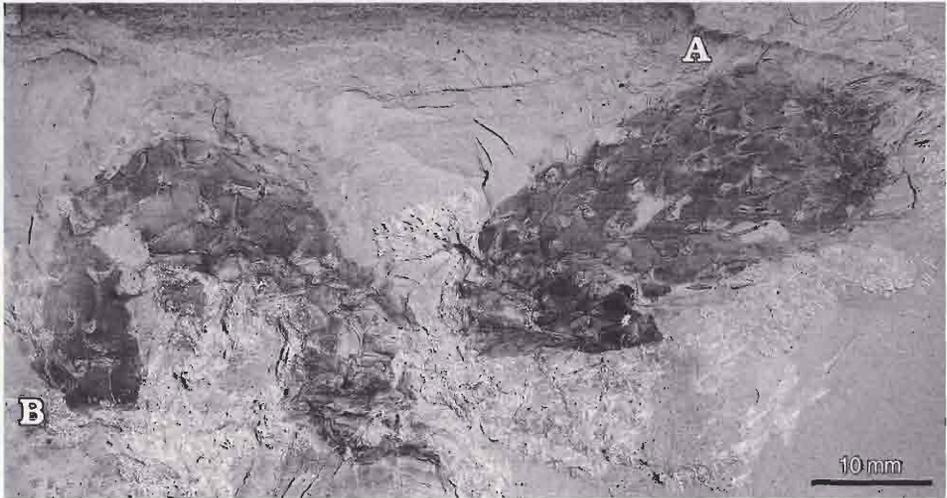


Fig. 3. *Allonnia phrixothrix* sp. n., part, holotype, RCCBYU 10160a (A), and paratype, RCCBYU 10160b (B). High-angled illumination, crossed nicols, green channel.

Fe of total weight) in comparison to the yellow areas, which have the same composition as the regular yellow mudstone matrix (5–8% Fe).

The EDS analyses revealed no significant trace of phosphorus, neither in the sclerites nor in the inter-sclerite integument. This is in contrast to Leslie *et al.* (1996), who found higher levels of phosphorus in originally non-mineralized cuticles of Chengjiang arthropods in relation to the surrounding matrix, and proposed that early precipitation of phosphate was responsible for the exquisite preservation of soft parts in the Chengjiang biota.

The inter-sclerite integument was clearly flexible, tending to become folded and draped around the mineralized sclerites (Fig. 4). At the edges of the fossils (e.g., Fig. 1A, top and right), sclerite rays are seen to protrude freely above the main body surface, showing that the sclerites were set in the soft integument, attached by their bases. Fig. 6 shows our interpretation of the taphonomy. Upon death the sacciform body (Fig. 6A) collapsed and flattened on the sea floor (Fig. 6B). The sclerites thus came to rest in two layers, pointing upwards and downwards, respectively, with sclerites at the edges of the flattened body pointing sideways. After embedding and compaction of the sediment, the sclerites became more or less compressed, depending on whether they were filled with sediment (Fig. 6C, D, sclerite ray 3) or empty (the other three rays). In the latter case, they may be either pressed flat (ray 2) or, if one of the sides withstood compression, collapsed into a crescentic cross section (rays 1 and 4). Fig. 6E shows alternative appearances of part and counterpart, depending on which planes the rock is subsequently split along.

In practice it is often difficult to determine whether a piece of soft integument or a sclerite belongs to the upper or lower side, particularly as the complete morphology of the sclerites is never preserved. For example, the sclerite ray (ray 3) preserved in full relief in Fig. 6 may appear to show the same relationship with the surrounding integument whether it adheres to the part or to the counterpart (Fig. 6E, a and b–c, respectively); and a concave furrow may reflect either an overlying non-compressed or

