HALKIERIIDS IN MIDDLE CAMBRIAN PHOSPHATIC LIMESTONES FROM AUSTRALIA

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ABSTRACT—Halkieriids are part of a distinctive Early Cambrian fauna, the “Tommotian fauna” sensu Sepkoski (1992), that is preserved mostly as phosphatic and secondarily phosphatized skeletal elements. The distinctiveness of the Tommotian fauna is ascribed, in part, to its preferential elimination during the end-Early Cambrian mass extinction event (the “Botomian extinction”). Newly discovered halkieriids in phosphatic limestones of the Middle Cambrian (Ptychagnostus gibbus Zone) Monastery Creek Formation, Georgina Basin, Australia, now indicate that this group not only survived the end-Early Cambrian extinction, but was at least locally abundant thereafter. Most of the Georgina halkieriid sclerites can be accommodated within a single species, Australohalkieria superstes new genus and species, described and partly reconstructed here. Remaining sclerites probably represent two additional but rare halkieriid species. Additional newly discovered sclerites may have affinities with the sachitid, another problematic “Tommotian” taxon related to the halkieriids. Rare wiwaxiid sclerites extend the taphonomic and geographic distribution of this clade. The Monastery Creek Formation provides a valuable window on Middle Cambrian life, both because it provides information that is distinct from but complementary to other, similarly aged windows (e.g., the Burgess Shale) and because it represents a taphonomic window similar to those that preserve Early Cambrian small shelly problematica. A decline during the Cambrian in conditions necessary for the early diagenetic phosphatization of shallow-shelf and platform limestones may have effectively closed this taphonomic window, potentially biasing apparent patterns of diversity change through the period.

INTRODUCTION

The Early Cambrian fossil record is characterized by unique skeletal assemblages that include the spongellike archaeocythans and a number of mostly problematic small skeletal elements, known collectively as small shelly fossils (SSFs; Matthews and Missarzhevsky, 1975). These assemblages are distinctive enough from Middle and Upper Cambrian assemblages that Sepkoski (1992) recognized the “Tommotian” fauna as a discrete evolutionary fauna separate from his Cambrian fauna s.s. In part, this distinctiveness reflects an extinction event at the end of the Early Cambrian [the “Botomian extinction” (Palmer, 1982; Signor, 1992; Zhuravlev and Wood, 1996)] that eliminated many “Tommotian” taxa s. Sepkoski (1992) (Zhuravlev and Wood, 1996). The extinction thus marks the evolutionary turnover from an early fauna populated mostly by skeletal problematica to the more familiar Cambrian fauna s.s.

To understand better the nature and extent of this turnover, it is important to control for preservational mode and environment, as taxa under consideration may be taphonomically or facies restricted. Because many elements of the “Tommotian” fauna appear to be both facies restricted and preserved by early diagenetic phosphatization (e.g., Brasier and Hewitt, 1979; Brasier, 1990; Landing, 1992; Mount and Signor, 1992; Dzik, 1994; Khomentovskii and Karlova, 1994), it is useful to compare them with taphonomically and environmentally comparable assemblages of Middle Cambrian age. The Monastery Creek Formation of the Middle Cambrian Georgina Basin, Australia, offers one such opportunity. It contains an SSF assemblage that, like many of its well-studied Early Cambrian counterparts, preserves secondarily phosphatized skeletal elements associated with condensed horizons in phosphatic limestones (Southgate and Shergold, 1991; Gravestock and Shergold, 2001).

For the most part, the Monastery Creek assemblage confirms the pattern highlighted by Sepkoski (1992): many of its dominant constituents, such as echinoderms, inarticulate brachiopods, nontrilobite arthropods, and trilobites, are typical of the Cambrian fauna s.s. Also present, however, at relatively high abundances, are halkieriids. Halkieriids were sluglike metazoans armored with a coat of mineralized sclerites and two prominent shells at either end (Conway Morris and Peel, 1990, 1995). Their phylogenetic affinities with modern groups are problematic, but they appear to fall somewhere within the Lophotrochozoa, possibly representing stem-group mollusces (e.g., Bengtson, 1992; Runnegar, 2000), stem-group annelids (e.g., Jell, 1981; Conway Morris and Peel, 1995), stem-group brachiopods (Williams and Holmer, 2002; Holmer et al., 2002; Cohen et al., 2003; Conway Morris and Peel, 1995), or a stem group of a combination of lophotrochozoan phyla (Conway Morris and Peel, 1995). Conway Morris and Peel (1995) argued for specific stem-group connections between the Sirius Passet halkieriid and brachiopods; between Thambetolepis and annelids (cf. Jell, 1981); and between a Siberian halkieriid species (Bengtson and Conway Morris, 1984) and the annelid+brachiopod clade. Halkieriids are a common and diverse component of the “Tommotian” fauna, where they are represented by abundant sclerites (e.g., Qian and Bengtson, 1989; Bengtson et al., 1990; Conway Morris and Chapman, 1997; Conway Morris et al., 1998) and rare articulated specimens (Conway Morris and Peel, 1990, 1995). However, with the exception of possible halkieriid shells reported from the Burgess Shale (Conway Morris, 1995), halkieriids have not been identified in post-Botomian successions. Their presence in the Monastery Creek Formation, thus, provides the first compelling evidence that halkieriids survived the end-Early Cambrian extinction.

GEOLOGY

The Georgina Basin, a shallow intracratonic basin covering ~325,000 km² in western Queensland and the Northern Territory, Australia (Fig. 1.1), formed during a Late Proterozoic phase of crustal extension (Lindsay et al., 1987; Southgate and Shergold, 1991). By Middle Cambrian time, marine conditions prevailed in the basin and phosphogenesis was widespread (Southgate and Shergold, 1991). Today, diverse assemblages of phosphatized fossils can be found in Middle Cambrian rocks throughout the basin (e.g., Fleming, 1973; Runnegar and Jell, 1976; Jones and Mackenzie, 1980; Henderson and Mackinnon, 1981; Shergold and...
PORTER—MIDDLE CAMBRIAN HALKIERIIDS FROM AUSTRALIA


Southgate, 1986; Southgate et al., 1988; Müller and Hinz, 1992; Hinz-Schalreuter, 1993; Müller and Hinz-Schalreuter, 1993; Kruse, 1998; Mehl, 1998; personal observations). A particularly diverse and well-preserved assemblage—and the focus of this study—occurs in the Monastery Creek Formation [formerly referred to as the Beetle Creek Formation (Russell and Trueman, 1971)] exposed in the Burke River Structural Belt ~140 km southeast of Mt. Isa, near the town of Duchess in western Queensland (Fig. 1.2). Although fossils have been reported from three localities in the Duchess region (Mt. Murray, Rogers Ridge, and Phosphate Hill), sample collection for this study was limited for logistical reasons to Rogers Ridge (Fig. 1.3).

