THE CANAL SYSTEM IN SCLERITES OF LOWER CAMBRIAN SINOSACHITES (HALKIERIIDAE: SACHITIDA): SIGNIFICANCE FOR THE MOLLUSCAN AFFINITIES OF THE SACHITIDS

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Abstract: The halkierids (Sachitida He, 1980) from the Early to Mid Cambrian possess a hollow sclerite with a complex branching canal system. An analysis of the canal system morphology in the halkierid Sinonachites (Thaumatocephalina) delicatus (Jell, 1981) from South Australia reveals similarities to the aesthetes canal system in the shell plates of chitons, which has been analysed in a number of extant taxa. The compartments, referred to as macro-aesthetes in chitons, and lateral canals in halkierids, have overlapping diameters and are constrained in morphology by the space of accommodation by maintaining a constant width, whereas length is more variable. Both canal systems are morphologically distinct from shell pores of other lophotrochozoans and known molluscan classes. Similarities in sclerite growth, microstructure and mineralogy further suggest that halkierids, along with the other sachitids, are molluscs, most likely stem aculiferans (Polyplacophora and Aplacophora).

Keywords: Lophotrochozoa, aesthetes, Halkieria, small shelly fossils, South Australia, Aculifera, Multiplacophora.

Chitons (Polyplacophora: Mollusca) are characterized by having a complex canal system of 'aesthetes' in their outermost mineralized shell layer. The aesthete canals consist of sensory and secretory cells, and are in contact with the shell-surface and the body of the animal. Aesthetes are derived from epithelial papillae (Fischer et al. 1980) present in the girdle epithelium (or perinotum) of both aplacophorans and polyplacophorans. These two groups comprise Aculifera Hatschek, 1891.

The evolution of the supposed monophyletic group Aculifera is poorly known from the fossil record, although a number of authors have recently described fossils that may be attributed to this group (i.e. Bengtson 1992; Vendrasco et al. 2004; Sutton et al. 2004; Porter 2004; Vinther and Nielsen 2005; Caron et al. 2006; Conway Morris and Caron 2007; Sigwart and Sutton 2007). One such fossil group is Sachitida He, 1980, which may represent stem aculiferans (Bengtson 1992; Runnegar 1996a, b; Vinther and Nielsen 2005). Sachitids are well known components of small shelly fossil assemblages from the Lower to Middle Cambrian and are characterized by hollow aragonitic sclerites, with an external restricted basal foramen that opens to the internal lumen. Both Wiwaxia and Halkieria were thought to be hyolith conchs, when first described as isolated sclerites (Matthew 1899; Poulsen 1967). Bengtson and Missarzhevsky (1981), Jell (1981) and Bengtson and Conway Morris (1984) suggested that the isolated sachitid sclerites were a part of a larger sclerite of a scaly metazoan, morphologically similar to the Middle Cambrian fossil Wiwaxia Walcott, 1911. Bengtson and Conway Morris (1984) provided a provisional reconstruction of Halkieria based on the morphology of Wiwaxia and a model of how the sclerites grew through a sort of moulding (see section on sclerite growth). When articulated specimens of Halkieria from Siriu Passet were subsequently discovered (Conway Morris and Peel 1990, 1995), the fossils revealed that halkierids also possessed an anterior and posterior shell plate. This led to a re-investigation of phosphatized small shelly fossil assemblages to identify possible shell plates from halkierids or other sachitids. Bengtson (1992) re-investigated the shell plates of Maikhanella, which was shown by Missarzhevsky (1989) to consist of merged sclerites identical to the co-occurring sachitid Siphogonuchites, and suggested that it provided evidence that molluscan shells (or more specifically chiton shells) evolved from merged sclerites.

History of phylogenetic debate

Runnegar et al. (1979) were among the first to speculate that sachitids were aculiferan molluscs. Bengtson and
Conway Morris (1984) were agnostic on the systematic relationships of sachitids to extant organisms, but stressed a phylogenetic link to Wiwaxia. Conway Morris and Peel (1990) proposed a molluscan affinity, which was maintained by Peel (1991). Later Conway Morris and Peel (1995) interpreted Halkieria evangelista as a stem group brachiopod; Wiwaxia and the remaining sachitids, were interpreted as a paraphyletic lineage subtending annelids and brachiopods. This theory evoked at a time where molecular analyses appeared and demonstrated that brachiopods, hitherto regarded as deuterostomes, were relatives of annelids and molluscs among others in the new group Lophotrochozoa (Halanych et al. 1995). Conway Morris and Peel doubted any relationship between sachitids and molluscs, contrary to the arguments presented by Bengtson (1992), instead resolving molluscs, however tentatively, as a sister clade to annelids plus brachiopods. The siphonogonchiidiids were questionable interpreted as stem representatives of the lineage subtending molluscs, annelids and brachiopods (Conway Morris and Peel 1995, p. 339, fig. 50). The prime argument presented by these authors for dismissing a relationship with the molluscs was that the growth mode of the halkieriid sclerites, as interpreted by Bengtson and Conway Morris (1984), was too different from the formation of aculiferan sclerites and that no equivalence to the halkieriid sclerite zones is apparent in the chiton girdle (Conway Morris and Peel, 1995, p. 338).

