SKELETAL MICROSTRUCTURE INDICATES CHANCELLORIIDS AND HALKIERIIDS ARE CLOSELY RELATED

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Abstract: Chancelloriids are problematic, sac-like animals whose sclerites are common in Cambrian fossil assemblages. They look like sponges, but were united with the slug-like halkieriids in the group Coeloscleritophora Bengtson and Missarzhevsky, 1981 based on a unique mode of sclerite construction. Because their body plans are so different, this proposal has never been well accepted, but detailed study of their sclerite microstructure presented here provides additional support for this grouping. Both taxa possess walls composed of a thin, probably organic, sheet overlying a single layer of aragonite fibres orientated parallel to the long axis of the sclerite. In all halkieriids and in the chancelloriid genus Archiasterella Sdzuy, 1969, bundles of these fibres form inclined projections on the upper surface of the sclerite giving it a scaly appearance. On the lower surface of the sclerite, the projections are absent. This microstructure appears to be unique to chancelloriids, halkieriids, and their relatives, siphogonuchitids and sachitids. (The sclerites of another putative halkieriid relative, Wiwaxia Walcott, 1911, are unmineralized, making direct comparisons impossible.) Thus, similarity both at the level of sclerite construction and the level of sclerite microstructure suggests that chancelloriid, halkieriid, sachitid, and siphogonuchitid sclerites are homologous. The difference in chancelloriid and halkieriid body plans can be resolved in two ways. Chancelloriids either represent a derived condition exhibiting complete loss of bilaterian characters or they represent the ancestral condition from which the bilaterally symmetric halkieriids, and the Bilateria as a whole, derived. The latter interpretation, proposed by Bengtson (2005), implies that coeloscleritophoran sclerites (‘coelosclerites’) are a plesiomorphy of the Bilateria, lost or transformed in descendent lineages. Given that mineralized coelosclerites appear in the fossil record no earlier than c. 542 Ma, this in turn implies either that the Ediacaran record of bilaterians has been misinterpreted or that coelosclerite preservability increased at the beginning of the Cambrian Period. The former is difficult to reconcile with Ediacaran trace and body fossil evidence, but the latter may be possible, reflecting either independent mineralization of organic-walled sclerites in chancelloriids and halkieriids or the opening of a taphonomic window that favours coelosclerite preservation.

Key words: chancelloriids, halkieriids, biomineralization, microstructure, sclerites, Coeloscleritophora.

Chancelloriids were Cambrian animals that possessed a radially symmetrical, sac-like body covered with an array of star-shaped sclerites. Their phylogenetic affinities are controversial; first interpreted as sponges (Walcott 1920; Sdzuy 1969), they were later united with the halkieriids, wiwaxiids, sachitids, and siphogonuchitids into the Coeloscleritophora Bengtson and Missarzhevsky, 1981, a group characterized by a multisclerite exoskeleton and mineralized sclerites displaying a prominent internal cavity, a restricted basal foramen, and no evidence of accretionary growth (Bengtson and Missarzhevsky 1981). Later, Bengtson et al. (1990) and Bengtson (2005) added some microstructural observations in support of the hypothesis.

The affinities between chancelloriids and other coeloscleritophorans have never been well accepted, however. Butterfield and Nicholas (1996) rejected a coeloscleritophoran affinity and instead supported the original interpretation of chancelloriids as sponges. Mehl (1996) also rejected a coeloscleritophoran affinity, and speculated that chancelloriids may be related to ascidians. Conway Morris and Chapman (1996) suggested that the chancelloriid and halkieriid body plans are so different that it is likely their sclerites are convergent. In a later paper, they recognized only halkieriids, siphogonuchitids, and wiwaxiids as a natural group (Conway Morris and Chapman 1997). Most recent systematic treatments are agnostic about the higher-level relationships of chancelloriids (e.g. Mehl 1998; Fernández Remolar 2001; Janussen et al. 2002; Randell et al. 2005); only Bengtson and Hou (2001) and Bengtson (2005) have argued recently in favour of a coeloscleritophoran affinity. Criticism of a
chancelloriid-coeloscleritophoran relationship has been based primarily on the dissimilarity between chancelloriid and wiwaxiid sclerites (a criticism that is undermined by the questionable status of the wiwaxiids themselves; see Butterfield 1990), but rejection of the concept reflects a more general unease about the fundamental difference in chancelloriid and halkieriid body plans (e.g. Dzik 1994; Conway Morris and Chapman 1996). Halkieriids clearly possessed bilateral symmetry and exhibited additional characters, including accretionary shells and a slug-like foot, that suggest a relationship with members of crown-group Bilateria, in particular, members of the Lophotrochozoa (Conway Morris and Peel 1995). They thus presumably possessed other bilaterian or eumetazoan characters such as a gut, internal organs, and a coelom. Chancelloriids, in contrast, lack bilateral symmetry, as well as a gut, internal organs, and a coelom (Bengtson 2005).