In the Burke River Outlier, the Monastery Creek Formation disconformably overlies the Thorntonia Limestone. It is overlain, with a conformable to laterally disconformable contact, by the organic-rich Inca Shale, which contains fossiliferous carbonate nodules in the Rogers Ridge area (Müller and Hinz-Schalreuter, 1993). The Monastery Creek Formation is divided into two members: the lower Siltstone Member, a 50–60-m-thick succession containing white fissile siltstone, chert, and minor pelletal phosphorite; and the upper Monastery Creek Phosphorite Member, a 10–15-m-thick unit comprising grainstone phosphorite, chert, phosphatic and siliceous siltstone, shale, sandstone, and phosphatic limestone (de Keyser and Cook, 1972; Soudry and Southgate, 1989). Phosphatized fossils occur throughout the Monastery Creek Phosphorite Member; the fossils discussed in this study come from two beds located at ~6 and ~7.5 m above the contact with the Siltstone Member, and ~8.7 and ~7.2 m, respectively, below a marker bed containing hollow chert nodules (noted in Müller and Hinz, 1992). The unit from which the fossils derive consists of tabular, fine-grained limestones ~10–15 cm thick, devoid of hummocky cross-stratification or other cross-lamination, suggesting deposition below fair-weather wave base. Some beds are siliciﬁed and most contain abundant ferruginized and phosphatic hardgrounds. Fossils occur in high concentrations in these rocks, with as many as ~20 fossils per mm² evident in thin section. Also present in varying abundance are nonskeletal phosphatic clasts.

Middle Cambrian phosphatic sediments from the Duchess Region were deposited in a restricted embayment that was bounded by land on its northern, western, and southern sides, and whose eastern connection with the Burke River Outlier, an appendage of the Georgina Basin (see Fig. 1.1, 1.2), was restricted by shallow banks (Russell and Trueman, 1971).
In the sequence stratigraphic framework formulated by Southgate and Shergold [1991; see also Gravestock and Shergold (2001)] for Middle Cambrian sediments of the Georgina Basin, the Monastery Creek Formation forms a progradational package (referred to as parasequence set 2) within the transgressive systems tract of their sequence 2. Phosphatic and glauconitic hardgrounds deposited on the transgressive surface of parasequence set 2 indicate sediment starvation; subsequent to this transgression, phosphatic carbonate beds, including the fossiliferous units from Rogers Ridge, were deposited in the structural lows, or subbasins, of the embayment (Russell and Trueman, 1971; Southgate and Shergold, 1991).

**Age**.—The Monastery Creek Formation contains Ptychagnostus gibbus, diagnostic of the Late Templetonian/Floran Stage of the Middle Cambrian of Australia (O’Pik et al., 1957; O’Pik, 1979). As yet, no formal stages have been recognized for the Cambrian System, but attempts at constructing internationally recognized divisions of Cambrian time have been made. The latest of these (Geyer and Shergold, 2000), based largely on trilobite biostratigraphy, correlates the Late Templetonian/Floran of Australia with intervals that all fall within the Middle Cambrian, wherever it is recognized (including the Delamaran/Early Marjuman of Laurentia, the Amgan of Siberia, the Acadian and St. David’s series of Avalonia, and the Taijiangian of South China; Geyer et al., 2000).

## THE ASSEMBLAGE

The Monastery Creek Phosphorite Member contains a diverse assemblage of fossils, representatives of which are shown in Figure 2. Bradorid head shields (or carapaces), including those of Zepaera and Monasterium (Fleming, 1973), are the most common fossil fragments (Fig. 2.1, 2.2). Occurring at lower abundances are shells of juvenile acrothelid (Fig. 2.3) and acrothelid brachiopods (Fig. 2.4), probable echinoderm fragments (Fig. 2.5), and hyolith shells similar to those of Hypothytheca and Actinothytheca spp. from the Early Cambrian of Australia (Fig. 2.6; Bengtson et al., 1990). Halkieriid sclerites (e.g., Fig. 2.7) are the fifth most abundant fossils, constituting about five percent of all identifiable specimens (of course, each halkieriid animal produced many sclerites). Present at lower abundance levels are trilobite fragments [including larval hypostomes; Fig. 2.8, 2.9; cf. Speyer and Chatterton (1989)], chancelloriid sclerites (Fig. 2.10), hollow spheres 50–100 μm in diameter that possibly represent egg capsules (Fig. 2.11; Roy and Fähræus, 1989; Walossek et al., 1993), cap-shaped fossils of possible molluscan affinities (Fig. 2.12; cf. Qian and Bengtson, 1989), and paleoscolecid worm fragments (Fig. 2.13). Many fragments (37 percent) are unidentifiable. All of these taxa have been preserved by phosphate, but their mode of preservation varies, possibly reflecting differences in original mineralogy.

### MATERIALS AND METHODS

Fossils were extracted from the carbonate matrix by maceration in 10–15 percent acetic acid, picked using a dissecting microscope, mounted on stubs, coated in gold and/or palladium, and viewed with a LEO 982 scanning electron microscope at 5 or 10 kV.

All figured specimens have been deposited in the Commonwealth Palaeontological Collections (CPC), Geoscience Australia, Canberra, under accession numbers CPC 37156–CPC 37228.

## SYSTEMATIC PALEONTOLOGY

Taxonomic treatment of disarticulated fossils is difficult and fraught with uncertainty (Bengtson, 1985a). This is particularly the case with halkieriid sclerites, which are known to be highly variable within a single scleritome. Nevertheless, early halkieriid taxonomies (e.g., Bengtson and Conway Morris, 1985; Qian and Bengtson, 1989; Bengtson et al., 1990) assumed that certain sclerite characteristics (e.g., the presence and nature of lateral zones and wall ornamentation) were uniform within a single species, an assumption supported by subsequently discovered articulated specimens (Conway Morris and Peel, 1995). Guided by both these taxonomies and descriptions of articulated halkieriids (Conway Morris and Peel, 1995), I use overall sclerite morphology, and in particular the nature of the lateral zones, as a species-level character.