Subsequently, there has been a division of opinion concerning the phylogenetic position of sachitids, interpreting them as stem brachiopods (Williams and Holmer 2002; Holmer et al. 2002; Usatinskaya 2002; Li and Xiao 2004), or as molluscs (Runnegar 1996a, b; Lindberg and Ponder 1996; Scheltema and Ivanov 2002; Lindberg et al. 2004; Vendrasco et al. 2004; Vinther and Nielsen 2005; Scheltema and Schander 2006; Caron et al. 2006; Sigwart and Sutton 2007; Parkhaev 2008; Ponder and Lindberg 2008; Todt et al. 2008; Vinther et al. 2008). A more, general stem lophotrochozoan affinity has recently been suggested by Conway Morris (2006), but still stressing the close affinities of Halkieri to brachiopods. Indeed, Bengtson (2005) has interpreted sachitids as a paraphyletic grade encompassing stem-members of all bilaterian lineages. This thesis is based on the similarities of the structure of sclerites of sachitids such as halkieriids, and chancelloridids – a group of sessile sponge-like metazoans. Bengtson (2005) argues that these similarities betray a common evolutionary origin of sachitids and chancelloridids, which he unites in Coelosclerithophora. Chancelloridids, with their sessile habit and apparent lack of internal organs, like a gut, could be basal eumetazoans apical to cnidarians, while sachitids are demonstrably bilaterians. The model therefore suggests that all eumetazoans evolved from an ancestor with hollow sclerites, but it is compromised by molecular clock estimates for the divergence of eumetazoans, which all require a pre-Cambrian origin (e.g. Peterson et al. 2004, 2008), long before the earliest sachitids appear in the stratigraphic record and also requires a subsequent loss in all recognized phyla. Sperling et al. (2007) presented arguments for convergence. Porter (2008) recently published additional examples of chancellorid and sachitid sclerites, showing similar structures as those imaged by Bengtson (2005) and summed up putative microstructural homologies. However many of these similarities are very general features of a mineralized ectodermal element (organic cuticle, a more knobby upper surface and smoother lower surface) or also seen in, for example, molluscs (longitudinal fibrous aragonite bundles) as discussed here. Although the similarities between these fossil groups are startling, differences are also apparent, and no evolutionary scenario suggesting relationship is particular congruent with our current knowledge of Cambrian metazoan biology. Thus it remains an unsolved palaentological problem.

Vinther and Nielsen (2005) reinvestigated published material of Halkieria evangelista from Sirius Passet. They demonstrated that, in direct contradiction of Conway Morris and Peel (1995), the morphological zonation of sclerites in H. evangelista is typical of the chiton girdle. Arguments were also presented that indicate the sclerites have been secreted the same way as in chitons. They concluded that the characters present in H. evangelista, in addition to an aragonitic biomineralogy and overall sclerite-tome, are compatible with their interpretation as molluscs, especially chitons, but not to annelids, brachiopods or tommotids (possible stem brachiopods). Vinther and Nielsen (2005) suggested a crown mollusc affinity, as a sister group to Polyplacophora. Conway Morris (2006) criticized Vinther and Nielsen (2005), claiming incorrectly that their core argument was based on a comparison of the sclerites in Halkieri to multiplyplacophorans (Conway Morris 2006). The spurious reference to multiplyplacophoran sclerites was reiterated by Conway Morris and Caron (2007), who described a new sachitid from the Burgess Shale. Conway Morris and Caron (2007) suggested that this new taxon Orthozouanulis reburrus had unmineralized sclerites, like Wiwaxia, (but see Vinther et al. 2008, supplement) and possessed an anterior shell plate, like Halkieri, supporting the contention that halkieriids and wiwaxiids comprise a clade of 'halwaxiids'. They provided two phylogenetic hypotheses for the placement of halwaxiids within Lophotrochozoa: (1) as stem molluscs; and (2) as stem annelids + brachiopods. The first hypothesis was suggested from the outcome of their cladistic analysis that could not resolve a monophyletic Halwaxiidae, resolving halkieriids and wiwaxiids in the total group Mollusca in one polytomy. The second hypothesis was not substantiated by any further evidence, but relies on
the argument presented by Conway Morris and Peel (1995). Conway Morris and Caron (2007) emphasized in their cladistic analysis and in their text that the sclerites of chitons are secreted in a manner quite distinct from sachtidis (always by a single cell in an invagination rather than through moultng, Bengtson and Conway Morris 1984). The problem with the arguments for a monophyletic clade is due to the fact that it is based on the putative intermediate morphology in Orthrozanclus and not any unequivocal homologies only seen in this group. The diagnosis by Conway Morris and Caron (2007) for Halwaxia would in fact include aplacophorans and chitons.

Sigwart and Sutton (2007) conducted a cladistic analysis of fossil and recent molluscs and in some permutations resolved halwaxiids as monophyletic and as stem molluscs, though the analysis assumes that the sclerites of halkieriids and molluscs are distinct from each other. In most permutations halwaxiids are also chosen as out groups in the analysis. The only conchiferan mollusc included in the analysis is the monoplacophoran Neopilina, which is problematic given its similarities to polyplacophorans, which not seen in other conchiferan taxa. The only molecular analysis to include a monoplacophoran also indicates intimate relationships with polyplacophorans (Giribet et al. 2006), which potentially compromises the choice of monoplacophorans as a representative for conchiferan diversity. Indeed, the long-assumed monophyly of Conchifera has yet to be demonstrated molecularly. A cladistic analysis in which the sclerites of aculiferans and sachtidis were coded as homologous recovered the halwaxiids as a paraphyletic lineage with respect to Aculifera plus Monoplacophora (Vinther et al. 2008). Wiwaxia has been suggested to be related to polychaete annelids due to the microstructure of the sclerites resembling microvillar secreted chitin, as in polychaete chaetae (Butterfield 1990, 2006, 2008). However, this chitinous microstructure is also seen in a number of other lophotrochozoans, such as in brachiopod setae (Nielsen 1991) and in hairs of the chiton girdle (Leise and Cloney 1982). The chitinous cuticle enveloping the calcareous sclerites also shows the regular microvillar microstructure (Fischer et al. 1980, abb. 9). This feature must be a lophotrochozoan plesiomorphy (Eibye-Jacobsen 2004). There are no other characters in Wiwaxia indicating a close relationship to annelids (also discussed in Eibye-Jacobsen 2004). Thus, Wiwaxia, along with the sachtidis, is more plausibly interpreted as part of the molluscan clade (Scheltema et al. 2003; Caron et al. 2005) as it possesses features, like sclerite organization in morphological zones, no obvious segmentation and a radula like feeding apparatus (although see Butterfield 2006 and response by Caron et al. 2007; Butterfield 2008). In fact typical modern aculiferan sclerites grow to a fixed size and are attached to the integument via a chitinous stalk with microvillar ultra-structure, just as in Wiwaxia (Blumrich 1891; Fischer et al. 1988).