Given such distinct differences in body plans, it is possible that the similarity in halkieriid and chancelloriid sclerite construction noted by Bengtson and Missarzhevsky (1981) is the result of convergent evolution. But even when skeletal elements are similar at one level, convergence can often be detected by examining other structural levels (Hickman 2004). Here, I build on the observations of Bengtson et al. (1990), Porter (2004b), and Bengtson (2005) as well as new observations of the chancelloriid, *Archiasterella hirundo* Bengtson, in Bengtson et al. 1990, presented here, to show that the sclerites of chancelloriids, halkieriids, sachitids, and siphogonuchitids not only have a unique mode of sclerite construction but also share a unique sclerite microstructure.

**MATERIAL AND METHODS**

Sclerites of *Archiasterella hirundo* were picked from acid maceration residues obtained during an earlier study of Early Cambrian fossils from South Australia (Bengtson et al. 1990). The fossils come from samples UNEL1763a and UNEL1848 from the Parara Limestone, Curramulka, Yorke Peninsula (localities described in Bengtson et al. 1990). Sclerites are preserved as phosphatic casts and moulds. Specimens were coated with gold and palladium and viewed using a JEOL JSM-6300V scanning electron microscope at 15 kV. Specimens of *Australohalkieria superstes* Porter, 2004b and *Wiwaxia* Walcott, 1911 were processed in an earlier study of Middle Cambrian phosphatized assemblages from the Georgina Basin, Australia (Porter 2004b).

Repositories. The specimens illustrated here are housed in the following repositories, which are abbreviated as follows: CPC, Commonwealth Palaeontological Collections, Geoscience Australia, Canberra; SAM, South Australia Museum, Adelaide; SMNH, Swedish Museum of Natural History, Stockholm; SM, Sedgwick Museum, University of Cambridge; GPIN, Nanjing Institute of Geology and Paleontology, Nanjing; and GSC, Geological Survey of Canada, Ottawa.

**MICROSTRUCTURE OF COELOSCLERITOPHORAN SCLERITES**

*Halkieriid sclerites*

Porter (2004b) studied well-preserved sclerites belonging to halkieriids from the Middle Cambrian Georgina Basin, Australia, and provided a reconstruction of sclerite microstructure. Comparison with other halkieriid species described in the literature indicates that there is a microstructural theme that characterizes the entire group. It consists of the following four characters (see Text-fig. 1):

1. A thin outer layer, possibly organic in original composition. Almost all halkieriid casts exhibit this outer layer, preserved through secondary phosphatization. It can be identified by its smooth or granular, wrinkled appearance. It is often partly degraded, particularly where it covers tubercles or plates (Pl. 1, figs 4, 6, 15, 17, 20); fibrous elements of the inner layer are occasionally visible beneath (Pl. 1, fig. 4). The outer layer is distinct from any secondary diagenetic coating, which is usually thinner, consists of radially orientated crystals, and obscures detail on the sclerite surface (e.g. Pl. 1, figs 7–8). A primary origin is also suggested by its contact with internal moulds (Porter 2004b). An originally organic composition, now replaced by calcium phosphate, is suggested by two observations. First, it sometimes appears wrinkled, indicating a degree of pliability (Pl. 1, figs 11–12). Second, its texture, consisting of spheroidal, randomly orientated calcium phosphate crystals, appears similar to that observed in secondarily phosphatized fossils known to have been originally organic (Porter 2004b). Whether or not the layer may have been lightly mineralized is unclear. For a more detailed discussion of primary versus secondary diagenetic coating and evidence for original composition, see Porter (2004b).

2. An inner layer composed of aragonite fibres orientated parallel to the long axis of the sclerite and either parallel to the sclerite surface or inclined toward its distal tip. Phosphatic casts of longitudinally orientated fibres may be observed where the outer organic layer is degraded (e.g. Pl. 1, fig. 4) or entirely gone (Pl. 1, figs 10, 22). Fibres may also be preserved as external moulds, giving steinkerns a ‘subdued fibrosity’ (Bengtson et al. 1990, p. 81, fig. 62F). Fibres may be either more or less parallel to the sclerite surface (Porter 2004b, fig. 6.5) or imbricated toward the distal tip of the sclerite (Pl. 1, figs 9–10, 14–
An originally aragonitic composition of the inner layer is suggested by its fibrous structure and ubiquitous remineralization (Bengtson and Conway Morris 1984; Runnegar 1985; Bengtson et al. 1990; Porter 2004b). Bumps on the surfaces of internal moulds suggest that this inner layer was either pitted or permeated by pores (Pl. 1, fig. 13; cf. Wrona 2004).