The majority of sclerites can be assigned to a single species, *Australohalkiera superstes* n. gen. and sp. In the following sections, I will describe the sclerites of this species in detail, reconstruct their original composition, morphology, wall structure, and position in the scleritome, and compare this species with Early Cambrian halkieriids. The remaining Georgina sclerites are distinctive enough to discourage their inclusion in *A. superstes*, but they are not abundant enough to provide detail sufficient for taxonomic description. These sclerites will be discussed briefly in the section, “Other sclerites.”

Terminology used in sclerite description is drawn from Bengtson and Conway Morris (1984) and illustrated in Figure 3. Briefly stated, one end of the sclerite is called the base, and the remainder, the blade (Fig. 3.1). The basal region can be identified by the presence of a flattened facet, typically with an indentation housing a foramen (Fig. 3.2). The concave side of the sclerite is defined as its lower surface, the convex side as upper (Fig. 3.3). The plane of the base is defined as that which is perpendicular to the basal facet and aligned along its longest dimension (Fig. 3.4); similarly, the plane of the blade corresponds to the dimensions of greatest flattening (Fig. 3.4). In most cases, the sclerites are asymmetric: the blade may curve within the plane of the blade. The side to which the blade curves is referred to as the inferior side because, when imbricated, this side lies below the adjacent sclerite (Bengtson and Conway Morris, 1984). Similarly, the superior side lies above the adjacent sclerite (Fig. 3.1).

**Family Halkieriidae** Poulsen, 1967

**Discussion.**—Poulsen (1967) erected the family Halkieriidae, but he did not provide a diagnosis for it, or for the genus Halkiera. In his restudy of the type material, Bengtson (1985b) published a diagnosis for the Halkieriidae, later used by Qian and Bengtson (1989). Bengtson et al. (1990) modified this diagnosis,
noting the presence of distinctive sclerite types and lateral sclerite zones that may comprise longitudinal canals (canals that flank the central canal) or may be divided into lateral canals or camerae (numerous canals extending outward from the central canal; these can be thought of as transversely divided longitudinal canals). The diagnosis presented in Conway Morris and Peel (1995, p. 310) modified those of both Bengtson et al. (1990) and Qian and Bengtson (1989), stating that halkieriid sclerites had “lateral canals of varying length.” It is unclear whether this diagnosis embraces sclerites with undivided, longitudinal canals (including the sclerites discussed here). The strong similarity between these sclerites and those with lateral canals, however, suggests that they do belong in the same family.

**Genus Australohalkieria** new genus

*Type species.*—A. superstes n. sp.

*Other species.*—Halkieria parva Conway Morris *in* Bengtson et al., 1990.

**Diagnosis.**—Halkieriids with lateral zones comprising undivided longitudinal canals.

**Etymology.**—Latin *australis*, southern, and *halkieria*, a reference to its geographic locality and its similarity to the genus *Halkieria*.

**Discussion.**—Early diagnoses for the genus *Halkieria* either explicitly (Bengtson et al., 1990) or implicitly (Bengtson, 1985b; Qian and Bengtson, 1989) included those halkieriids with *longitudinal canals* (Bengtson et al., 1990). Conway Morris and Peel (1995), however, restricted the diagnosis of *Halkieria* such that only those halkieriids with “short lateral canals” are included (p. 310). Under this restricted definition, those sclerites with longitudinal canals (including the Georgina sclerites and the Australian species originally described as *Halkieria parva* (Bengtson et al., 1990)) must be placed in a new genus.

**Australohalkieria superstes** new species

*Figures* 2.7, 4, 6, 8, 9

**Diagnosis.**—Species of *Australohalkieria* *n.* gen. with sclerites that possess a flattened central canal. Flattening begins at midpoint of blade, where longitudinal canals originate, and is only visible on the upper surface of the sclerite.

**Description.**—Longitudinal canals are cylindrical in shape and extend beyond the central canal, resulting in a distal sclerite tip with two points separated by a rounded valley. Includes four variable sclerite types, distinguishable from each other by base-blade transition and shape of basal facet. Basal facet commonly with indentation, perforated by a small (5–10 μm diameter) foramen connected to a short tube. Wall composed of fibrous plates imbricated in the distal direction, resulting in appearance of parallel transverse lineations on both upper and lower sclerite surfaces. Sclerites range from ~250 to ~1,000 μm in length.

**Etymology.**—From the Latin *superstes*, surviving, with reference to the fact that this species is part of a lineage that survived the end-early Cambrian extinction event.

**Types.**—*Holotype:* CPC 37189, *Figure* 4.4. *Paratypes:* CPC 37159, 37161, 37169–37171, 37173–37184, 37190–37200, 37211–37216, 37219, 37222, 37224. From samples PK98–41 and PK98–42; *Figures* 2.5, 4.1–4.3, 4.5, 4.6, 8, 9.

**Other material examined.**—Two hundred and forty-five sclerites. Sclerites are represented by internal molds (e.g., Figs. 4.3, 4.6, 8.1–8.4, 8.9, 8.11, 9.4, 9.12, 9.16, 9.17), with, in some cases, part or all of the phosphatized wall (e.g., Figs. 4.1, 4.2, 4.4, 4.5, 8.5–8.8, 8.10, 8.12–8.21, 9.1–9.3, 9.5, 9.6, 9.8, 9.9, 9.11, 9.13–9.15, 9.18, 9.19). Outer surfaces may also be encrusted with diageneric apatite (e.g., Figs. 10.12–10.14).

**Occurrence.**—Middle Cambrian (Late Templetonian/Floran) Monastery Creek Phosphorite Member, Rogers Ridge, Burke River Outlier (samples PK98–41, 42, 44, 45, 47, 48).

**Australohalkieria parva** (Conway Morris, 1990) new combination


**Diagnosis.**—Species of *Australohalkieria* *n.* gen. with sclerites that possess an unflattened central canal; longitudinal canals arise at or near base of blade.