Recently, articulated sclerites of the tommotiid Eccentrotheca were described by Skovsted et al. (2008). These indicate that the sclerites or shell plates are merged together to form an encrusting tube and it is therefore believed that they had a sessile life mode. Skovsted et al. (2008) suggested that the scleritomes of tommotids and the halkieriid-tommotid-brachiopod model of Williams and Holmer (2002) and Holmer et al. (2002) should be revised, which was performed by Holmer et al. (2008), who reconstructed Micrina as a sessile bivalved stem brachiopod.

Molecular analyses have not been able to resolve the issue of molluscan relationships (Okusu et al. 2003; Passamanec et al. 2004; Giribet et al. 2006). Such studies suggest (albeit with low precision) that both aplacophorans and chitons are derived within the molluscs and not basally diverging forms, thus, given their relationship to Aculifera, sachtidis should be resolved as crown molluscs as the sclerite bearing morphology is not a molluscan plesiomorphy. However this remains an unresolved issue and until accurate relationships of the molluscs are clarified at class level and thus the morphological polarity resolved with the aid of informative fossil stem groups, it will be impossible to determine whether sachtidis and wiwaxiids are stem or crown molluscs. Better knowledge of the morphology of the fossil taxa will be valuable for future phylogenetic discussion.

Scope of this analysis

One of the intriguing characters of the halkieriids is their possession of an elaborate canal system inside the mineralized sclerite (Plates 1 and 2), extending from the internal cavity out through the sclerite walls; these canals are suggested to have housed tissue (Bengtson and Missarzhevsky 1981; Bengtson and Conway Morris 1984). The canal system shows some remarkable morphological variation among genera, but also seems to be clearly constrained, as will be demonstrated here. Canals inside a mineralized matrix housing cellular structures are a common feature of the Metazoa, but the canal system in sachtidis has some specific similarities to the aesthetral canal system in chitons. Porter (2004) speculated that the canals housed tissue that served a sensory function analogous with that of arthropod setae and chiton aesthetes. Bengtson (1992) drew attention to the previous studies of Haas and Kriesten (1975) and Fischer et al. (1980) that demonstrated the girdle papillae of chitons to be similar to the aesthetes and that the arrangement of aesthetes in a quincunx pattern in the shell plates mimics that of fused sclerites in Maihkanella and also the organization of
papillae in the girdle of chitons and the sclerites of Haliceria evangelista (i.e. Bengston 1992).

Here the halkieriid canal system is shown to possess a number of morphologically similarities to the aesthetacial canal system in chitons. Material of Sinosachites (=Thambetolepis) delicatus (Jell, 1981) from Ardrossan, South Australia is abundant, exquisitely preserved and shows the internal canal system in great detail. An analysis of the aesthetace canal system in a number of extant chitons was performed to define the morphological diversity, constraints and formation of the aesthetes. This analysis provides a template for a comparison with Sinosachites and other well known halkieriids. Published descriptions of shell pores in other molluscs and lophotrochozoans are also discussed.

MATERIAL AND METHODS

Sinosachites

Acid residue from limestones of Sinosachites delicatus (Jell, 1981) from localities in South Australia: Yorke Peninsula, near Ardrossan, in the Flinders Ranges and Mt Scott Range (see Bengston et al. 1990 for details). The material was studied with a dissecting microscope and reposited in Naturhistoriska Riksmuseet in Stockholm (abbreviated NRM). The fauna has been correlated with Atdabanian faunas elsewhere (Bengston et al. 1990). Where preservation allowed, the length and width were measured and the number of lateral canals were counted (Table 1 and Text-fig. 2). Some specimens were coated with gold/palladium and studied using a scanning electron microscope (Hitachi S-4300, 10 kV) that allowed precise measurement of canal size and assessment of sclerite microstructure. Figured specimens are reposited in Naturhistoriska Riksmuseet, Stockholm and are designated NRM-PZ X3832-X3839, X3860 and X3861.

Chitons

A number of extant chitons representing the major groups, Lepidopleurida and Chitonida (Acanthochitonina and Chitonina), were studied. Classification of chitons is under marked change with the use of molecular techniques and additional morphological classification. The classification of Sireko (2006) is followed herein.

The studied species are listed below together with the accession numbers for the studied specimens (first number is the collection the studied specimen is part of, the second is the remaining isolated shell plates of the individual studied, NA denotes specimens without museum numbers): Nierstraszella lineata (Nierstrasz, 1905) ZSM Mol 20034397 and NA, Leptochiton asellus (Gmelin, 1791) YPM IZ 043611 and YPM IZ 043614, Hanleya nagelfar (Lovén, 1846) NA and YPM IZ 043620, Notopliax violaceus (Quoy and Gaimard, 1835) ZSM Mol 20040567 and YPM IZ 043615, Lepidochitona cinerea (Linnaeus, 1767) ZSM Mol 20050528 and YPM IZ 043616, Nuttallochiton mirandus (Thiele, 1906) ZSM Mol 20008157 and YPM IZ 043617, Schizopliax brandtii (von Middendorf, 1847) ZSM Mol 20050464 and YPM IZ 043618, Tonicella marmorata (Fabricius, 1780) YPM IZ 043612 and YPM IZ 043619, Cryptopliax larvaeformis (Burrow, 1815) ZSM Mol 20033107 and YPM IZ 043621, Callotoglyptis septenuvalvis (Montagu, 1803) euplaccæ (O. G. Costa,1829) ZSM Mol 20040239 and NA, Ischnochiton elizabethensis Pilsbry, 1894 ZSM Mol 20050840 and YPM IZ 043622, Stenochiton longicymba (de Blainville, 1825) ZSM Mol 20041373 and YPM IZ 043623, Acanthopleura gemmata (de Blainville, 1825) ZSM Mol 20033115 and YPM IZ 043624, Lucilina lamellosa (Quoy and Gaimard, 1835) ZSM Mol 20033148 and YPM IZ 043625 and Rhysopliax olivacea (Spengler, 1797) YPM IZ 043613 and YPM IZ 043630.