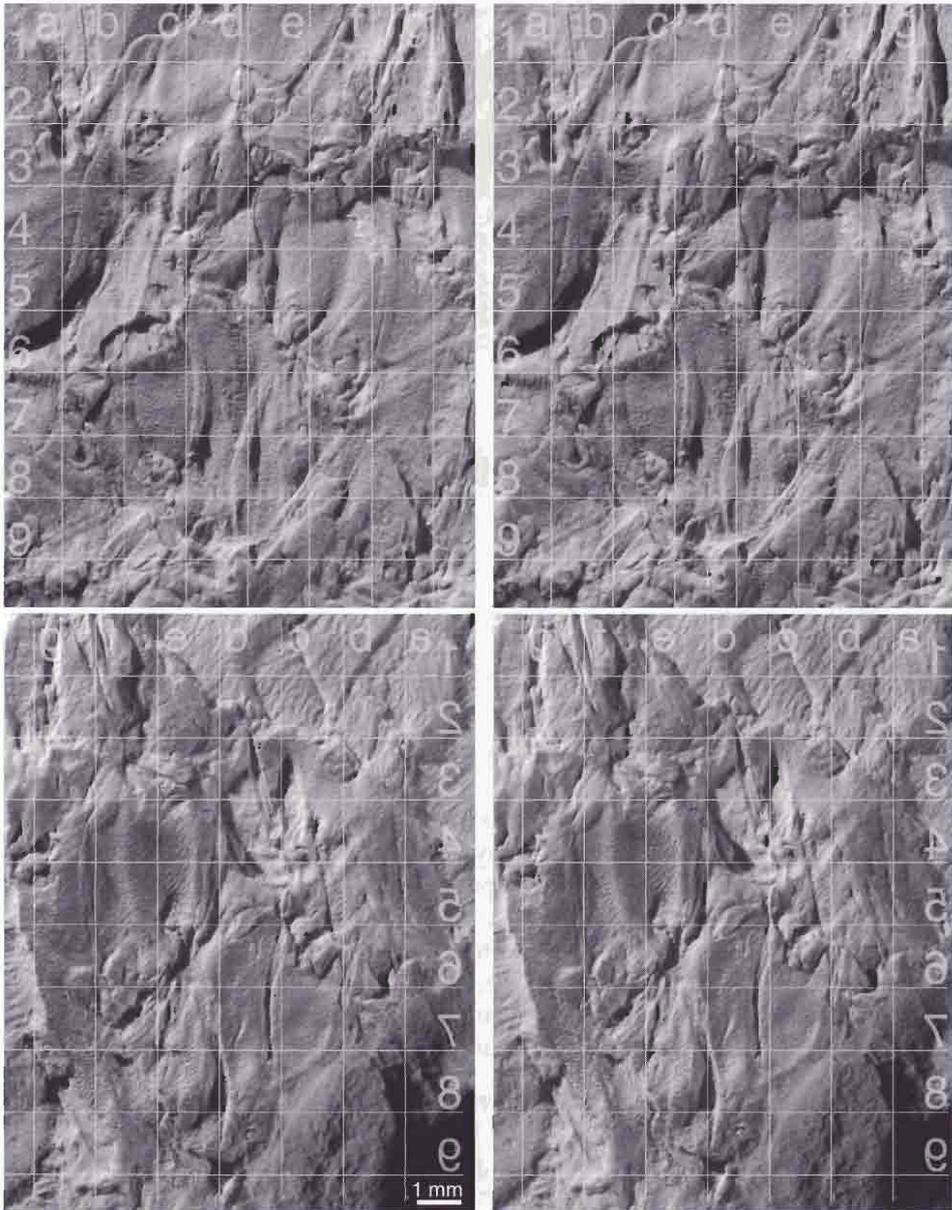


Fig. 4. *Allonnia phrixothrix* sp. n., holotype, part (top) and counterpart (bottom), RCCBYU 10160a. Stereo pictures; low-angled illumination from NW, plain light.

crescentically compressed ray (Fig. 6E, a, lower part, depressions formed by rays 1 and 3), or an underlying, crescentically compressed ray (ray 4). The frequent folding of the integument (not shown in the diagram) further complicates the interpretation. The complex relationships between sclerites and soft integument in the fossil are illustrated by the stereo close-ups of part and counterpart in Fig. 4.

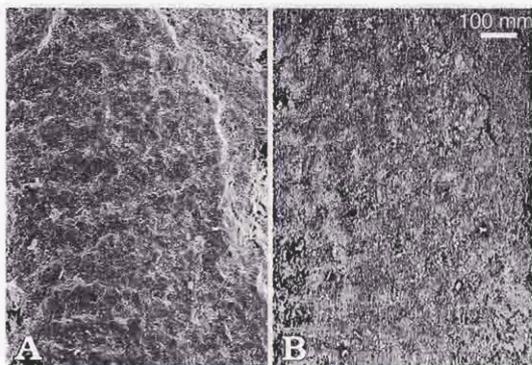


Fig. 5. *Allonnia phrixothrix* sp. n., paratype, part, RCCBYU 10161. Detail of area shown in Fig. 7B. A. Secondary electron image. B. Backscattered electron image.

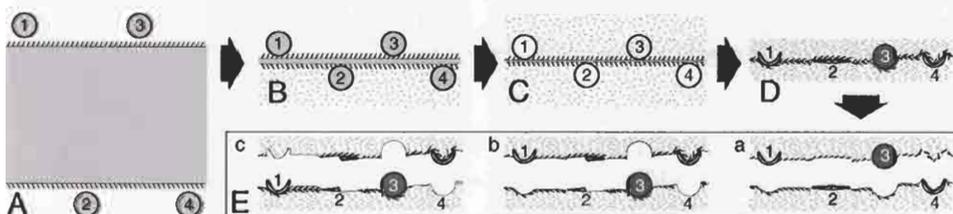


Fig. 6. Taphonomy of Chengjiang chancelloriids. See text on pp. 6–7 for discussion.

Structure of the integument

The preservation of the Chengjiang chancelloriids thus confirms that the integument consists of a flexible skin beset with hard, spiny sclerites projecting outwards. The sclerites are almost always crushed or incompletely preserved. Their detailed shape therefore cannot be exactly determined. Nonetheless, the best preserved sclerites (Figs. 2C, 9A₁) all show a maximum of three rays, corresponding to the typical *Allonnia* pattern with two lateral rays almost parallel to the body surface, and one middle ray protruding from it (Fig. 11B). The recognition of two species, *Allonnia phrixothrix* and *Allonnia* sp., is based on differences in the structure of the soft integument.

Platelets in the integument. — In *Allonnia phrixothrix*, the inter-sclerite integument is conspicuously textured over the whole body of the animal (Fig. 1B). The texture consists of a generally rhombic pattern (e.g., Figs. 2, 7D), individual elements, platelets, being about 60 μm apart. Over a larger stretch of surface, the different alignment directions of the pattern are variously accentuated; for example, in Fig. 2A the NNW–SSE direction is most prominent, but a band immediately below the middle accentuates instead the roughly perpendicular direction. The alignments may also be curved in different directions (Fig. 2A, top left; 2B, lower left). A scale-like imbrication is often discernible (Figs. 2B, E, 7D).

The shape of the individual platelets is difficult to make out. Whereas under an optical microscope they may appear as smooth granulae (Figs. 7A, 8C), examination of the same surface under the SEM reveals that the individual platelets are poorly preserved (Fig. 7E) and that the appearance of smoothness may be an effect of their regular arrangement.

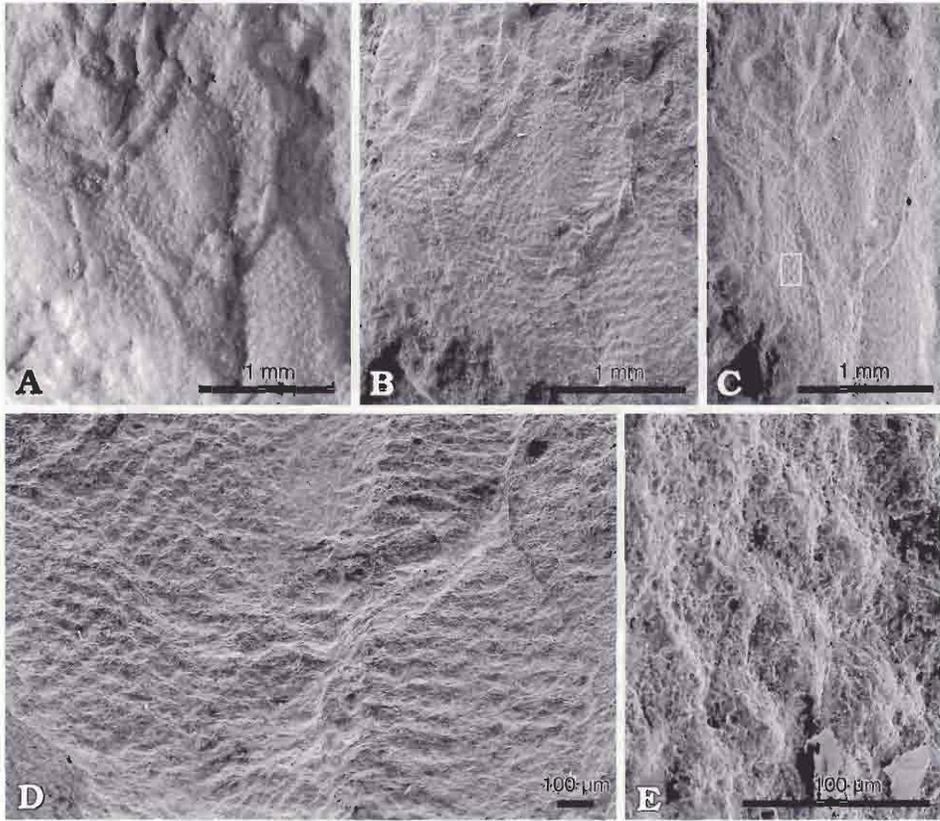


Fig. 7. *Allonnia phrixothrix* sp. n., paratype, part, RCCBYU 10161. A. Low-angled illumination from SW, plain light. B–E. SEM micrographs. C and D show approximately the same areas as in B, under different tilt. E shows detail of C (position indicated by frame in C).