**Material examined.**—Bengtson et al. (1990) examined material from acid maceration residues. For this publication, figures 41–48 in Bengtson et al. (1990) were examined.
Porter—Middle Cambrian Halkierids from Australia

**Occurrence.**—*Australohalkiera parva* n. comb. occurs in Early Cambrian rocks in the Flinders Ranges (Ajax Limestone: Mt. Scott Ranges locality) and Yorke Peninsula (Parara Limestone: Curramulka, Horse Gully, and Kulpara localities); South Australia (Bengston et al., 1990).

**Discussion.**—See Bengtson et al. (1990) for a detailed description of this species.

**DESCRIPTION AND RECONSTRUCTION OF AUSTRALOHALKIERIA SUPERSTES SCLERITES**

**Original composition.**—Halkierid sclerites were originally calcareous in composition (e.g., Bengtson and Missarzhevsky, 1981; Bengtson and Conway Morris, 1984; Bengtson et al., 1990; Conway Morris and Peel, 1995). An aragonitic mineralogy is indicated by the presence of <1-μm-diameter needlelike fibers suggestive of fibrous aragonite in the wall of *Australohalkiera superstes* sclerites (Fig. 6.2, 6.6, 6.10; cf. Runnegar, 1985) and by the preservation of *A. superstes* sclerites, similar to that of other taxa in the assemblage known to be originally aragonitic (e.g., hyoliths and chancelloriids; James and Klappa, 1983; Bengtson et al., 1990; Mehl, 1996; Kouchinsky, 2000a, 2000b), and distinct from that of calcitic taxa. In addition to an aragonitic layer, there is evidence for an outer organic coating (see the section, *Wall structure*, below).

**Morphology.**—Proximally, the sclerites of *Australohalkiera superstes* n. gen. and sp. have a single internal cavity. At the midpoint of the blade, the cavity divides into three roughly equal parts: a central canal flanked by two longitudinal canals. At the point of division, the upper surface of the central canal slopes sharply downward and comes in close contact with the lower surface such that the canal becomes extremely flattened; indeed, in internal molds, the prong that represents the central canal is commonly broken off [Figs. 4.3, 4.6, 8.1, 8.2, 8.9–8.11, 9.4, 9.16 (although see Fig. 9.7)]. No pores that connect longitudinal canals to the central canal have been observed (cf. *A. parva*; Bengtson et al., 1990), although the extremely close proximity (~1–2 μm separation) of canals suggests a very thin intervening wall. The three-part blade structure is limited to the internal part of the sclerite. On the outer surface of the sclerite, the wall is continuous; only the flattened aspect of the central canal, visible on the upper surface of the sclerite, and the two-pointed tip hint at this internal structure (e.g., Figs. 4.4, 4.5, 8.6, 8.8, 8.14, 9.19). On the lower surface, the wall lacks any indication of the inner compartmentalization (e.g., Figs. 4.1, 8.5, 8.7, 8.12, 8.13, 8.15, 9.3, 9.5, 9.18, 10.3).

The basal region is variable in structure (indeed, this is the basis for distinguishing sclerite types; see next section), but can be identified by the presence of an indentation (e.g., Fig. 8.12, 8.13, 8.18, 8.19) and/or a foramen (e.g., Figs. 8.2–8.4, 8.10, 8.11, 8.16, 8.20, 8.21, 9.10, 9.16, 9.17). The foramen is most obvious in internal molds (although see Fig. 8.20) where it takes the form of a sharply delineated circular depression, 5–10 μm in diameter and at least as deep. This suggests that the sclerite wall curved into the cavity, forming a short canal or tube (cf. fig. 7.1 in Conway Morris and Chapman, 1997). The presence on one specimen of wall fragments that curve inward into the foramen (Fig. 8.21) and the presence of phosphatic infill (of the tube) in the center of the foramen (Fig. 8.3), surrounded by a narrow valley where the original tube wall was located, confirm this interpretation. A reconstruction of *A. superstes* sclerite morphology is illustrated in Figure 5.

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**Figure 4**—Examples of *A. superstes* blade structure. 1–3, views of the lower surface of siculate sclerites with varying degree of wall preservation; 1, CPC 37211; 2, CPC 37212; 3, CPC 37170. 4–6, as in 1–3, but for the upper surface of cultrate sclerites; 4, CPC 37189; 5, CPC 37190; 6, CPC 37171. Scale bar represents 150 μm for 1, 2, 4, 5; 110 μm for 3; and 90 μm for 6.
The most distinctive aspect of *A. superstes* n. gen. and sp. is the flattened central canal that forms a depression on the upper distal surface of the sclerites. Ascribing function to this structure has obvious difficulties, but one possible explanation is that the depressions were involved in sensory activity (cf. Jell, 1981). As discussed below, what is interpreted to be the mineralized part of the sclerite does not extend across the depressed region; only the outer layer of the wall, interpreted to be originally organic (see below), extends across it. Thus, the depression represents an area where there might have been easy exchange of gases, ions, or simple biomolecules, possibly through a permeable organic layer, between the sclerite’s internal tissue and the external environment. The restriction of the sclerite’s internal cavity—thought to have been tissue- or fluid-filled during life and have aided in sclerite mineralization (Bengtson and Missarzhevsky, 1981). Their restriction to the upper distal surface of the sclerite suggests that, like the depressed area of the sclerite discussed above, the spaces may have been involved in sensory reception. The lowermost part of the inner layer appears to have been continuous (e.g., Figs. 6.5, 7), although ~1-µm bumps on the surface of some internal molds (Figs. 6.4, 8.9) suggest that the inner surface of this layer was pitted.

Covering both the rows and the spaces between them is the second outer layer of the sclerite wall. In well-preserved specimens, this layer forms an undulating cover that covers the entire sclerite (Fig. 6.11). Possibly, this layer is a diagenetic encrustation, but several features argue against this. First, internal molds of the central canal are regular and smooth on their upper, flattened surface, indicating the presence of a primary boundary layer, on which the mold templated. The lower, fibrous layer of the wall is not present in this region; only the outer layer is. Collectively, these observations suggest that the thin outer layer is a primary feature of the sclerite wall. Second, the outer layer does not fill in the spaces between the rows, as would be expected if it were an encrustation. Instead, it extends straight from one ridge to the next, bridging the intervening spaces (Fig. 6.8). In sclerites where the spaces are represented by secondary phosphatic infill (e.g., Fig. 6.9, 6.10, 6.12), there is a sharp line of contact between the outer layer and the infill (see, in particular, Fig. 6.12), suggesting the outer layer acted as a template for the phosphatic infill.