ZSM is the Bavarian State collection of Zoology, Munich, Germany; ZMUC is the Zoological Museum in Copenhagen, Denmark; YPM is the Yale Peabody Museum, New Haven, USA.

An intermediate shell plate from each species was dissected and treated in 5% bleach (sodium hypochlorite) to remove the external organic matter and the tissue within the aesthetcan canals. Subsequently, the shell plate was rinsed in water and dried at room temperature. The dried shell plate was placed on a glass slide and submerged in molten lakeside resin heated over an ethanol candle. The sample was reheated and cooled two to four times to allow the

EXPLANATION OF PLATE 1

Sinosachites delicatus (Jell, 1981) from the Parana Limestone, Yorke Peninsula, South Australia.

Figs 1–4. NRM-PZ X3832 Partially formed asymmetric cultrate sclerite. 1, lower surface in oblique view. 2, close up, arrows indicate lateral canals terminating on basal secretion front. 3, lower surface seen from above. 4, close up of outer phosphatic coating preserving delicate growth lines, underneath is lateral canals attaching to central canal.

Figs 5–7. NRM-PZ X3833, Internal steinkern of palmate sclerite. 5, entire sclerite. 6, closeup of lateral canals attached to central canal by connecting pores. 7, NRM-PZ X3834. Asymmetric cultrate sclerite, internal steinkern, mineralized matrix replaced by phosphate in proximal part. Scale bars represent 100 µm.
VIN ThER, Sinosachites
molten resin to fill in the aesthetical canals by expansion of the air inside and subsequent contraction. After last cooling,
the surface was cleaned for excess resin with a sharp
scalpel and treated in acetic acid (8–10%) to expose the
casts of aesthetical canals. After rinsing in water to wash away
the acid, the sample was dried and coated with platinum
for study under the scanning electron microscope (see mea-
surements in Table 2). The resin casting technique used
here was first used and described in Hansen and Lykke-
Andersen (1976). The shape, size, and interrelationships of
the macro- and micro-aesthete as well as the basal canals
were observed and measured.

**SINOSACHITES DELICATUS (JELL, 1981)**

**Morphology**

*Sinosachites delicatus* was first described as *Thambetolepis
delicata* by Jell (1981) from the Lower Cambrian of Ardd-
rossan, South Australia. Better material of the Chinese
species *Sinosachites flabelliformis* He, 1980 was described
by Yue (2004), who demonstrated that the internal canal
system and overall morphology of *Thambetolepis* is so
similar to that of *Sinosachites*, it should be considered a
junior synonym if classification were based on the canal
system alone. *Sinosachites* is very similar in sclerite
morphology to *Halkieria* (having cultrate, palmate and
sicatele sclerite types with an internal branching canal
system) and is therefore assigned to the same family,

The overall anatomy of the sclerites has been described in
Bengtson *et al.* (1990) and only a short description of
the sclerite morphology is provided here, with a focus on
the internal canal system, taphonomy, original mineralogy
and growth of the sclerites.

The scleriteome consists of three sclerite forms: palmate,
cultrate and sicatele. The palmate sclerite is triangular in
outline with a sub-equal length and width, whereas the
cultrate is more elongate. Cultrate sclerites are up to
1.6 mm in length whereas palmates are up to 1.2 mm in
length. Both sclerites have a base that varies from promi-
inent to recessed (see Bengtson *et al.* 1990 for excellent
examples of sclerite morphologies). The sicatele sclerite is
more slender, asymmetric and can be much longer than
the other sclerite types (more than 2 mm). At the base of
all sclerites there is an external foramen, which connects
to the internal canal system (Bengtson *et al.* 1990).

The external upper surface is ornamented with either
longitudinal ribs, commonly associated with transversely
arranged knobs, or a more irregular transversely arranged
set of ribs (Pl. 2, fig. 7). The under-surface and the base
of the sclerites are preserved with delicate transverse
increments (Pl. 1, figs 1–4) that are interpreted as growth
lines (Vintner and Nielsen 2005).

The internal canal system consists of a central canal,
lateral canals and smaller tubules (Text-fig. 1). The central
canal occupies the median area of the sclerite and extends
from the basal foramen to the distal tip of the sclerite,
tapering in both directions. Lateral canals (Bengtson *et al.*
1990) project from each side of the central canal and
trend distally. The central and lateral canals are connected
with each other by narrow connecting pores (Pl. 1, figs
4–6). It has been observed in both *S. delicatus* and *S.
flabelliformis* that small tubules extend from the lateral
canals through the sclerite wall on both the lower and
upper surface (Text-fig. 1). These tubules are very densely
packed at the lateral margins (Bengtson *et al.* 1990, figs
52, 55M, O–P; Yue 2004, pl. 3R). The tubules may be
diagenetic, representing a partial replacement of the
mineralized sclerite wall by phosphate, but the consistent
pattern, with which these tubules are organized in both the
Australian and Chinese material, plus their presence in
the genus *Halkieria* (Bengtson and Conway Morris 1984;
Bengtson *et al.* 1990; Conway Morris and Peel 1995; Con-
way Morris and Chapman 1997) indicates that they are
an original feature of the canal system. It could be sug-
gested that the small tubules are aragonite fibres replaced
by phosphate, but their morphology and regular spacing

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**EXPLANATION OF PLATE 2**

*Sinosachites delicatus* (Jell, 1981) from the Parara Limestone, Yorke Peninsula, South Australia.