Nonetheless, certain characteristics of shape are possible to distinguish. The imbricating platelets in Fig. 2B and E are 50–60 μm long and 30–40 μm wide, and appear to have thickened rims and a central depressed part. In several places, particularly where the integument is folded into a crest, the elements appear like fine rods, about 100 μm long and 25 μm wide (Fig. 2D). We interpret these rods as representing the distal parts of the integumental platelets, forming short spinules protruding from the surface. They are probably equivalent to the 120 μm long spines reported by Chen & Zhou (1997) from a Chengjiang cancelloriid, although the considerably larger size of the basic units in Chen & Zhou's specimen, 150 μm , suggests a taxon other than *Allonnia phrixothrix*, in which the elements in the soft integument are only about 60 μm wide.

Platelets in sclerites. — Although the preservation of the sclerites in the Chengjiang *Allonnia* does not reveal details of the sclerite surfaces, well-preserved cancelloriid sclerites from other deposits typically are beset with fine spinules or granules. Fig. 10 shows such a sclerite of *Archiasterella hirundo* Bengtson, 1990 (in Bengtson *et al.* 1990), from the Lower Cambrian of South Australia. The spinules are spaced at about 10–30 μm from each other and appear to be the tips of elements embedded in the

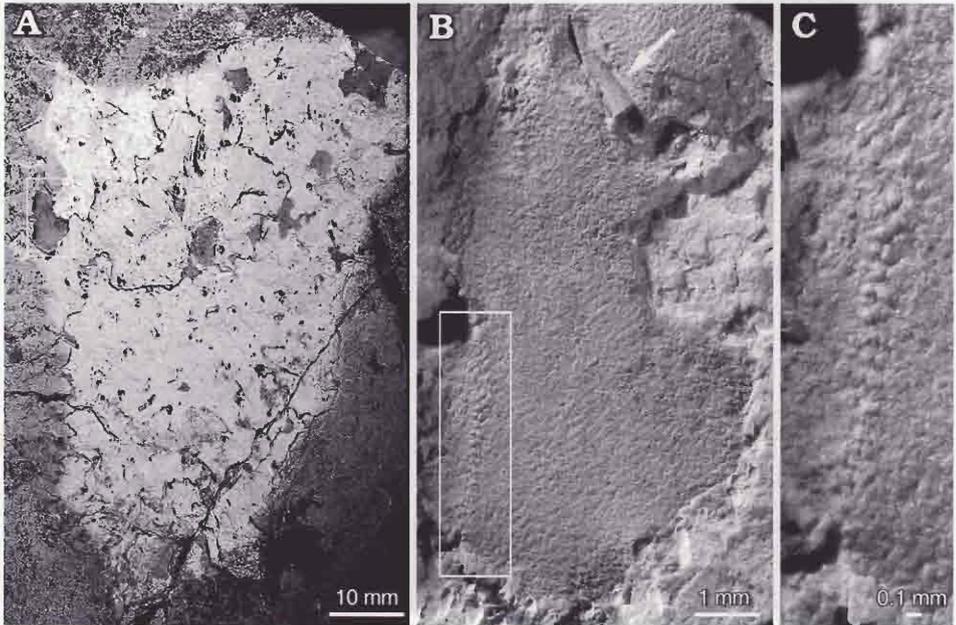
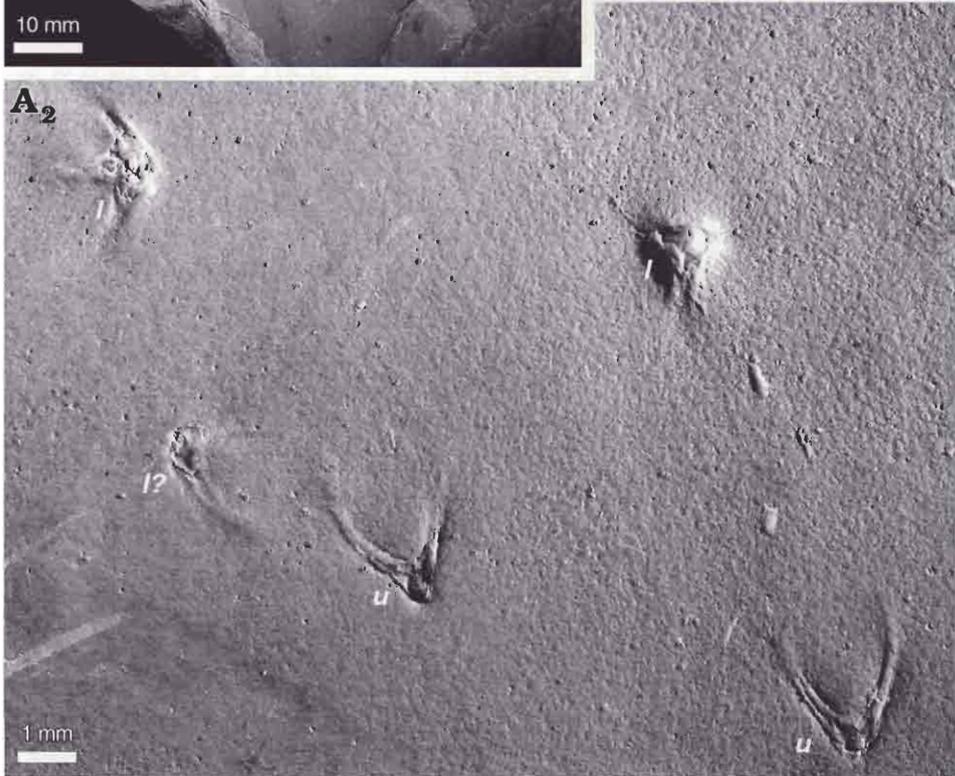
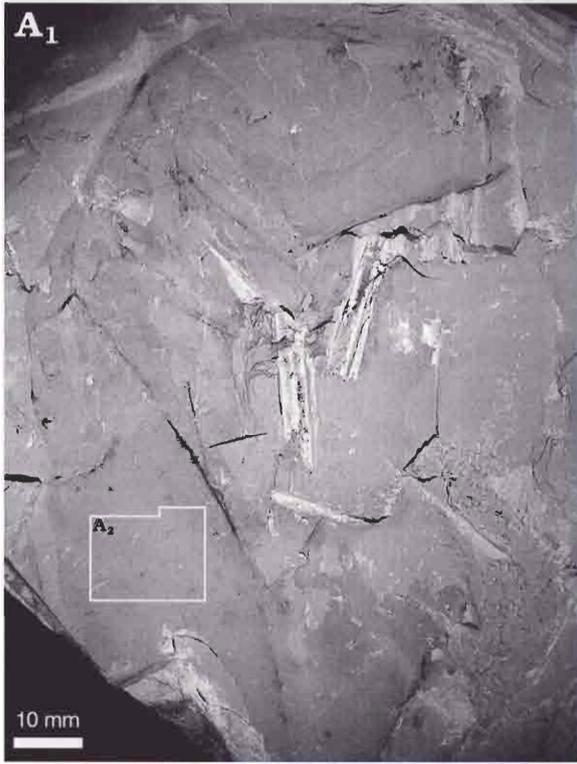