3. Aragonite fibres bundled into discrete ‘projections’ that are commonly inclined from the vertical toward the distal tip of the sclerite. Sclerites may exhibit just one kind of projection (e.g. lamellae, Pl. 1, fig. 14; the ‘rows’ of Porter 2004b), or a combination: plates in the central region of the sclerite flanked by tubercles on its outer rims and central ribs (Pl. 1, figs 16–18); plates that trend distally into tubercles (Pl. 1, figs 19–20), or tubercles interspersed with spines (Pl. 1, fig. 21). In some cases, these projections are missing, probably incompletely phosphatized and thus dissolved during acid maceration, leaving holes in the outer organic layer indicating where they once were (e.g. Pl. 1, figs 6, 12; Bengtson et al. 1990, fig. 48A–E). The projections appear to be formed by bundles of fibres, seen beneath the degraded outer layer (e.g. Pl. 1, figs 4, 15; Bengtson et al. 1990, fig. 51l), and are not simply thickened outgrowths of the organic layer. It is not clear how these bundled fibres interact with the other fibres that make up the wall; they may form a separate entity embedded within the larger wall (cf. the ‘platelets’ of Bengtson 2005, fig. 6, and the ‘oblong structures’ of the chancelloriid Archiasterella Sdzuy, 1969; noted by Randell et al. 2005, fig. 4) or they may be continuous with it (cf. Porter 2004b, fig. 7). Projections are commonly inclined from the vertical toward the tip of the sclerite (Pl. 1, figs 3–4, 14–15, 18, 21; Bengtson et al. 1990, figs 46F, 48F–G).

4. A lower surface where the projections are absent. No tubercles, spines, plates or lamellae are observed on the underside of halkieriid sclerites. Instead, there are thin, imbricated layers of fibres (Pl. 1, fig. 22), which impart an undulating appearance to the overlying organic layer (Pl. 1, figs 1–2). Other authors have noted that the lower surface appears to be covered in fine transverse lineations (Jell 1981; Bengtson and Conway Morris 1984; Bengtson et al. 1990; Conway Morris and Chapman 1997); these are interpreted here to reflect the imbricated layers of fibres (Text-fig. 1B).

**Sachitid and siphogonuchitid sclerites**

A survey of published photographs and descriptions suggests that sachitids and siphogonuchitids exhibit the same microstructure as halkieriids. Most sclerites of the sachitid Hippophasrangites dailyi Bengtson, in Bengtson et al. 1990, for example, exhibit a thin outer layer comparable to the organic layer seen in halkieriids (Text-fig. 2A–B, H–J). Longitudinally orientated fibres visible in some partially eroded specimens of *H. dailyi* (Text-fig. 2C–D) and in a specimen of *Sachites proboscideus* Meshkova, 1969; (Text-fig. 2E–G) are consistent with an inner layer composed of...
fibrous aragonite (also see Bengtson et al. 1990, p. 63, who inferred that the sclerites were originally calcareous and that their inner surfaces had ‘fine longitudinal striations’). Sclerites of H. dailyi display prominent, flattened tubercles on their upper surfaces that imbricate toward the distal tip of the sclerite (Text-fig. 2A–B, H–I; S. proboscideus lacks projections). As with halkieriid sclerites, the tips of these tubercles are often eroded, leaving holes beneath where aragonite fibres presumably had been (Text-fig. 2B, H). The lower surface of the sclerite is smooth (Text-fig. 21–J).

Siphogonuchitid sclerites also possess a thin, smooth outer covering comparable to the outer layer observed in halkieriids (Text-fig. 3A–F, H). One species, Siphogonuchites cf. triangularis Qian, 1977, possesses prominent, inclined tubercles on the upper surface of their sclerites (Text-fig. 3A–C), although in most species, these are subdued (e.g. Text-fig. 3D–E) or absent (Text-fig. 3G–I). An inner fibrous microstructure is evident in some specimens (Text-fig. 3F, H–I; also see Qian and Bengtson 1989, fig. 16A to 16C; and Conway Morris and Chapman 1996, fig. 9H–I).