**Figs 1–3.** NRM-PZ X3835 asymmetric cultrate sclerite. Mineralized matrix replaced by phosphate in the proximal part, gradually disappearing in distal direction, in the distal part of the sclerite in the right side of the image longitudinal rods is present, which is interpreted as moulds of original mineralized microstructure. 2, detail of longitudinal rods. 3, detail of single rod, consisting of microcrystalline apatite.

Fig. 4. NRM-PZ X3836, sicatele sclerite, internal steinkern.

Fig. 5. NRM-PZ X3837, asymmetric cultrate sclerite, mineralized matrix replaced in proximal part of sclerite.

Fig. 6. NRM-PZ X3838, cultrate sclerite, internal steinkern.

Fig. 7. NRM-PZ X3839, sicatele sclerite upper side, preserving external ornamentation.

Scale bars represent 100 μm, except for fig. 3, which is 5 μm.
VINTHER, Sinosachites
Table 1. Sclerite dimensions of Sinosachites delicatus (Jell, 1981) measured under dissecting microscope.

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<td>'L1871,2'</td>
</tr>
<tr>
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<td>600</td>
<td>24</td>
<td>43</td>
<td>cul</td>
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<td>pal</td>
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<tr>
<td>1120</td>
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<td>36</td>
<td>ass cul</td>
<td>'L1872,2'</td>
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<tr>
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<td>1430</td>
<td>29</td>
<td>30</td>
<td>pal</td>
<td>'L1871,1'</td>
</tr>
</tbody>
</table>

Cul, cultrate sclerite; ass cul, asymmetric cultrate sclerite; pal, palmate sclerite; sic, siculo sclerite.

Collections are at the Naturhistoriska Riksmuseet in Sweden.

Sample information: see Bengston et al. (1990) for details.

Measured widths of the lateral canals are prone to some error due to the magnification of the dissecting microscope.

All measurements are the maximum width of the given object.

differs from previous descriptions of secondarily phosphatized aragonite fibres.

At the base of palmate and cultrate sclerites there is sometimes a structure, which has been previously interpreted as a lumen, termed the basal cavity (Bengston et al. 1990; Yue 2004). The relation to the other parts of the internal canal system remains poorly resolved, and the

Table 2. Measured widths of aesthetes in living chitons studied in this article, spectrum of maximum measures.

<table>
<thead>
<tr>
<th>Species/width</th>
<th>Macro-aesthete/μm</th>
<th>Micro-aesthete/μm</th>
<th>Basal canal/μm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nierstrasella lineata</td>
<td>25–30</td>
<td>3</td>
<td>15–25</td>
</tr>
<tr>
<td>Lep tochiton asellus</td>
<td>30</td>
<td>3</td>
<td>10–30</td>
</tr>
<tr>
<td>Nuttallochiton mirandus</td>
<td>15?</td>
<td>?</td>
<td>40–60</td>
</tr>
<tr>
<td>Tonicella marmorea</td>
<td>25–30</td>
<td>3–7</td>
<td>30–50</td>
</tr>
<tr>
<td>Hanleya nagelfar</td>
<td>50–80</td>
<td>5</td>
<td>12</td>
</tr>
<tr>
<td>Cryptopax larviformis</td>
<td>15–70?</td>
<td>5–10?</td>
<td>10</td>
</tr>
<tr>
<td>Callochiton septemvalvis</td>
<td>30–40</td>
<td>5–8</td>
<td>15–25</td>
</tr>
<tr>
<td>euplaeae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ischnochiton elizabethensis</td>
<td>20</td>
<td>2</td>
<td>8–30</td>
</tr>
<tr>
<td>Stenochiton longicymha</td>
<td>15</td>
<td>2–3</td>
<td>8–25</td>
</tr>
<tr>
<td>Acanthopleura gemmata</td>
<td>35 (70)</td>
<td>2–10</td>
<td>?</td>
</tr>
<tr>
<td>Lucinula lamellosa</td>
<td>25–30 (55)</td>
<td>5</td>
<td>10–25</td>
</tr>
<tr>
<td>Rhysopax olivacea</td>
<td>25–30</td>
<td>5</td>
<td>10–25</td>
</tr>
</tbody>
</table>

Parentheses in second column are the measured width of the larger ocelli in the genus Lucinula and Acanthopleura.

Text-fig. 1. Schematic sections through a sinusachitid sclerite, indicating the relation and position of elements of the internal canal system. A, view from the underside. B, lateral view, median section. Abbreviations: bf, basal foramen; cc, central canal; lc, lateral canal; t, tubules.
exact nature of the basal cavity is highly dubious. Many sclerites of Sinosachites evidently do not possess this basal cavity and so it may be surmized that the basal cavity was formed due to dissolution and replacement of the mineralized matrix by phosphate (see Preservation, below).

The width and depth of the lateral canals are, in most sclerites, more or less the same within a single sclerite, whereas the length varies with long canals in the basal part, and shorter distal canals. The width is typically between 20 and 40 µm (up to 60 µm), whereas the depth varies according to the thickness of the sclerite so that a thin sclerite will have rounded lateral canals in transverse section and a thicker sclerite will have a more elongate rectangular cross section (Bengtson et al. 1990, fig. 62B). Asymmetric culturate sclerites tend to have thinner lateral canals on the concave side than on the convex side. Some sclerites tend to have slightly thinner lateral canals in the distal part compared to those in the proximal portion (Bengtson et al. 1990).

Text-figure 2 plots the length of the sclerite vs the number of lateral canals for 20 culturate and 14 palmate specimens. It indicates that there is a linear relationship between the number of canals and the length of the sclerite. This implies that during growth the animal did not retain a finite number of lateral canals irrespective of size of the sclerite, but incorporated more canals into the sclerite matrix when secreting a larger sclerite. This is consistent with the observation that the widths of the canals are very regular.