Third, unlike diagenetic encrustation observed on some fossils in the Rogers Ridge assemblage (e.g., Fig. 10.14) and elsewhere (e.g., Xiao and Knoll, 1999), apatite crystals forming the layer are not elongate or oriented perpendicular to the coated surface but instead are spherical and randomly oriented, a fabric typical of phosphatized organic material (Fig. 6.13; Allison, 1988; Martill, 1988; Wilby, 1993; Wilby and Briggs, 1997; Xiao and Knoll, 1999; Zhao and Bengtson, 1999). Collectively, these features suggest that the outer layer represents a primary organic layer that coated the sclerite. An outer organic layer has also been observed in sclerites of chancelloroids (J.-Y. Chen, personal commun., cited in Mehl, 1996, although see Bengtson and Hou, 2001); metazoans which may be closely related to the halkieriids (Bengtson and Missarzhevsky, 1981; Bengtson and Hou, 2001; although see, e.g., Butterfield and Nicholas, 1996). Its function is unknown, but it may have been involved in sclerite mineralization or protection, similar to the molluscan periostracum (Taylor and Kennedy, 1969; Tevesz and Carter, 1980; Bottjer, 1981). Indeed, if halkieriids are

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**Figure 5**—A reconstruction of *A. superstes* blade structure, including cross sections at two different locations (indicated by the dashed lines). See text for explanation.

**Figure 6**—Details of *A. superstes* sclerite wall structure. 1, detail of sclerite shown in Figure 8.7; 2, detail of sclerite shown in Figure 9.1; 3, detail of sclerite shown in Figure 9.9; 4, detail of sclerite shown in Figure 9.7; 5, detail of sclerite shown in Figure 8.16; 6, CPC 37172; 7, CPC 37221; 8, detail of sclerite shown in Figure 9.2; 9, detail of sclerite shown in Figure 9.2; 10, detail of sclerite shown in Figure 2.5; 11, detail of sclerite shown in Figure 9.5; 12, arrows point to line of contact between the phosphatic infill and the outer layer; CPC 37220; 13, cross section of outer layer; CPC 37223. Scale bar represents 20 µm for 1, 5, 10; 4 µm for 6, 7; 15 µm for 2, 8; 30 µm for 3; 50 µm for 4, 11; 10 µm for 9; 2 µm for 12; and 3 µm for 13.
stem-group molluscs (Bengtson, 1992; Runnegar, 2000), the organic layer may be homologous with the periostracum. A tentative reconstruction of the sclerite wall is illustrated in Figure 7.

**RECONSTRUCTION OF THE AUSTRALOHALKIERIA SUPERSTES SCLERITOME**

Specimens of articulated halkieriids (Halkieria evangelista Conway Morris and Peel, 1995) from the Early Cambrian Sirius Passet fauna, Greenland, provide a useful guide for reconstructing the scleritome of *A. superstes* n. gen. and sp. The scleritome of *H. evangelista* is bilaterally symmetric, and on either side it is composed of three zones, each consisting of a distinctive sclerite type. “Palmate” sclerites are situated in the dorsal zone of the animal’s body. These are smaller than other sclerite types, bear prominent ribs on their upper surfaces, and are tightly adpressed to the animal’s body (Conway Morris and Peel, 1995). “Cultrate” sclerites are situated on the lateral surfaces of the animal’s body. They also bear prominent ribs and are tightly adpressed to the body, but are larger than the palmate sclerites. “Siculate” sclerites are situated on the ventrolateral margin on either side of the animal’s body. They are approximately the same size as cultrate sclerites, but lack prominent ribs. Rather than being tightly adpressed to the animal’s body, siculate sclerites appear to have extended outward at a 45°–90-degree angle. In addition to the scleritome, the articulated specimens bear two bilaterally symmetric shells, one at the anterior and the other at the posterior end of the body.

Using these sclerite characteristics, I have divided the *A. superstes* sclerites into palmate, cultrate, and siculate types. Each sclerite type includes roughly equal numbers of right- and left-handed forms (e.g., see symmetry pairs in Fig. 8.10–8.13), as would be expected if the scleritome of *A. superstes* n. gen. and sp. were bilaterally symmetric.

**Palmate sclerites** (Fig. 8.1–8.7).—Twelve specimens, ~250–650 μm in length. In these sclerites, the basal facet is long and narrow, mirroring the flattened cross section of the blade. On one side of the sclerite the base may extend beyond the width of the blade, forming a projection, or “auricle” (e.g., Fig. 8.1–8.6, Bengtson and Conway Morris, 1984). A shallow indentation on the basal facet is long and narrow, like the facet itself (faintly visible in Fig. 8.2–8.4, 8.5, 8.6). The foramen is located within this indentation, offset to one side toward the auricle (Fig. 8.2, 8.4). The base is offset from the blade by a ~90-degree bend, such that the plane of the base is perpendicular to the plane of the blade. Other than at the blade-base transition, the blade is not strongly curved. On the upper surface of the blade, a central rib may run from the basal transition to the flattened central canal.

These sclerites are assigned to the palmate type because they exhibit the same characteristics as palmate sclerites of *H. evangelista*. They are the smallest of the sclerite types and have prominent ribs on their upper surface. The sharp angle between the blade and the basal facet suggests that, like the palmate sclerites of *H. evangelista*, they were adpressed to the body surface. Finally, these sclerites share a number of features with Early Cambrian sclerites from disarticulated assemblages identified as pal- mate, including a strongly flattened base and an auricle (Bengtson and Conway Morris, 1984; Qian and Bengtson, 1989; Bengtson et al., 1990).