Fig. 8. *Allonnia phrixothrix* sp. n., paratype, part, RCCBYU 10162. A. High-angled illumination, crossed nicols; outline of preserved body indicated by darkening of surrounding matrix. Frame indicates position of B. B. Detail of A; low-angled illumination from NW, plain light. Frame indicates position of C; arrow points to broken sclerite ray. C. Detail of B.

sclerite wall. Butterfield & Nicholas (1996: fig. 5.2) illustrated a portion of a demineralized chancelloriid sclerite showing a similar pattern of apparently imbricating structures, 10 μm broad and about 20 μm long. We interpret these structures as homologous to the platelets in the flexible integument of *Allonnia phrixothrix*. The differences in spacing between the platelets in the *Allonnia* integument (about 60 μm) and those in the isolated sclerites (10–30 μm) may be due to taxonomic differences, or to the fact that the sclerite surface structure became fixed at the time of formation of the sclerite, which took place in the apical end of the body (Bengtson *et al.* 1996).

Smooth integument. — The surface of the integument of *Allonnia* sp. illustrated in Fig. 9 is without regular patterns. The surface may have a fine irregular granularity (Fig. 9A₂), but this is similar to that exhibited by the surrounding sediment matrix and is therefore likely to be of secondary, non-biological origin. Also, the inter-sclerite integument is more flat than in *Allonnia phrixothrix*, even around sclerites (cf. Fig. 9A₂ with Fig. 4). The density of sclerites in *Allonnia* sp. is low, and it is usually possible to distinguish between sclerites of the ‘upper’ (Fig. 9A₂, u) and ‘lower’ (Fig. 9A₂, l) surface of the flattened body. In contrast to the preservation in *Allonnia phrixothrix*, where the distal parts of the rays are often better preserved than the somewhat crushed

Fig. 9. *Allonnia* sp. A₁, A₂. Part, RCCBYU 10163. A₁. High-angled illumination, crossed nicols. Frame shows position of A₂. A₂. Detail, low-angled illumination from E, plain light. B. Part, RCCBYU 10164. High-angled illumination, crossed nicols. Abbreviations: *u*, sclerites of upper side; *l*, sclerites of lower side. (‘Upper’ and ‘lower’ arbitrarily defined, based on position of flattened body on slab.)



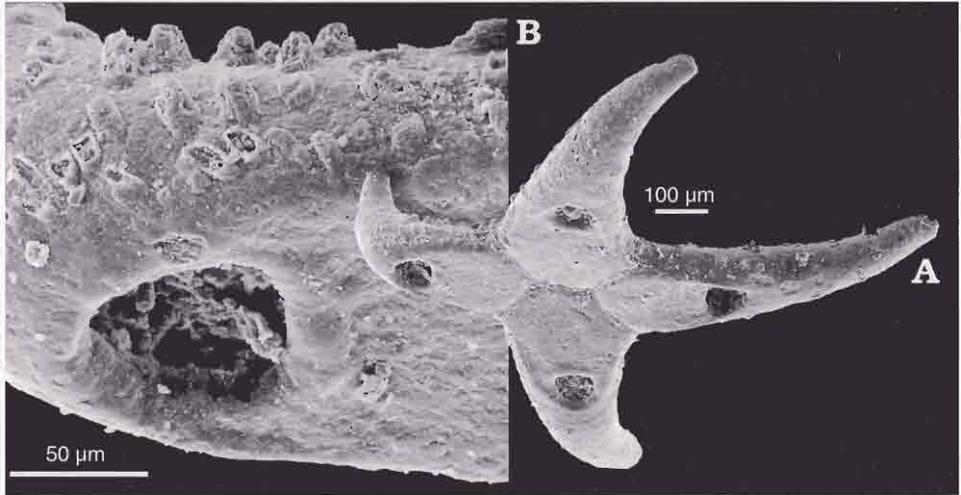


Fig. 10. Sclerite of *Archiasterella hirundo* Bengtson, 1990 (in Bengtson *et al.* 1990), holotype, SAMP 30307, from the Lower Cambrian Parara Limestone of Curramulka, South Australia; SEM pictures. **A.** Whole sclerite, viewed from lower (basal) side, showing the basal surface and the basal openings of the four rays. **B.** Detail of A, showing one basal opening and protruding platelets. Specimen also figured by Bengtson *et al.* (1990: fig. 30E, F).

bases, the sclerites of *Allonnia* sp. preferentially display their bases and impressions of the proximal parts of the rays. We interpret this to reflect a difference in the nature of the inter-sclerite integument: that of *Allonnia* sp. was thicker, the basal parts of the sclerites being sunk into the soft integument.

Another interpretation of the differences between *Allonnia phrixothrix* and *Allonnia* sp. is that only one species is present and '*Allonnia* sp.' represents more inflated specimens, accounting for the smoothness of the soft integument and the large distances between the sclerites. This would be in conflict, however, with our interpretation of the soft integument in this form being thicker than in *Allonnia phrixothrix* and the platelets being solid elements in the integument, which would not disappear by stretching.