**Chancelloriid sclerites**

The chancelloriid Archiasterella hirundo, from the Early Cambrian of South Australia, exhibits all four microstructural characters found in other Coeloscleritophora:

1. A thin outer layer, possibly organic in original composition. A thin outer layer is observable in casts of most A. hirundo sclerites (Pl. 2, figs 1–10, 13). This layer is closely comparable to the outer layer found in halkieriids: it is <1 μm thick, has a smooth or granular texture, and may be partly degraded (e.g. Pl. 2, fig. 3) or absent (Pl. 2, figs 5–6, 13) where it covers tubercles. Interestingly, the organic coating covers the entire sclerite rosette in a single continuous layer, rather than wrapping each individual ray. This is also true for the inner fibrous layer (Pl. 2, fig. 11), suggesting that the rosette was mineralized as a whole, rather than fused together after ray mineralization (Mehl 1996). Its consistent thickness and lack of radially orientated crystals (Pl. 2, fig. 10 vs. Pl. 1, fig. 8) suggests that, as inferred for halkieriids, it is a primary component of the sclerite wall, now secondarily phosphatized, rather than a product of diagenetic overgrowth by phosphate.

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**EXPLANATION OF PLATE 1**

Scanning electron microscopy (SEM) images of diagenetically phosphatized halkieriid sclerites.

Figs 1–2, 7–8, 13–15, 22. Australohalkiera superstes Porter, 2004b, 1–2, CPC 37219. 7–8, CPC 37205. 13, CPC 37214. 14, CPC 37216. 15, CPC37180. 22, CPC 37174. Specimens in 1–2 from sample PK98-42, all others from PK98-41. All specimens from the Middle Cambrian Monastery Creek Formation, Rogers Ridge, Duchess Embayment, Georgina Basin, Australia. Images originally published in Porter (2004b) as figs 9.5, 6.11, 10.12, 10.14, 6.4, 7, 6.8, and 6.1, respectively, and reprinted here by permission of the Association of Australasian Palaeontologists.


Figs 5–6. Halkieriid sclerite. SAM P41615, sample UNEL 1848, Abadiella huoi Zone, Lower Cambrian Parara Limestone, Curramulka Quarry Section, Curramulka, Yorke Peninsula, South Australia.


Figs 11–12. Possible halkieriid spine. SAM P42162, sample UNEL 1763a, Abadiella huoi Zone, Lower Cambrian Parara Limestone, Curramulka Quarry Section, Curramulka, Yorke Peninsula, South Australia.


Fig. 18. Halkiera mira (Qian and Xiao, 1984). SM X26087, sample X1/91/44, Xiaoerbulak phosphorite mine, Lower Cambrian Yurtus Formation, Xinjiang, China. Image originally published in Conway Morris and Chapman (1997) as fig. 6.10, and reprinted here by permission of the Paleontological Society.

Fig. 21. Halkieriid sclerite. SM X26111, sample X1/91/17, Aksu phosphorite mine, Lower Cambrian Yurtus Formation, Xinjiang, China. Image originally published in Conway Morris and Chapman (1997) as fig. 8.2, and reprinted here by permission of the Paleontological Society.
PORTER, halkieriid sclerites
Porter (2004b). Its original composition is unknown, but is assumed to have been organic because of its similarity to the presumed organic layer of halkieriids.

Butterfield and Nicholas (1996) isolated organically preserved chancelloriid sclerites from the Mount Cap Formation, north-west Canada, that exhibit what they referred to as a ‘cellular’ pattern on their outer surface (Text-fig. 4; see also Butterfield and Nicholas 1996, fig. 5.2). This surface is interpreted here to be the outer organic layer; the ‘cellular’ pattern is interpreted to be impressions of the fibrous aragonite layer (no longer present) that lay just beneath. Note that the Mount Cap specimens comprise more than simply the outer organic layer; some specimens preserve remnants of soft tissue that filled the interior of the sclerite (Butterfield and Nicholas 1996).

Many authors have noted the presence of a tough, organic integument covering intersclerite areas of the chancelloriid body (Walcott 1920; Butterfield and Nicholas 1996; Bengtson and Hou 2001; Janussen et al. 2002; Randell et al. 2005). It is possible that this is continuous with the outer organic layer of the sclerite discussed here (Mehl 1996; Bengtson and Hou 2001; Janussen et al. 2002; Bengtson 2005), as it also exhibits imbricated projections similar in size to those on the surface of Archias-terella sclerites (see below).