Preservation

The material studied of S. delicatus is preserved as secondary phosphate. The phosphate has replaced the sclerites to varying degrees. Typically, the internal canal system is preserved as an internal lining (Pl. 2, figs 1, 6) or more solid steinkern. The external surface is preserved as a delicate coat of phosphate (Pl. 1, figs 1–4). The gap between the internal steinkern of the canal system and the outer coating is commonly filled by calcium carbonate, observed in thin sections, which is macerated away in the acetic acid extraction. The gap is interpreted as representing the originally mineralized wall (Bengtson and Conway Morris 1984) that sometimes also is partially replaced by phosphate to various degrees. Mineral replacement always occurs in the basal part of the sclerites, where there is connection to the internal canal system via the basal foramen, replaced in various grades from proximal to distal (Pl. 1, fig. 7; Pl. 2, figs 1, 5). The characteristic replacement of carbonate by phosphate suggests that the phosphatization took place early when, for example, an organic cuticle was present. The only physical connection to the mineralized matrix would then be through the basal foramen, as the cuticle would protect the mineralized matrix from dissolution, only allowing percolating fluids to replace the mineralized matrix by phosphate from the base and progressing in a distal direction to various degrees. Some fossils seem to exhibit phosphate replacement of the organic cuticle, described as the outer phosphatic coating (evidenced by Porter 2004; but see Runnegar and Bentley 1983), which preserves delicate surface textures (Pl. 1, fig. 4), like the surface ornamentation and growth lines. Phosphate replacement of mineralized and organic structures needs to be experimentally studied in more detail to be fully understood. The suggested preservational sequences are depicted in Text-figure 3. The veracity of the basal cavity as a biological structure is dubious, as mentioned above. Yue (2004) suggested that the basal cavity had a different composition than the remaining canal system because of the different colour of the replacing phosphate. This colour difference may be related to partial infill of sediment grains in the canal system, which gives the phosphate a browner colour, whereas the putative basal cavity corresponds much more in colour to the replaced mineralized matrix. The phosphatized basal area is therefore more likely a replacement of the mineralized matrix and thus a secondary artefact. This would explain why the basal cavity is typically indistinct in morphology (as, for example Pl. 1, fig. 7).

**TEXT-FIG. 2.** Diagram with the relationship between the number of lateral canals (y-axis) and the length of the sclerite (x-axis). Left, culturate sclerites; right, palmate sclerites. Grey points fall out of the linear trend and are believed to be related to incomplete hosting of lateral canals due to incomplete preservation.
Mineralogy of sclerites

Jell (1981) suggested that the central and lateral canals of Sinosachites (= Thambetolepis) were fluid-filled, the carbonate-filled gap was occupied by soft tissue, and the outer phosphatic coating perhaps a weakly mineralized layer. Later, Bengtson and Conway Morris (1984) and Bengtson et al. (1990) interpreted the carbonate-filled gap as representing the originally mineralized part of the sclerites and the internal canal system to have been occupied by soft tissue, which is the generally accepted interpretation today (although see Ushatinskaya 2002 for a different interpretation).

The inferred mineralized part of the sclerites was replaced by either sparry calcite or secondary phosphate, but there are a number of clues that allow inference of the original mineralogy. Shells and sclerites that were originally organophosphatic are known from the same deposits and are preserved with sub-original ultra-structure (like tommotids and nonarticulate brachiopods). Hexactinellid sponges typically have their opaline spicules replaced by quartz in otherwise phosphate bearing deposits (Bengtson et al. 1990). Therefore, most researchers have argued that the sachitid sclerites had an original composition of calcium carbonate rather than silica or phosphate (Bengtson and Missarzhevsky 1981; Bengtson and Conway Morris 1984; Bengtson et al. 1990; Porter 2004). This is consistent with the preservation of other taxa known to have original carbonate shells, for example, the molluscs, whose calcareous shells are typically preserved as phosphatic steinkerns that preserve moulds of the original microstructure (Runnegar 1985; Bengtson et al. 1990; Feng and Sun 2003). The internal steinkerns of sachitids often preserve dense longitudinal striations (i.e. Pl. 1, fig. 3), which are interpreted as moulds of original mineralized microstructures, which have previously been interpreted as having been fibrous aragonite (Porter 2004). The material studied here also preserves casts of original microstructure. An asymmetric cultrate sclerite
(shown in Pl. 2, fig. 1) is preserved with longitudinal bundles of fibres in the distal area. The texture of the apatite in these fibres is microcrystalline (Pl. 2, figs 2–3) and therefore the fibres must be an infill of secondary phosphate into structures that mineralogically had a larger original fibrous nature. Fossil groups that had an original mineralogy of calcite quite often preserve the original shell microstructure in the carbonate fossils, whereas ancient aragonitic forms are typically replaced with sparry calcite, like the sachitids (see example in Bengtson and Conway Morris 1984).

It has been demonstrated that microbially induced acidic and anoxic environments associated with rich sources of phosphate ions from decayed organic matter can lead to dissolution of the calcium carbonate shell and direct precipitation of apatite in the locus of dissolution, which results in replication of original structures (Lucas and Prevot 1985). Apparently, the mineralized matrix was replaced quite early, when there was an outer organic cuticle still present (see discussion above). Since aragonite is less stable than calcite in sedimentary environments, the early replacement of the mineralized matrix by phosphate favours an original aragonitic composition for the sachitid sclerites.

Sclerite growth of sachitids

The growth of the scleritone in Halkieria evangelista was inferred by Vinther and Nielsen (2005) from a comparison of small and large specimens and with data from sclerite anatomy. The animal grew by marginal accretion of the shell plates, whereas the sclerites were continually replaced by larger successors. Vinther and Nielsen (2005) did not observe any indication of apparent interpolation of sclerites as suggested by Conway Morris and Peel (1990) and Bengtson (2005). Bengtson and Missarzhevsky (1981) proposed that in coeloscleritophorans, after a sclerite had been formed with its restricted base and constriction of the internal canal system, no more growth was possible. Bengtson and Conway Morris (1984) followed up on this model of sclerite growth by suggesting that the sclerites were formed and mineralized from soft tissue inside the internal canal system: the soft tissue would contract and withdraw from the former mineralized matrix, which was shed and the soft tissue would then expand to secrete the subsequent larger sclerite. The model is very close to the concept of ecdysis in arthropods and has been discussed, too, by Bengtson (2005). Arthropod exoskeletal morphology is an exact reflection of the underlying morphology of the body. If sachitid sclerites were secreted by the internal canal system, it would be expected that the external ornamentation and shape is consistently reflected by the internal canal morphology. This is not observed. It should also be noted that the orientation of the lateral canals is directed in different angles as compared to the external transversely arranged morphology of ornamentation (Pl. 1, figs 1–4; or see for example Bengtson et al. 1990, fig. 54c).