Reconstruction of the integument. — The body of the Chengjiang *Allonnia* is here interpreted to have been covered with a continuous cuticle, which was mineralized in the sclerites and flexible between them. At least in *Allonnia phrixothrix* the cuticle contained small, fairly regularly disposed platelets protruding as more or less prominent spinules.

The nature of the underlying soft tissue is not evident from the Chengjiang material; the roughly rhombic disposition of the platelets does not seem to reflect an arrangement of underlying epithelial cells. However, the organically preserved chancelloriid sclerites from the Middle Cambrian Mount Cap Formation in northwestern Canada reported by Butterfield & Nicholas (1996) give important clues. The sclerites, isolated from shales by gentle HF etching, show the same basic structure as the ones known from mineralized preservation, a thin wall surrounding an inner space, which opens through a constricted basal foramen. The wall surface structure consists of rectangular, apparently imbricating elements aligned along the axis of the ray; as discussed above, these elements are interpreted to be homologous to the platelets observed in the soft integument and sclerites of

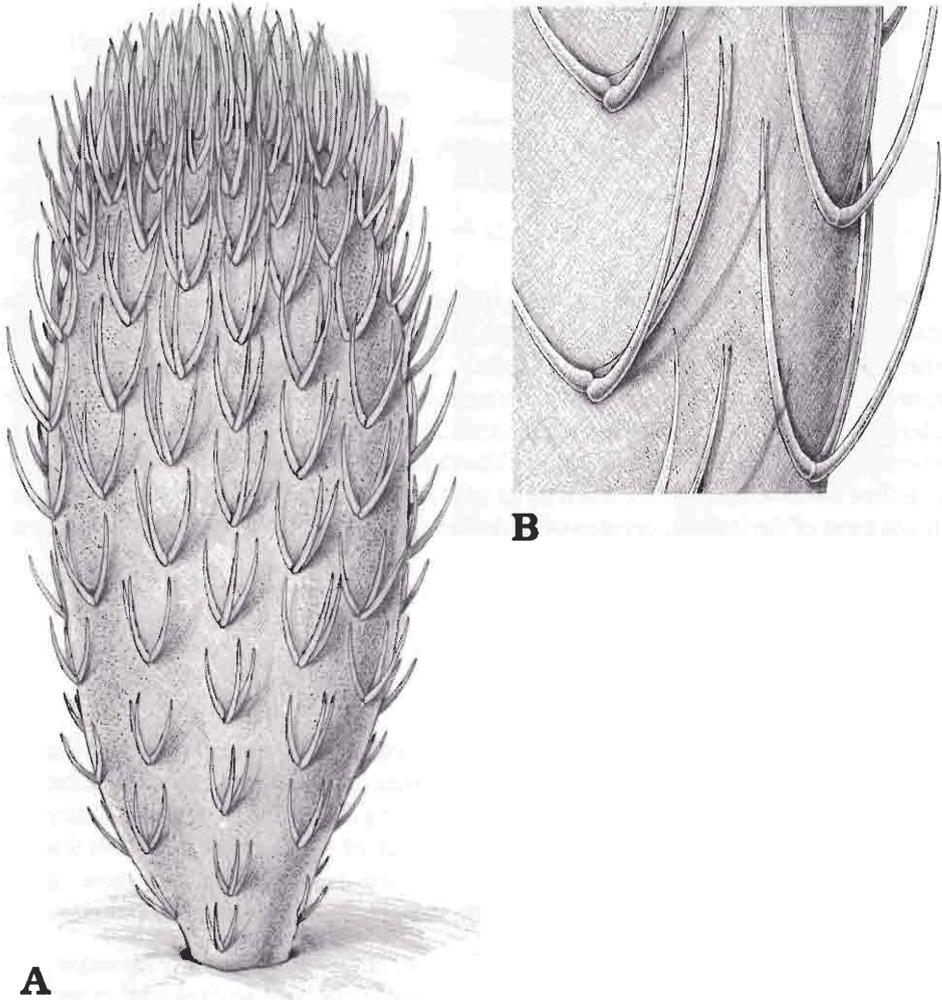


Fig. 11. *Allonnia phrixothrix* sp. n., reconstruction of whole body (A) and detail of body surface (B). Drawings by Pollyanna von Knorring.

other chancelloriids. In addition, the internal cavity is filled with dark granular material, which appears non-cellular and shows a weak striation that may represent lamination (Butterfield & Nicholas 1996: fig. 5.5). This material suggests the presence of an additional non-mineralized cuticular layer, underlying the mineralized layer.

In at least four of the sclerites illustrated with transmitted light microscopy (Butterfield & Nicholas 1996: figs. 5.1, 5.3, 5.5, and 5.7) there is a central light zone, approximately 5 μm thick, in the dark material filling the sclerites. Butterfield & Nicholas commented on this zone in only one instance, suggesting it to be a taphonomic feature (Butterfield & Nicholas 1996: caption to fig. 5.5). In view of its persistence, we suggest instead that it reflects an original feature of the tissue, probably formed by cellular extensions from the secreting epidermis, active in the secretion and sclerotization of the cuticle.

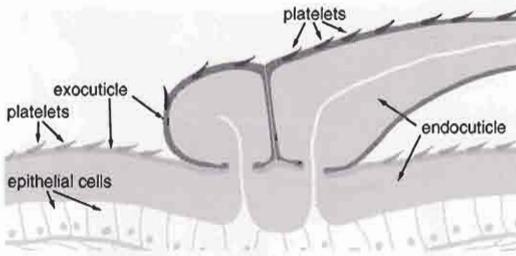


Fig. 12. Hypothetical reconstruction of chancelloriid integument, showing section through epithelium (cellular) plus soft skin and sclerite (both consisting of exo- and endocuticle). Mineralization of exocuticle and platelets in sclerite indicated by darker colours; non-mineralization of the same in flexible integument indicated by lighter colours.

Fig. 12 shows a reconstruction of the chancelloriid integument, based on the above observations and considerations. The epidermal epithelium is covered by a cuticle, which is divided into exo- and endocuticle. The exocuticle is 5–30 μm thick, non-mineralized in the soft parts of the integument and mineralized (with aragonite) in the sclerites. At least in some forms, the exocuticle is invested with imbricating platelets protruding from the surface as spinules. The thicker endocuticle is non-mineralized. It underlies the exocuticle in the sclerites as well as the inter-sclerite integument, and occupies most of the internal cavities of the sclerites, where it is penetrated by cellular extensions of the epithelium.