2. An inner layer composed of aragonite fibres orientated parallel to the long axis of the sclerite and either parallel to the sclerite surface or inclined toward its distal tip. In *A. hirundo* sclerites with an outer layer that is missing or partly degraded, an inner layer consisting of c. 1-µm-thick fibres may be visible (Pl. 2, figs 3, 11–12). The fibres are orientated parallel to the long axis of each ray in the compound sclerite. Similar fibres have been observed in other chancelloriid species; in addition to their longitudinal orientation, these fibres are inclined toward the tip of each ray, similar to those observed in halkieriids (Bengtson et al. 1990; Mehl 1996, 1998; Kouchinsky 2000a; Janussen et al. 2002; Wrona 2004). There is a general consensus that these fibres were originally aragonitic, as suggested by their acicular morphology (Bengtson et al. 1990; Mehl 1996; Kouchinsky 2000a; Janussen et al. 2002; Wrona 2004). Primary aragonite mineralogy is also indicated by chancelloriid specimens from the Early Cambrian Forteau Formation in Canada, which are preserved as calcite spar-filled moulds and co-occur with primary calcite skeletons exhibiting fabric retention (James and Klappa 1983).

3. Aragonite fibres bundled into discrete ‘projections’ that are commonly inclined from the vertical toward the distal tip of the sclerite. The upper surface of *A. hirundo* sclerites is covered with c. 20-µm-long tubercles, which, like

the tubercles, plates, and lamellae of halkieriid sclerites, appear to be composed of bundled fibres and covered by an organic layer (Pl. 2, fig. 3; see also Pl. 2, figs 1–2, 7–9). The tubercles are often arranged in a roughly regular pattern of transverse rows (Pl. 2, figs 2, 6, 13), and may be more concentrated in the centre part of the compound sclerite, particularly where the rays join (Pl. 2, figs 8, 13). As with halkieriids, most tubercles are inclined, although rather than inclining in four different directions toward the distal tip of each ray, the tubercles tend to be inclined in the same direction, toward the tip of the larger median ray and away from the strongly recurved ray (Pl. 2, figs 1, 7; see also Bengtson et al. 1990, figs 29–30). This is consistent with the observation, noted above, that the sclerite rosette was mineralized as a single unit. Tubercles are often missing, represented only by holes in the outer layer (Pl. 2, figs 5–6, 9, 13).

Randell et al. (2005) described regularly spaced, 40–50 µm ‘oblong structures’ on the surfaces of both the intersclerite areas and the sclerites of Archiasterella fletchergyllus Randell et al., 2005. Their size and distribution suggest that they may be homologous to the tubercles observed in Archiasterella hirundo (Bengtson and Hou 2001; Bengtson 2005). Similar structures have been noted in the intersclerite areas of the chancelloriid Alonnia Dore´ and Reid, 1965 (Bengtson and Hou 2001; Janussen et al. 2002).

Note that the tubercles observed in A. hirundo are different from, and not necessarily related to, the prominent bumps commonly found on chancelloriid steinkerns (e.g. Pl. 2, fig. 15; see also Wrona 2004, fig. 6M–O, Q, and Bengtson et al. 1990; fig. 35). These are likely to be moulds of pores in the inner wall (Wrona 2004). Steinkerns of halkieriid sclerites may exhibit similar bumps on their surface (Pl. 1, fig. 13); these were interpreted by Porter (2004b) to represent moulding of a pitted surface on the inner wall, and were speculated to mirror the projections above (Text-fig. 1).

4. A lower surface where the projections are absent. The sides of Archiasterella hirundo sclerites may be covered in tubercles, but with the exception of the ray tips, the lower surface of the sclerite is devoid of them (Pl. 2, figs 4–5).

Wiwaxiid sclerites

The relationship between wiwaxiids and other coeloscleritophorans is in dispute (Butterfield 1990, 2006; Bengtson