There is another model of sclerite growth that was mentioned in Vinther and Nielsen (2005) and explained here further: namely that the sclerites were secreted by the underlying basal epithelium, implying that the sclerite is secreted from one tip to the other, starting with formation of the distal tip of a sclerite, with growth continuing at the base until sclerite secretion was terminated with the formation of the restricted basal area and foramen. A number of observations support this model, for example, the external ornamentation of transverse ribs appear to represent incremental growth lines (Pl. 1, figs 1–4, Pl. 2, fig. 7). The ornamental pattern of knobs arranged in transverse rows on the upper side would then reflect a cyclic event of contemporary secretion (see examples of such ornamentation in Bengtson et al. 1990). The apparent transverse growth lines can be traced along the entire sclerite, from the base to the tip.

The original mineralogical microstructure of sachitids is interpreted as longitudinal fibres of aragonite. Modern taxa, like polyplacophoran molluscs, secrete aragonite arranged in fibrous bundles. They secrete an aragonite crystallite fibre from one tip to the other with the crystallographic c-axis aligned to the length of the fibre (Treves et al. 2003). This shows that an aragonite fibre would be oriented perpendicular to the secreting epithelium. Seeding a sclerite from the basal epithelium, as suggested, would make longitudinal aragonite fibres, as observed. If, rather, fibrous aragonite is secreted from the internal canal system, according to the model of Bengtson and Conway Morris (1984) the orientation of the fibres would be expected to be oriented radially in transverse section of the sclerite and from the internal canal system to the exterior surface. This has not been observed.

During secretion of the sclerite, the internal canal system would gradually have been incorporated. Fossils of partly secreted sclerites should potentially occur. Plate 1, figure 1 shows an asymmetric cultrate sclerite, evidenced by the different thicknesses of the lateral canals on both sides and the arcuate distal tip. This sclerite may be only partially formed. Asymmetric cultrate sclerites are characterized by being longer than they are wide, which is not the case for this sclerite. Moreover, the sclerite lacks the restricted base evident on most other sclerites. The basal surface is aligned with the external growth lines indicating that this sclerite was not randomly fractured. The basalmost lateral canals terminate at the basal surface instead of connecting to the central canal (Pl. 1, fig. 2). This demonstrates that the canal system is passively incorporated soft tissue during the basal secretion of mineralized
matrix. The incorporation of the aesthetes into the chiton shell plate is very similar to this (Blumrich 1891; Baxter and Jones 1984), as will be discussed below.

*Constraints on the sinosachitid sclerite canal system*

As discussed earlier, the sinosachitid canal system consists of a central canal connected to the body via the foramen at the attachment base. The lateral canals are connected to the central canal through the narrow connecting pores, and to the exterior through the tubules perforating the sclerite wall. Apparently the canal system was open and connected to the body and the exterior. The lateral canals have a relatively constant thickness throughout a single sclerite, tapering slightly at the distal tip and constricting basally into the connecting pore. The length of the lateral canal becomes gradually shorter in a distal direction. The thickness of the lateral canal is relatively constant in sclerites of different size and the morphometric diagram (Text-Fig. 2) shows a linear relationship between sclerite length and number of lateral canals (see also Tables 1 and 2). The length of the lateral canal varies according to the overall morphology of the sclerite. Thus, the principal constraint on the architecture of the sinosachitid canal system is the thickness of the lateral canals, which remained constant with respect to growth. The canal systems appear to accommodate their morphology to the space available within the sclerite, changing the length of the lateral canal, but not its thickness. The central canal serves to connect all the lateral canals to the body of the animal through the basal foramen.

*Shell pores in other sachitids*

There are a number of forms within Halkieriidae that have a more complex canal system. Most specimens only preserve the cavity as crude steinkerns, which do not allow detailed analysis of any internal canal system. Sclerites of *Australohalkieria parva* Conway Morris (in Bengtson et al. 1990), from the same deposits as *S. delicatus*, possess a pair of longitudinal canals arranged on each side of the central cavity, that are about 35 μm in maximum width and thereby fall within the same size class as *Sinosaechites*. Evidently, this arrangement of longitudinal canals (instead of oblique lateral canals as in *Sinosaechites*) relates to the smaller size of the sclerite and the adaptation of the canal system to the smaller accommodation space. The Middle Cambrian *Australohalkieria superstes* Porter, 2004 displays a similar pair of longitudinal canals within the same size range.

The same feature of longitudinal lateral canals is present in the palmate sclerites of *Halkieria* sp. (in Bengtson and Conway Morris 1984). A cultrate sclerite described in this paper (Bengtson and Conway Morris 1984, fig. 9c) shows lateral openings, consistent with laterally arranged tubules that open to the exterior in *Sinosaechites*. One specimen of *Halkieria evangeliast* has been shown to possess laterally arranged tubules or canals (Conway Morris and Peel 1995) and the same is apparent in *H. mira* (Conway Morris and Chapman 1997). In other sachitids, like siphonochitits, sclerite cavities are relatively simple, lacking complex branching canals. An undescribed form from South Australia in the collection of Naturhistoriska Riksmuseet, Stockholm, similar to the co-occurring *Hippopharangites* (Text-fig. 4) has regular pores corresponding to the tubules of *Sinosaechites*, extending from the internal cavity through the shell wall. The external surface ornamentation shows regular pits that could be the location of the pore openings.