Significance of the chancelloriid integument for interpretations of affinity

The support of the sponge interpretation of chancelloriids (Butterfield 1995; Butterfield & Nicholas 1996; Conway Morris & Chapman 1997) is based on interpretations of the sclerite structure. Mehl (1996), in suggesting a possible ascidian affinity, referred to sclerite structure as well as to the presence of a soft integument. We discuss both these proposals below in the light of the new evidence on the nature of the chancelloriid integument and on the integrated nature of sclerites and soft integument.

The skin of sponges. — Sponges (except hexactinellids) are externally bounded by a pinacoderm, consisting of pinacocytes that are flattened or have an expanded outer part, giving them a T-shaped cross-section (Bergquist 1978: p. 53). A cuticle is usually lacking, although some demosponges may form an outer collagenous cuticle. This is often very thin; a cuticle about 25–30 nm thick covering the exopinacoderm has been reported from some demosponges (Lévi & Porte 1962; Bagby 1970), and De Vos *et al.* (1991: pl. 7) figured a 100–200 nm thick impermanent cuticle from *Cacospongia*. Vacelet (1971b) described a thicker cuticle, up to 1–1.5 μm , in *Verongia*. This cuticle appeared mostly structureless in TEM preparations but contained fine irregular fibres and stained positively for collagen/spongin. It was developed over parts of the sponge body, sealing off the inhalant ostia, thus shutting off the water circulation, at least locally.

According to Bergquist (1978: table 2.1), the T-cells have diameters at the epithelial surface of 3.5–30 μm , though De Vos *et al.* (1991: pl. 7) figure an epithelium with up to 75 μm wide pinacocytes. These, however, are arranged in an irregular polygonal pattern, in contrast to the generally rhombic pattern seen in *Allonnia phrixothrix*. In addition, the *Allonnia* inter-sclerite integument has a considerable relief of the individual platelets, sometimes with a topography suggesting imbrication.

In *Allonnia phrixothrix* and *Allonnia* sp, there is no sign of holes that might correspond to the inhalant ostia of sponges. Sponge ostia, however, rarely exceed 50 μm in diameter (Bergquist 1978), and given the preservation of the Chengjiang *Allonnia*, smaller holes in soft integument may not be retained as visible structures. The punctae reported from isolated chancelloriid soft integument (Butterfield & Nicholas 1996: p. 896) might conceivably represent ostia, but they are larger (about 200 μm) than most ostia, and the lack of further detailed information on them prevents closer comparisons.

Many sponges have only a single exhalant osculum, situated in the apical portion of a cylindrical or bag-shaped body. If chancelloriids were sponges, the expected position for an osculum on *Allonnia* would be at the apex, within the mass of apically pointing sclerites. Such a spine-protected osculum is found in some sponges (Jones 1970). In any case, the lateral compression of the fossils leaves the presence of an opening in this region of the body conjectural.

Chancelloriid sclerites and demosponge 'horn cells'. — In his first report of organic-walled chancelloriid sclerites from the Mount Cap Formation, Butterfield (1995) claimed that the sclerites 'exhibit an essentially one-to-one comparison, not with the spicules, but the *fibres* of certain horny sponges'. He further remarked that the modern demosponge *Darwinella* "produces non-mineralizing and effectively hollow 'spiculoids', apparently derived from the fibres, which approximate intriguingly the form of chancelloriid sclerites".

Bengtson *et al.* (1996) maintained that the arguments against homology of sclerites with sponge spicules are equally valid with regard to homology with spongin fibres, since both spicules and fibres in sponges are formed in similar ways by sclerocytes and spongocytes, respectively. Butterfield & Nicholas (1996) further elaborated on Butterfield's (1995) interpretation, and Conway Morris & Chapman (1997: p. 8) also concurred with this view: 'The sac-like body [of chancelloriids], rooted to the sea floor, is closer to the Porifera in organization, and comparisons also may be drawn between their sclerites and sponge spicules (Butterfield 1995).'

Butterfield & Nicholas's (1996: p. 898) crucial assertion, backed up by reference to 'unpublished observations', is that the spongin 'horn cells' of the demosponge *Darwinella* 'express the same topological relationships as multi-rayed chancelloriid sclerites'. Therefore they concluded that sponge spicules and chancelloriid sclerites are both derived from spongin fibres and are thus homologous structures. N.J. Butterfield has kindly lent us micrographs of these 'horn cells', which show clearly that they consist of solid fibres built up of concentric spongin layers indicating growth by external deposition from spongocytes, as described by Carter (1881) and Vacelet (1971a). There are no internal cavities, and consequently no double walls or openings to the exterior. Nor do they approximate the form of chancelloriid sclerites. The 'unpublished observations' Butterfield (personal communication, 1998) explains as follows: 'if the components of chancelloriid sclerites are like fibres, and the components of composite horn cells are like fibres, then the two might reasonably be expected to have the same topological relationships'. In his view, 'individual components of chancelloriid sclerites [were] built from the outside, in the same manner as sponge fibres'.

The geometric term 'topological' refers to connectedness of surfaces. Topologically identical surfaces can have any shape and size, and can be transformed into one another by stretching without breaking. A sphere is topologically identical with a cube

but not with a torus. Biological structures of different topology may well be homologous (for example, an abalone shell, containing a row of perforations, is considered homologous with a limpet shell having no such perforations); topological relationships are thus not particularly useful to assess biological homology. We take Butterfield & Nicholas's (1996) claim of the same topological relationships being expressed in *Darwinella* 'horn cells' and chancelloriid sclerites to mean that the two can be transformed into one another without a radical shift in the geometry of formation.

The original claim for non-homology of chancelloriid sclerites with sponge spicules (Bengtson & Missarzhevsky 1981) was based on just such a geometrical difference. Sponge spicules consist of layers successively deposited on the outer surfaces, whereas the double walls between adjacent rays in the chancelloriid sclerites, and the presence of basal pores, show that the walls must have been formed by surficial mineralization of organic precursors which are continuous with soft tissue external to the sclerites. The same argument as for spicules applies to the organic skeletal elements in sponges, because these are formed in the same way as spicules, i.e. by external deposition from amoeboid cells, in this case termed 'spongocytes' (Carter 1881; Vacelet 1971a; Bergquist 1978: pp. 88–90). The fibrous composition of the two structures referred to by Butterfield is irrelevant to the question of their geometric relationships. Butterfield & Nicholas's (1996) 'unpublished observations' of topological identity between sponge 'horn cells' and chancelloriid sclerites are thus mistaken, and Butterfield's connected viewpoint that chancelloriid sclerites are built from the outside remains unsubstantiated.