2005; Caron et al. 2006; Conway Morris and Caron 2007). Because wiwaxiid sclerites are unmineralized (Conway Morris 1985), their microstructures cannot be directly compared with those of other Coeloscleritophora. However, it is noteworthy that the sclerites of some wiwaxiid species do exhibit micro-scale patterns that are broadly similar to the microstructural theme described above (see also Bengtson 2005). The phosphatized and organically preserved sclerites of Wiwaxia corrugata (Matthew, 1899), for example, exhibit sub-µm-scale, longitudinally orientated lineations (Text-fig. 5B; also see Butterfield 1990, fig. 3B) that could be homologous to the longitudinally orientated aragonite fibres found in other Coeloscleritophora. Similarly, some wiwaxiid sclerites exhibit tubercles on their surface (Text-fig. 5C–F; Butterfield 1990, fig. 3B), in some cases arranged in prominent transverse rows (Text-fig. 5E–F; Butterfield 1994); these are reminiscent of the transverse rows of tubercles exhibited by the sclerites of sachitids and halkieriids. A third wiwaxiid species, represented by a single, secondarily phosphatized specimen, has a very different microstructure, however: no longitudinal lineations and transverse rows of pits instead of tubercles (Text-fig. 5G–H). In addition, this species has longitudinally orientated channels instead of longitudinally orientated ribs observed in other wiwaxiid species and other Coeloscleritophora. Assuming this fossil is indeed a cast of a wiwaxiid sclerite (and not an external mould), its microstructure bears little resemblance to that of the halkieriids and other Coeloscleritophora.

**Summary**

Table 1 summarizes microstructural data for halkieriids, sachitids, siphogonuchitids, and chancelloriids; wiwaxiids are not included as their unmineralized sclerites are not directly comparable. Each family includes at least some species that exhibit all four microstructural characters. Sachitids, siphogonuchitids, and chancelloriids also include species with simpler microstructures: they lack the projections (character 3) that are so prominent in other species and which give them their ‘scaly’ appearance. (Interestingly, not only do all halkieriids exhibit this character but also the family as a whole displays a much wider diversity of projection ‘types’.) Whether the simpler microstructure is derived or whether it represents the primitive condition for the Coeloscleritophora is not known.

**COELOSCLERITOPHORAN MICROSTRUCTURE IS UNIQUE**

Similar microstructure in the chancelloriids, halkieriids, and other Coeloscleritophora would not be remarkable if such microstructure were widespread. But even among Cambrian animals, which might be expected to have similar microstructures given their relatively recent common ancestor, coelosclerite microstructure is unique. Although...
many Cambrian skeletal elements appear to have been composed of fibres, reflecting the common crystal habit of aragonite (e.g. hyoliths, anabaritids, cambroclaves, and several mollusc and mollusc-like taxa), the arrangement of these fibres in most taxa differs substantially from that of coelosclerites (Runnegar 1985; Conway Morris and Chen 1989; Bengtson et al. 1990; Kouchinsky 1999, 2000a, b; Feng et al. 2001; Kouchinsky and Bengtson 2002; Feng and Sun 2003).

Two exceptions are some cambroclaves and ‘cap-shaped fossils’. Like coelosclerites, cambroclave sclerites appear to be composed of fibres, reflecting the common crystal habit of aragonite (e.g. hyoliths, anabaritids, cambroclaves, and several mollusc and mollusc-like taxa), the arrangement of these fibres in most taxa differs substantially from that of coelosclerites (Runnegar 1985; Conway Morris and Chen 1989; Bengtson et al. 1990; Kouchinsky 1999, 2000a, b; Feng et al. 2001; Kouchinsky and Bengtson 2002; Feng and Sun 2003).

Similarity between cap-shaped fossil and coelosclerite microstructure would not be surprising given that representatives of the former have been hypothesized to be part of a coeloscleritophoran scleritome (Bengtson 1992; Conway Morris and Chapman 1996). Some cap-shaped fossils possess a fibrous texture (e.g. Maikhanella Zhegallo, in Voronin et al. 1982 and Ramenta Jiang, in Luo et al. 1982; see Bengtson 1992; Feng et al. 2002) and are covered in granules, scales, or spicules reminiscent of the inclined projections on most coelosclerites (e.g. Ernogia Jiang, in Luo et al. 1982; Maikhanella; see Qian and Bengtson 1989; Bengtson 1992). The spicules of Maikhanella are thought to be homologous with entire coelosclerites, however; the spine-like projections seen in phosphatic specimens have been interpreted to be internal moulds of a siphogonuchitid-like spine (Bengtson 1992). The microstructure of Ramenta appears to be much more complex, with a crossed lamello-fibrillar inner layer covered by an outer layer of vertical fibres (Feng et al. 2002).