**Cultrate sclerites** (Figs. 4.4–4.6, 8.8–8.21).—Eighty-eight specimens, ~300–1,000 μm in length. In these sclerites the basal facet is circular to polygonal in shape, with an even rim, ~10 μm wide, around the facet border (Fig. 8.12, 8.13, 8.18, 8.19). The foramen is located in the center of the facet. Like the palmate sclerites, the plane of the base is oriented perpendicular to that of the blade, but it may be offset from the blade by a broad constriction (e.g., Fig. 8.10, 8.11, 8.15–8.17). Most sclerites, when viewed from either the upper or lower surface, have a proximal end that is angular in shape, with the sides of the sclerite bending sharply toward each other to meet in a point (Figs. 4.4–4.6, 8.8–8.16). The sclerite edge dips more steeply away from this point on the inferior side of the sclerite; the sclerite base is oriented such that the longest dimension of the facet is parallel to this edge (Fig. 8.10–8.13, 8.16, 8.18). The upper surface commonly has a central rib, extending from the proximal point to the inferior side of the central canal (Figs. 4.4–4.6, 8.8, 8.9, 8.14).

These sclerites are considered cultrate because, like cultrate sclerites of *H. evangelista*, they are larger than the palmate scler- rites, exhibit prominent ribs, and have an angle between the basal facet and blade that suggests adpression against the animal’s body. In addition, these sclerites are similar to cultrate sclerites identified in other disarticulated assemblages (Bengtson and Conway Morris, 1984; Bengtson et al., 1990; Conway Morris and Peel, 1995), particularly in the appearance of their proximal tips (see especially fig. 51 in Bengtson and Conway Morris, 1984), the shape of their basal facets, and their base-blade transition (e.g., figs. 44c and 45g in Bengtson et al., 1990).

**Siculate sclerites** (Figs. 2.5, 4.1–4.3, 9.1–9.19).—Sclerites consistent with a siculate assignment can be divided into two groups, although rare transitional forms exist.

Group 1 (Figs. 2.5, 4.1–4.3, 9.1–9.10).—Eighty-four specimens, ~400–1,000 μm in length. The basal facet is circular to elliptical and indentation is faint or lacking. The foramen is offset...
Figure 10—Other sclerites. Type I (1–16); variant A (1–14); variant B (15, 16). Type II (17–23). 1, CPC 37185; 2, CPC 37186; 3, 4, CPC 37201; 5, 6, CPC 37187; 7, CPC 37202; 8, CPC 37203; 9, 10, CPC 37204; 11–14, CPC 37205; box in 13 indicates area shown in 14; 15, CPC 37206; 16, CPC 37188; 17, CPC 37168; 18, CPC 37162; 19, 20, CPC 37207; 21, CPC 37208; 22, 23, CPC 37227. Scale bar represents 140 μm in 1; 120 μm for 2, 3; 35 μm for 5; 50 μm for 4, 11, 20, 23; 100 μm for 6, 12, 13, 21, 22; 150 μm for 7, 8; 125 μm for 9, 25 μm for 10; and 75 μm for 17–19.

Figure 9—Siculate (1–10) and possible siculate (11–19) sclerites of A. superstes n. gen. and sp. 1, CPC 37161; 2, CPC 37180; 3, CPC 37181; 4, CPC 37159; 5, CPC 37219; 6, CPC 37213; 7, CPC 37214; 8, CPC 37182; 9, CPC 37183; 10, detail of specimen in Figure 4.3; 11, CPC 37196; 12, CPC 37197; 13, CPC 37198; 14, CPC 37184; 15, CPC 37199; 16, 17, CPC 37200; 18, CPC 37215; 19, CPC 37216. Scale bar represents 100 μm for 1, 3; 150 μm for 2, 5, 6; 200 μm for 4, 7; 125 μm for 8, 11, 12, 18; 350 μm for 9; and 25 μm for 10; 160 μm for 14, 16, 19; 65 μm for 17; 140 μm for 15; and 90 μm for 13.
toward the upper surface of the sclerite (Fig. 9.10). The most distinctive aspect of these specimens, however, is the sigmoidal curve that distinguishes the base from the blade: distally the blade curves sharply away from the upper surface of the sclerite and then curves back such that the basal facet is perpendicular to the plane of the blade. In some cases, the base is also offset by a broad constriction (e.g., Fig. 4.1, 4.2). The degree of sigmoidal curvature varies among sclerites from barely perceptible (Fig. 9.6–9.8) to strongly pronounced (Figs. 2.5, 4.1–4.3, 9.1–9.5, 9.9). Like palmate and cultrate sclerites, these are asymmetric: the curvature is commonly more pronounced on one side than on the other (Fig. 9.6–9.8) and the plane of the blade may be twisted slightly. In all of these specimens, the upper surface lacks a rib.

Group 2 (Fig. 9.11–9.19)—Twenty-eight specimens, ~400–500 μm in length. In these specimens the shape of the basal facet reflects the roughly elliptical cross section of the blade. A shallow, broad indentation on the facet is similar in shape to the facet, and the foramen is slightly offset toward the inferior side of the sclerite (Fig. 9.16, 9.17). The sclerite bends sharply between the base and the blade such that the plane of the base is offset from that of the blade by ~45–90 degrees. The longitudinal axis of the base (perpendicular to the plane of the basal facet) is also bent ~45 degrees relative to the longitudinal axis of the blade, toward the inferior side of the sclerite. In some specimens, a central rib may be present on the upper surface of the sclerite, extending from the edge of the basal facet to the base of the central canal (Fig. 9.12, 9.13).

Like the siclelate sclerites of H. evangelista, these sclerites are comparable in size to the cultrate sclerites and ribs are rare or absent. In addition, the position of the basal facet in these specimens suggests that they projected outward from the animal’s body at a ~45–90-degree angle, like siclelate sclerites on H. evangelista. Finally, the sigmoidal curvature typical of Group 1 is observed in sclerites from disarticulated assemblages that are also identified as sicleate (Bengtson et al., 1990), fig. 47b, c).