Chancelloriid sclerites and ascidian spicules. — Mehl's (1996) comparison of chancelloriid sclerites with ascidian spicules was based on the following observations and reasoning. (1) Photographs of a Chengjiang chancelloriid show that there is a smooth, skin-like layer 'between and partly also above the sclerites', suggesting that the sclerites were covered by dermal tissue or epidermis. (2) No outer suture is visible at the joints between rays of chancelloriid sclerites, indicating that sclerite formation was under the control of inner secreting cells as well as of an outer dermal tissue layer. (3) Ascidian spicule biomineralization takes place within an outer covering of dense extracellular material under the control of a mineralizing organic matrix.

We disagree that chancelloriids and ascidians form their skeletal elements in similar ways. First, in none of the actual Chengjiang specimens that we have studied is there evidence that the skin covers the sclerites; at the edges of the flattened specimens it is particularly obvious that the sclerite rays protrude above the soft integument (Fig. 1, top and right). In the remaining parts of the fossilized body, where two layers of hard sclerites and soft epithelium have been pressed into one another (cf. Fig. 4), it is difficult to sort out their spatial relationship even when working with actual specimens; attempting to do so from photographs seems nearly impossible (Mehl 1996 did not include the photographs in her publication).

Secondly, the lack of visible outer sutures in many chancelloriid sclerites is not evidence that the material was deposited from the outside. The walls are very thin (about 5–30 µm) and were clearly initiated as a non-mineralized organic matrix, as evidenced both by the adpression of the rays to one another and the residues of organic matter in demineralized specimens (Butterfield & Nicholas 1996). Such a layer, probably consisting of structural proteins, would have been plastic before sclerotization, and would thus easily obscure ray boundaries. Even the suture between adjacent walls is only oc-

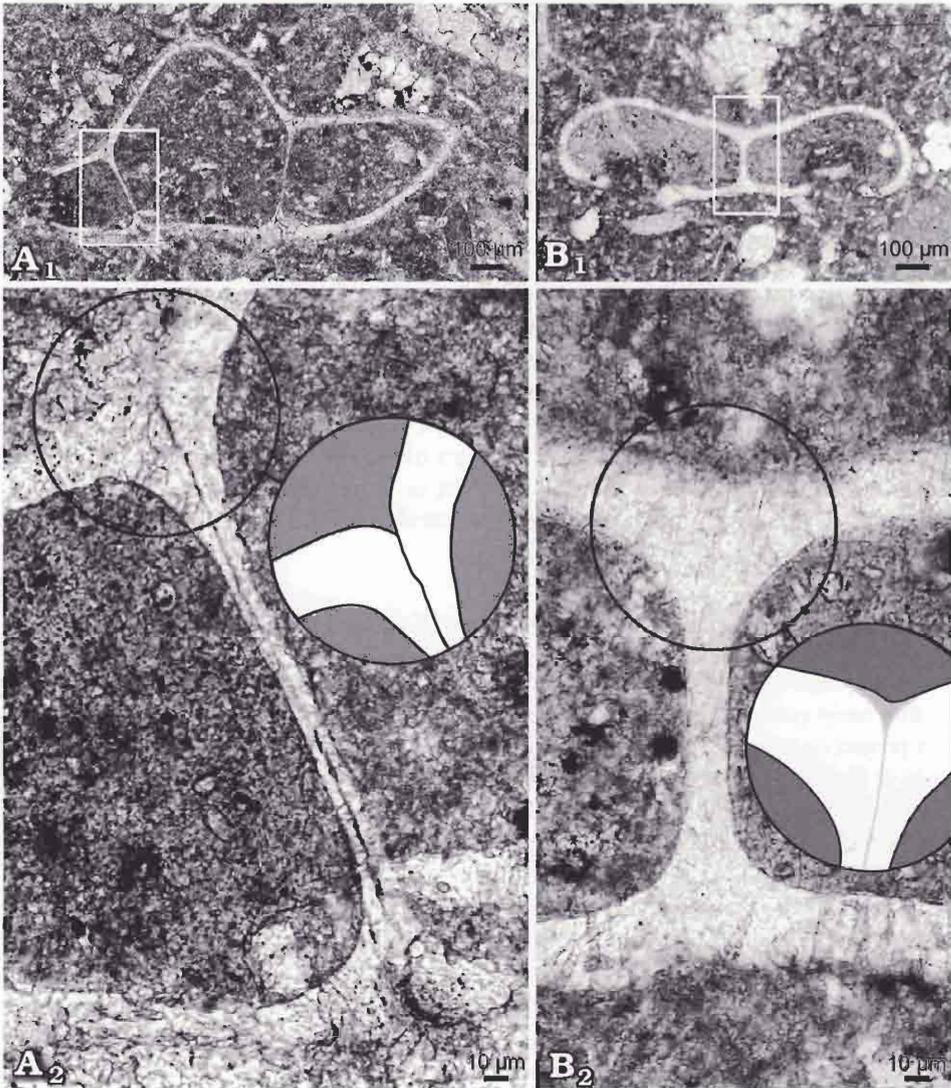


Fig. 13. Sclerites of cancelloriids from the Lower Cambrian of Horse Gully, South Australia, in petrographic thin sections; plane polarized light. SAMP 30332 (**A₁**, **A₂**). SAMP 30334 (**B₁**, **B₂**). Diagrams in enlargements show traced outlines of walls. Light grey area in outline diagram shows the maximum extent of the matter that needs to be accounted for by merging of organic matrix before mineralization (cf. discussion). Sections also figured by Bengtson *et al.* (1990: fig. 37A, B, D, E).

asionally preserved (cf. Fig. 13A₁, A₂ and B₁, B₂). The matter obscuring the ray boundaries is accounted for by a wedge less than 10 μm thick (Fig. 13B₁, B₂); it is not necessary to invoke a different secretory regime for this wedge, which in all respects seems to be part of the originally mineralized organic matrix.

Thirdly, ascidian spicule formation is basically similar to that in most other metazoans, i.e. the spicules are built from the outside, without any deposition from the inside

(Lambert *et al.* 1990; Lambert 1992). In at least one species of ascidian, the sclerocytes remain in contact with the spicules, allowing the latter to continue growing during the growth of the animal (Lambert 1992: p. 241). Following Lambert (1992), Mehl (1996) wrote about a 'deuterostomian system' of biocalcification, represented by echinoderms and ascidians (which she assumes to be directly derived from an echinoderm) and compares this with the biomineralization in chancelloriids. Mehl acknowledges that 'no evidence exists to decide if any homology of these two systems can be established' (Mehl 1996: p. 383). We agree, and stress that the fundamental differences between the two systems make a homology between them extremely unlikely.