COELOSCLERITOPHORAN SCLERITES ARE HOMOLOGOUS

If it is true that chancelloriids and halkieriids are unrelated, then sclerite similarities reflect convergent evolution. The idea of convergent sclerites by itself is not surprising; biomineralization evolved independently many times in animals (Bengtson and Conway Morris 1992) and multi-element skeletons in particular seem to be widespread (Kingsley 1984; Bengtson and Conway Morris 1992). But chancelloriid and halkieriid sclerites appear to share both macrostructural similarities (i.e. those noted by Bengtson and Missarzhevsky 1981) and microstructural similarities, and it seems unlikely that both arose by convergent evolution. Convergence arises either because similar characters experienced similar selective regimes or because of a limited number of ways a character can be made (cf. Hickman 2004). The latter explanation is unlikely to be true for coelosclerites; the variety of sclerite

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Table 1. Distribution of microstructural characters 1–4 in mineralized coeloscleritophorans (the wiwaxiids are excluded because of their questionable status and because their sclerites are unmineralized).

<table>
<thead>
<tr>
<th>Character #</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Thin outer organic layer</td>
<td>Single inner layer of longitudinally orientated aragonitic fibres</td>
<td>Projections</td>
<td>Lower surface smooth</td>
</tr>
<tr>
<td>Halkieriidae</td>
<td>Yes</td>
<td>Yes</td>
<td>Lamellae</td>
<td>Yes</td>
</tr>
<tr>
<td>Sachitidae</td>
<td>Yes</td>
<td>Yes</td>
<td>Platelets</td>
<td>Tubercles</td>
</tr>
<tr>
<td>Siphogonuchitidae</td>
<td>Yes</td>
<td>Yes</td>
<td>Tubercles</td>
<td>None</td>
</tr>
<tr>
<td>Chancelloriidae</td>
<td>Yes</td>
<td>Yes</td>
<td>Tubercles</td>
<td>None</td>
</tr>
</tbody>
</table>

‘Yes’ indicates there is evidence for this character in at least one species in the family. For character 3, the type of projection is listed for each family. Note that some species of sachitids, siphogonuchitids, and chancelloriids do not exhibit this character, as indicated by ‘none’.

Macro- and microstructures encountered in metazoa suggests there are many ways to make a sclerite (e.g. Lowenstam 1989; Lowenstam and Weiner 1989). This is true even for the earliest animals, whose skeletons exhibit a wide range of constructional types (Thomas et al. 2000) and microstructures (Runnegar 1985; Kouchinsky 1999, 2000a, b; Feng et al. 2001; Kouchinsky and Bengtson 2002; Feng and Sun 2003). Furthermore, skeletal macro- and microstructures often behave as independent characters; congruence, therefore, cannot simply be explained by constraints imposed by one structural level dictating the design of the other. For example, the trabecular bone of vertebrates, the ossicles of echinoderms, and the skeletons of acroporid scleractinians are all similar in their open framework architectures, although their mineralogy and length scale of the supporting elements are quite different and, indeed, taxon-specific (Lowenstam and Weiner 1989; J. Weaver, pers. comm. 2007). Likewise, similar microstructures do not necessarily induce similar macrostructures, as evident by, for example, the variety of skeletal architectures built from spherulites (Lowenstam and Weiner 1989). Thus, if chancelloriid and halkieriid sclerites are convergent, their sclerites must have been subject to remarkably similar selection regimes operating at both the macrostructural and microstructural level. This seems unlikely given their rather different life habits.

Discussion

If chancelloriids and halkieriids are closely related, then the difference in chancelloriid and halkieriid body plans can be resolved in one of two ways, both with challenging implications. The first possibility is that chancelloriids represent a derived body plan relative to halkieriids (Text-fig. 6A; Bengtson and Conway Morris 1984). In this case, halkieriid-like ancestors of chancelloriids lost bilateral symmetry and, presumably, changed their mode of feeding as they switched from a vagrant to a sessile lifestyle. Loss of overt bilateral symmetry is common in animals (e.g. echinoderms, priapulids, and kinorhynchs), but even so, these taxa retain vestiges of their former symmetry as well as other key features that indicate membership in the Bilateria, such as a gut and internal organs. Chancelloriids, in contrast, betray no evidence of a bilaterian ancestry, despite their exceptional preservation (Bengtson 2005). Thus, if chancelloriids are secondarily derived, their transformation from an ancestral bilaterian body plan is unparalleled.

The second possibility, recently suggested by Bengtson (2005), is that chancelloriids represent the ancestral body plan from which halkieriids were derived (Text-fig. 6B–C). If halkieriids are at least stem-group bilaterians, the hypothesis implies that the transformation between chancelloriids and halkieriids captured the evolution of bilateral symmetry, a gut, and internal organs that we know must have occurred at some point in bilaterian ancestry (Bengtson 2005). Furthermore, it implies that coelosclerites are a symplesiomorphy of crown group Bilateria, secondarily lost or transformed in descendent lineages (Bengtson 2005). Significantly, the evolution of coelosclerites would predate that of other bilaterian characters, including those assumed to be lacking in chancelloriids: bilateral symmetry, a gut, and internal organs (Text-fig. 6B–C).