Shells.—A distinctive feature of articulated Early Cambrian halkieriids is the presence of two symmetric shells, one at either end of the body (Conway Morris and Peel, 1990, 1995). Since this discovery, putative halkieriid shells have been identified in a number of disarticulated assemblages (e.g., Bengtson, 1992; Conway Morris, 1995; Conway Morris and Chapman, 1997; Conway Morris et al., 1998). No shells that might be ascribed to halkieriids are rare. This could reflect either postmortem sorting of sclerite types (palmate sclerites are on average smaller than the other types) or, more likely, a sclerite whose ventral-lateral zone is expanded in area relative to lateral and dorsal zones. A. superstes sclerites are significantly smaller than Early Cambrian halkieriid sclerites (250–1,000 μm vs. 600–3,000 μm; the presence of larger fossils in the Georgina assemblage and the fact that most Early Cambrian halkieriids are less phosphatized suggests that this difference is not due to taphonomic selectivity). This suggests that the individual(s) represented in the Georgina assemblage were juvenile, their sclerite was composed of many more sclerites than those of Early Cambrian halkieriids, or the species was relatively small.

**Comparison with other halkieriids**

All halkieriids possess calcareous, hollow sclerites arranged in a tightly imbricated, differentiated scleritome. In addition, their sclerite walls share a similar ultrastructure, consisting of distally inclined, fibrous elements—a pattern also observed in chancelloriids (Bengtson et al., 1990; Mehl, 1996; Bengtson, 1999; Kouchinsky, 2000a; Bengtson and Hou, 2001), siphonochitids (Qian and Bengtson, 1989), and sachtids (Bengtson et al., 1990).

There is substantial variation within the halkieriids, however. Sclerites may have lateral zones consisting of longitudinal canals (e.g., Australohalkieria parva (Bengtson et al., 1990)) or multiple lateral canals (e.g., Halkieria mira (Conway Morris and Chapman, 1997); Thambetolepis delicata (Jell, 1981; Bengtson et al., 1990)), or lateral zones may be absent altogether (e.g., Fig. 10.17–10.22). Sclerite walls may be composed of distally inclined rows (A. parva (Bengtson et al., 1990)), plates (e.g., H. sp. (Bengtson and Conway Morris, 1984); H. sthenobasis (Qian and Bengtson, 1989)), or tubercles, or a combination of these (e.g., A. parva, T. delicata (Bengtson et al., 1990); H. mira). Sclerites may also vary in size (~250 mm to ~3,000 mm in length) and in relative numbers of palmate, cultrate, and siclelate types.

**Other sclerites**

Two other morphologically distinct blade types occur in the Georgina assemblage, each with either one or two sclerite morphologies. While it cannot be ruled out that these sclerites belong to A. superstes n. gen. and sp., their inclusion would imply a sclerite that was much more complex (with respect to structural variability as well as the number of sclerite types) than those of Early Cambrian halkieriids. More likely, the structural types correspond to species that were rare in the assemblage and, therefore, are only represented by sclerite types that were most abundant in the scleritome. Lack of information on the range of sclerite variability cautions against erecting species names for these specimens, and, therefore, only a form classification is presented (cf. Bengtson, 1985a).

**Type 1** (Fig. 10.1–10.16)—The internal structure of these sclerites is difficult to discern due to the absence of specimens preserved only as internal molds; in all specimens of this type the wall is preserved, almost always in its entirety. The few specimens that expose part of the internal mold show that, like the
blade of *A. superstes* n. gen. and sp., the distal section is divided into three canals (Fig. 10.11). This is also suggested by the distal tips of the sclerites that, like those of *A. superstes* n. gen. and sp., feature two points (representing each side canal) separated by a valley (Fig. 10.9, 10.10, 10.13). Unlike *A. superstes* n. gen. and sp., however, the middle canal is not flattened. The upper surface of sclerites of this type instead may exhibit a broad central rib or swelling (Fig. 10.7, 10.12, 10.13), probably representing the central canal. The wall structure appears comparable to that of *A. superstes* sclerites (note e.g., the imbricated fibrous rows on the sclerite in Fig. 10.2).

There are two variants with this kind of blade, which differ in base shape:

Variant A (Fig. 10.1–10.11).—Fourteen specimens. In these specimens, the basal facet is not distinct from the surface of the blade. Instead, the proximal part of the blade curves smoothly around a 180-degree angle and tapers to a subrounded point, maintaining the same cross-sectional thickness throughout. The foramen is triangular in shape, about 15 μm at its widest, and is situated at this proximal point, on the upper surface of the blade (Fig. 10.3–10.6, 10.9, 10.12).

Variant B (Fig. 10.15, 10.16).—Only two specimens of this type have been identified, but they are distinctive enough to warrant separation from the specimens mentioned above. Although the sclerite blade is flattened as in variant A, the base is cylindrical with a rounded basal facet. In addition, at the base-blade transition, the sclerites only curve around a 90-degree angle (rather than 180 degrees), such that the presumed basal facet is oriented parallel to the plane of the blade. No information is known about the shape, size, or position of the foramen.

The sharp angle between the base and the blade of both of these variants suggests that they probably occupied the dorsal or lateral zones, where the palmate and cultrate sclerites occur. It is not clear whether these sclerites occupied additional distinctive *A. superstes* sclerite zones or whether they belong to an additional, rare *Australohalkieria* species.

Type II (Fig. 10.17–10.23).—Seven specimens. In these sclerites there are no distinct lateral zones. Instead, the flattened canal remains undivided throughout, tapering distally to a single point. A central rib may be separated from thickened margins by two broad depressions (Fig. 10.22), or may slope evenly to thin edges (Fig. 10.18). Proximally, the blade curves slightly (Fig. 10.17–10.19) or strongly (Fig. 10.21, 10.22) and ends in a flattened base (Fig. 10.19–10.21), comparable to palmate sclerites in Early Cambrian halkieriids. On some sclerites, the base may flare on one (Fig. 10.21) or both (Fig. 10.19) sides so that it is wider than the blade. A small (~5 μm diameter) foramen lies in the center of the basal facet, within a linear indentation that extends the width of the facet (Fig. 10.19, 10.20). The wall is generally not well preserved in these sclerites, with the exception of one specimen that possesses small (7 μm) holes (Fig. 10.22, 10.23) in a phosphatic matrix (a structure similar to that of putative sachitid sclerites, described below).

Assuming that the presence and nature of the lateral zones is a genus-level character of halkieriids, these specimens, which lack lateral zones, represent an additional Middle Cambrian halkieriid genus, distinct from *Australohalkieria* n. gen.