Conclusion. — The chancelloriid integument, with its resilience and structural complexity, is clearly different from the sponge exopinacoderm, with its occasional thin structureless cuticle. The sclerites are an integral part of the integument, formed in continuity with the soft integument, and they are homologous neither with sponge spicules, nor with spongin fibres or ascidian spicules. Homologues of the chancelloriid sclerites appear instead to be those of the other coeloscleritophorans, on basis of the structural, compositional and morphological similarities (Bengtson & Missarzhevsky 1981; Bengtson *et al.* 1990).

Functional and ecological considerations

In contrast to sponge spicules, which permeate the soft tissue and only in some cases form a spiny body surface, chancelloriid sclerites are positioned on the body surface and the rays project outwards. Sponge spicules often have a supportive role; in fact, their importance in deterring predators seems to be limited, at least in the Recent biota (Chanas & Pawlik 1995, 1996; Waddell & Pawlik 2000a, b). Chancelloriid sclerites are too scattered to have had any supportive function. The composite nature of the material that built up the rays – an organic core capped by a thin mineralized wall – would have rendered them comparatively hard, tough and stiff. An analogy with stiff cactus spines – which closely resemble chancelloriid sclerites in morphology as well as position on the surface of the organism, and which are known to deter herbivores (e.g., Theimer & Bateman 1992; LeHouérou 1996) – suggests that a prime function of chancelloriid sclerites was to ward off predators (see also Bengtson 1994).

Specimens in the Burgess Shale demonstrate that at least some species of *Allonnia* had the basal end (the one opposite the apex) anchored in soft sediment (Bengtson *et al.* 1996). The apparent lack of bilateral symmetry also testifies to a sedentary mode of life. This suggests that chancelloriids may have been suspension feeders. There is no evidence of external filtering structures (such as tentacles). Consequently, if *Allonnia* was a suspension feeder, it would be expected to bring the nutrient-laden water insided the body. The Chengjiang material has not revealed any body openings that could allow water currents to pass through. As discussed above, one possible place for such an opening would be within the apical tuft of sclerites, where details of the soft integument are obscured by the mass of sclerites in the fossils. However, suspension feeding through a single, restricted opening is very inefficient, because exhalant and inhalant currents need to be separated. The flexible integument of the Chengjiang specimens does not reveal any structures that could be interpreted as indicating the position of a second body opening. Nor does it show any sign of more numerous, smaller body

openings. As discussed above, however, the presence of ostium-sized openings (50 μm or smaller) cannot be ruled out, because of the relative coarseness of the preservation. The available evidence thus does not rule out a sponge-type circulatory model (with numerous very small inhalant pores and one or a few exhalant ones).

An alternative mode of feeding is predation, as known from cnidarians, which manage the task through a single body opening. However, with few exceptions cnidarians use external tentacles to capture their prey, and such structures are absent in *Allonnia*.

The presence of a thick, leathery, integument would seem to argue against the chancelloriids obtaining a significant part of their nutrition by uptake of dissolved organic matter directly through the skin. There is, however, a possibility that *Allonnia* and other chancelloriids were closely associated with bacterial or algal symbionts. This would relieve them of the need for an elaborate food-capturing system and digestive tract, as in the case of the gutless vestimentiferan 'rift worms', which obtain the bulk of their nutrition from bacterial symbionts (Bright *et al.* 2000). The high levels of ambient nutrients in the Early and Middle Cambrian seas, as suggested by the globally extensive phosphorite deposits (Cook & Shergold 1986), may have made such a mode of living feasible.

Further considerations of the feeding modes of chancelloriids will rely heavy on more detailed evaluations of their anatomy and of their contentious relationships with halkieriids and other coeloscleritophorans. This is beyond the scope of the present article.

Systematic palaeontology

Family Chancelloriidae Walcott, 1920

Genus *Allonnia* Doré & Reid, 1965

Allonnia phrixothrix sp. n.

Figs. 1, 2, 3, 4, 5, 7, 8, 11.

Derivation of the name: Greek *phrixos*, standing on end, shivering, and *thrix*, hair, alluding to the bristly surface of the cuticle.

Material. — Holotype RCCBYU 10160a (Hou *et al.* 1999: p. 155, fig. 225; Figs. 1, 2, 3a, 4). Paratypes RCCBYU 10160b (Fig. 3B), RCCBYU 10161 (Figs. 5, 7) and RCCBYU 10162 (Fig. 8).

Type occurrence. — Lower part of the Yu'an-shan Member, Qiongzhusi Formation, Xiaolantian Section, Chengjiang, Yunnan, China.

Diagnosis. — Species of *Allonnia* with large, robust sclerites (fully formed rays about 8 mm long; basal width of rays about 400 μm). Rhombically arranged integumental platelets, 50–60 μm long and 30–40 μm wide, carrying 100 μm long spinules. Width of body up to 50 mm or more.

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Pokrywa ciała u kambryjskich Chancelloriidae

STEFAN BENGTON i XIANGUANG HOU

Streszczenie

Przedstawiono wyniki badań pokrywy ciała u doskonale zachowanych okazów Chancelloriidae z rodzaju *Allonia*, z wczesnego kambru południowo-zachodnich Chin (tzw. fauna Chengjiang). Pokrywa ciała tych zwierząt składała się z drobnych elementów (ok. $30 \times 60 \mu\text{m}$ średnicy) ułożonych w rombowy wzór. Elementy te zinterpretowano jako nakładające się na siebie płytki (skleryty) mające w swej dystalnej części kolcowate wyrostki. Porównania z innymi Chancelloriidae sugerują, że aragonitowe skleryty tkwiły na powierzchni elastycznej pokrywy ciała, na wzór kolców kaktusa, i obie te struktury (tj. skleryty i elastyczna pokrywa) były wytworami ciągłego, wewnętrznego i zewnętrznego oskórka. W sklerytach, zewnętrzny oskórek był zmineralizowany, zaś do ich wnętrza wnikał niezmineralizowany wewnętrzny oskórek oraz komórki epitelialne. Elastyczną pokrywę ciała tworzyły niezmineralizowane warstwy wewnętrznego i zewnętrznego oskórka. Przedstawiona interpretacja budowy pokrywy ciała oraz sklerytów jest zgodna z interpretacją Chancelloriidae jako Coeloscleritophora (enigmatycznej grupy organizmów kambryjskich), nie zgadza się zaś ze spotykaną niekiedy interpretacją tych organizmów jako gąbek lub zachw.