This poses a conundrum. Mineralized coelosclerites appear no earlier than c. 542 Ma, yet Ediacaran trace fossils and body fossils suggest that bilaterally symmetric animals had evolved by c. 555 Ma (Narbonne 2005),
and molecular clock analyses suggest an even earlier date, >570 Ma (Peterson et al. 2004). This means that either the Ediacaran fossil record has been misinterpreted and bilaterally symmetric (stem- or crown-group) Bilateria did not appear until Early Cambrian time or there is a hidden Precambrian record of coelosclerites (and chancelloriids) (Bengtson 2005). While the evidence for crown group Bilateria during Ediacaran time has been challenged (see Budd and Jensen 2000, and Benton and Donoghue 2007 for reviews), evidence for bilaterally symmetric stem-group bilarians is difficult to dismiss (e.g. Fedonkin and Waggone 1997; Jensen 2003; Droser et al. 2005). On the other hand, the abundance and widespread occurrence of coelosclerites in Lower Cambrian rocks suggests that unless these animals were extremely rare, their sclerites should have been preserved, unless sclerite preservability itself changed at the beginning of the Cambrian Period. Bengtson (2005) proposed that chancelloriids and halkieriids may have independently evolved mineralized sclerites from organic-walled precursors. In other words, while the macro- and microstructure of chancelloriid and halkieriid sclerites would be homologous (dictated by their homologous organic framework), the impregnation of bimineral would not (Text-fig. 6B). Their appearance in the Early Cambrian would thus reflect the convergent evolution of biomineralization in the two groups, not the initial evolution of coelosclerites.

**TEXT-FIG. 6.** Possible reconstructions of coeloscleritophoran and bilaterian relationships and character evolution. Of the Coeloscleritophora, only halkieriids and chancelloriids are shown because these are the only taxa whose body plans are known. A, halkieriids and chancelloriids are both crown-group bilarians; chancelloriid morphology reflects loss of several bilaterian synapomorphies. B–C, bilaterians are nested within the Coeloscleritophora (Bengtson 2005); chancelloriids are outside crown-group Bilateria and halkieriids may be within the stem- or crown-group. Coelosclerites are a plesiomorphy of crown-group Bilateria, lost or transformed in multiple clades. B, mineralized coelosclerites evolve independently in halkieriids and chancelloriids from an organic-walled precursor. C, mineralized coelosclerites are homologous in chancelloriids and halkieriids but do not appear in the fossil record until secondary phosphatization of fossils is widespread.
Alternatively, sclerite preservability may have changed at the beginning of the Cambrian owing to the opening of a ‘phosphatization window’ (Text-fig. 6C; Porter 2004a). Preservation and sampling of many small shelly fossils, including coeloscleritophoran sclerites, is largely dependent on their secondary phosphatization; the apparent decline of small shelly fossil diversity at the end of the Early Cambrian may have been exaggerated by the closure of this phosphatization window (Porter 2004a). It is likewise possible that the appearance of small shelly fossils at the beginning of the Cambian was influenced by increasing prevalence of phosphatization; indeed, more than 25 phosphatized biotas have been described from Namkit-Daldynian and Tommotian rocks (c. 542–521 Ma; Porter 2004a), but only one is known from c. 555–542-Ma rocks (e.g. Hua et al. 2003, 2005; dates from Maloof et al. 2005).

CONCLUSIONS

Secondary phosphatization of halkieriid and chancelloriiid sclerites permits detailed reconstructions of original sclerite microstructures. The sclerites of both taxa share a similar microstructure characterized by four components: (1) an outer organic layer; (2) an inner layer of aragonitic fibres oriented parallel to the long axis of the sclerite; (3) an upper surface that may exhibit projections composed of bundled aragonitic fibres; and (4) a lower surface that lacks projections. The mineralized sclerites of other coeloscleritophoran taxa, in particular sachitids and siphogonuchitids, also exhibit this microstructure; otherwise it is unique among the earliest mineralizing animals. Despite the significant difference between chancelloriiid and halkieriid body plans, the similarity in both sclerite construction (Bengtson and Missarzhevsky 1981) and sclerite microstructure makes it unlikely that their sclerites are convergent. Chancelloriiids may represent either a highly derived bilaterian clade or the ancestral condition from which crown-group Bilateria were derived (Bengtson 2005).

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