**OTHER NEW TAXA**

*Sachitids* (Fig. 11.1–11.6).—Two distinctive, spiniform specimens have also been recovered from the assemblage. These sclerites are roughly circular in cross section, long and narrow in dimension, and they lack a distinctive basal region. The distal region of the sclerites exhibits roughly triangular holes, ~7 μm wide, regularly arranged in a phosphatic matrix (Fig. 11.3–11.5). These holes appear to represent tubercles that did not become phosphatized and were dissolved during maceration. Partially

**FIGURE 11**—Putative sachitid sclerites (1–6) and wiiwaxiid sclerites (7–11). 1, 2, CPC 37209; 3–6, CPC 37210; in 4, upper box indicates area shown in 5, lower box indicates area shown in 6; 7, 9, 10, wiiwaxiid specimen 1; note complex tubercles in 9, indicated by arrows; note fine parallel lines in 10. Unfortunately, specimen was destroyed during manipulation (sample PK98–41; SEM stub PK98–41-HP2); 8, 11, wiiwaxiid specimen 2; CPC 37228. Scale bar represents 400 μm for 1; 60 μm for 2; 40 μm for 3; 450 μm for 4; 10 μm for 5, 9; and 20 μm for 6; 100 μm for 7; 50 μm for 8; 4 μm for 10; and 30 μm for 11.
phosphatized tubercles can be seen in Figure 11.3. (The surrounding phosphatic matrix may represent a diagenetic encrustation that molded the tubercles, or, as in the halkieriid sclerites, it may represent an outer organic layer.) On the proximal part of the sclerite, the wall structure is similar to that of *A. superstes* sclerites, suggesting that the tubercles coalesced into imbricated plates (Fig. 11.6).

While it is plausible that these specimens represent rare spiniform sclerites belonging to *A. superstes* n. gen. and sp. or another halkieriid (cf. Bengtson et al., 1990), they are most similar, both in morphology and wall structure, to sclerites of the coeloscleritophoran family Sachitidae (cf. *Hippopharangiites* Bengtson in Bengtson et al., 1990), previously known only from the Early Cambrian.

**Wiwaxiids.**—Of special note are two wiwaxiid sclerites, each possibly representing a distinct species [Fig. 11.7–11.11; *Wiwaxia* sp. from the Monastery Creek Formation is also reported but not figured in Southgate and Shergold (1991)]. These originally organic sclerites (Conway Morris, 1985) are preserved as secondarily phosphatized casts, comparable to the phosphatized paleoscoledidan cuticles and possible eggs also found in the assemblage (Fig. 2). Their presence in the assemblage extends not only the taphonomic distribution of this group (known previously only from organic specimens in siliciclastic sediments) but also, together with articulated specimens from the Early Cambrian Emu Bay Shale, Australia (C. Nedin, personal commun., 2000), their geographic range. [Wiwaxiids were known previously only from North America and China (Conway Morris, 1985; Butterfield, 1994; Zhao et al., 1994).] One specimen exhibits the same fine structure observed in sclerites from the Burgess Shale (Butterfield, 1990), including longitudinal ribs, rows of tubercles, and submicrometer lineations (Fig. 11.7, 11.9, 11.10). The other (Fig. 11.8, 11.11) is similar to a specimen from the Mount Cap Formation, northwestern Canada, figured in Butterfield (1994, fig. 2b).

**Conclusions**

The phosphatic limestones of the Monastery Creek Formation, Georgina Basin, provide a window on Middle Cambrian life that is valuable for at least three reasons. First, like other phosphatized assemblages (e.g., Müller, 1985; Xiao et al., 1998), the Monastery Creek Formation preserves a diverse array of taxa, many of which are not preserved under conventional circumstances. Many are preserved in very fine detail, providing insight into the structure and function of their skeletal parts (cf. Müller and Hinz, 1992; Hinz-Schallreuter, 1993; Müller and Hinz-Schallreuter, 1993; Walossek et al., 1993).

Second, the Monastery Creek Formation complements other preservational windows on life during this time. For example, articulated halkieriids in fine-grained siliciclastics from Greenland (Conway Morris and Peel, 1990, 1995) provide unique information about sclerite organization that can be used as a guide to reconstruct halkieriid species from disarticulated assemblages. They provide little information, however, about sclerite morphology and wall structure, information that can be helpful in elucidating phylogenetic relationships. For this, we must rely on phosphatic preservation. Combining information from different preservational windows, then, provides an integrated view not available from any single window.

In addition to providing complementary views of single organisms, different windows may give us different perspectives on community structure. The Burgess Shale is approximately the same age as the Monastery Creek Formation, but it does not provide definitive evidence for halkieriids (Conway Morris, 1995). It also lacks the diversity of molluscs that is recorded in phosphatic rocks of the same age from Australia (Runnegar and Jell, 1976; personal observations). This may be due to a restriction in the geographic range of these taxa, but it also likely reflects environmental differences between the Burgess Shale and the Monastery Creek Formation. Clearly, to get a more complete view of Middle Cambrian communities, we must sample more than one window. A single assemblage, no matter how well preserved, allows a glimpse of only one environment.

Finally, because the Monastery Creek Formation preserves taxa in the same way and in the same environment as most Early Cambrian small-shelly-fossil-rich successions, it allows us to view Cambrian life through a single taphonomic window. Because unique taphonomic windows can preserve taxa that otherwise may not be represented in the fossil record, the opening and closing of these windows, i.e., temporal variation in the prevalence of specific taphonomic conditions, can bias the fossil record (e.g., Cherns and Wright, 2000). One condition necessary for phosphatization of small shelly taxa, namely the availability of phosphate, may have decreased through Cambrian time (Cook and McElhinny, 1979). If so, this may have contributed to the pattern of “Tomмотian” faunal decline (Sepkoski, 1992). By comparing faunas of differing age through the same window we are able to control for these variations. The discovery of halkieriids in the Monastery Creek Formation suggests that further exploration of Middle and Upper Cambrian phosphatic limestones may yield more “Tomмотian” taxa, indicating that, rather than short-lived experiments that gave way to successful crown-group taxa, these problematic organisms may have been long-lived and important components of Cambrian communities. Certainly, this appears to be true of the Halkieriidae.

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**References**


MULLER, K. J., AND I. HINZ-SCHALLREUTER. 1993. Palaeoecocoleid...
worns from the Middle Cambrian of Australia. Palaeontology, 36:549–592.


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