**POLYPLACOPHORA**

*General morphology*

Modern polyplacophorans or chitons are distinct in having eight dorsal shell plates (or valves; setting aside teratological deviations). The shell plates are surrounded by a fleshy girdle, called the perinotum (Text-fig. 4), covered by cuticle and containing calcareous sclerites, chitinous hairs and other embedded sensory processes (Leise and Cloney 1982; Fischer et al. 1980, 1988). The term sclerite is used here in place of the traditional term spicule because there is no obvious morphological or ontogenetic difference between spicules and sclerites in the case of chitons and sachitids. Chiton scales are secreted with an initial formation from invagination of a single cell, but are immediately transferred to an extracellular secretion from multiple cells, especially in large scales (Haas 1981). A number of workers have tended to treat spicules and sclerites as different structures in cladistic and morphological analyses (Conway Morris 2006; Conway Morris and Caron 2007; Sigwart and Sutton 2007). The perinotum extends to the ventral side where it surrounds the muscular foot; between them is a mantle cavity in which serial ctenidia (gills) are situated and through which a posteriorly-directed ventilatory current flows. The typical chiton is dorso-ventrally flattened with the shell plates overlapping from anterior to posterior. The shell plates are subdivided into four mineralized layers: the dorsal-most tegumentum, then articularum, hypostromaticum and myostromaticum (Text-fig. 5B) made of fibrous aragonite arranged in some layers into a cross-lamellar structure. The outermost shell layer is occupied by the aesthetes which form a branching canal system housing sensory
TEXT-FIG. 4. Undescribed sachitids from the Early Cambrian of South Australia, stored at NRM Stockholm. The form is similar to *Hippopharangites* (Bengston *et al.* 1990). A, NRM-PZ X3860, complete sclerite, preserved as an internal steinkern of the cavity and an outer phosphatic coating. In the gap in between extend numerous pores from the internal cavity. B, NRM-PZ X3861, another sclerite showing the external ornamentation. C, detail of the distal tip of the sclerite figured in A. D, detail of the regular pits in the surface of the sclerite figured in B. Detail of sclerite figured in B. Scale bars represent 200 μm in A–B, 100 μm in C, 20 μm in D and 50 μm in E.

and secretory cells, which are connected to the animal by basal canals that contain fluids and nerve processes (Text-fig. 5C). The shell surface leaves little evidence of the underlying canal system when observed under the SEM if the outer organic layer, the proaperistomtriacum is present.

**Perinotum**

The perinotum possesses a thick glycoproteinaceous cuticle with the sclerites and other sensory processes situated within it. The perinotum elements are all secreted by epidermal papillae, sometimes also termed epithelial packets (Text-fig. 5D). The sclerites vary in morphology from flat and scale-shaped to cylindrical and elongate. They are arranged in different morphological zones: a ventral, marginal and dorsal zone. The dorsal zone can be subdivided into two zones in many forms (Kaas and Van Belle 1987). The marginal zone of sclerites is minute and spinose, whereas the ventral zone of sclerites is flat with a quadratric shape (see Vinther and Nielsen 2005, fig. 1). The ventral zone is absent in *Ferreiraelia* (Ermisse and Reynolds 1994; Schwabe and Wanninger 2006). Many girdle elements are unmineralized, like the setae or hairs, which sometimes have smaller mineralized bodies within. They form a morphological continuum with the more elaborate mineralized sclerites. The mineralogical microstructure of the sclerites is composed of fibrous bundles of crystalline aragonite (Treves *et al.* 2003). The fibres are arranged longitudinally throughout the sclerite in some forms and can be inclined from the longitudinal axis along the margins, while in others the bundles can be shorter. A sclerite is initially secreted by one cell of the epithelial papilla, the cell then clones a number of mineral secreting cells in order to form larger sclerites. Adjacent cells with numerous microvilli secrete the enclosing chitinous cuticle (Haas 1981). The sclerite is continuously secreted until achieving a certain size, when a thickened basal cuticle is formed, enclosing the mineralized body; a stalk is formed continuing the attachment to the papillae (Text-figure 5D; Haas 1981; Fischer *et al.* 1980, 1988). During growth, the sclerites are continually replaced by larger successors, which displace the old sclerites (Blumrich 1891; Fischer *et al.* 1980). Additional sclerites can be added at the margin from a groove between the shell and the perinotum and at the peripheral margin of the perinotum (Fischer *et al.* 1988). Bergenhayn (1937) has described what seems to be a generative zone between the two dorsal sclerite zones in *Tonicina zschau*, but this has to be reconfirmed. Fischer *et al.* (1980) described the epithelial papillae in the perinotum of *Acanthochitona fascicularis* that secretes the sclerites. They noticed large secretory cells with droplets and peripheral photoreceptor cells. The sclerite is attached to the epithelial papillae, via the organic stalk, to the so-called spine cell next to another cell with a distal cilium that functions as a mechanoreceptor (Fischer *et al.* 1988). The morphology of the epidermal papillae with slender sensory cells having a distal cilium, large central secretory cells and the peripheral photoreceptor are quite similar to the morphology of an aesthete (Text-fig. 5C) suggesting homology (Fischer *et al.* 1980).
The aesthetes

The aesthetes are cells incorporated into the shell plates during marginal accretion, forming a canal system that connects the epithelium to the external surface of the shell plates. They are imbedded in the outer mineralized shell layer, called the tegmentum. The aesthetes are connected to each other by a basal canal, which lies in the border between the tegmentum and the underlying shell layer, the articulamentum and connects to the epithelium.
at the shell margin (Text-fig. 5B; Pl. 3, figs 1, 5–6; Pl. 4, figs 1, 3–4). In forms with thin shells, some aesthetes join together to form a basal canal, which traverse the underlying shell layers to connect to the underlying epithelium. The row of pores formed on the lower shell surface is termed a slit ray (Pl. 4, figs 1–2, 5).

An aesthete consists of a main body, termed the macro-aesthete and smaller side branches called the micro-aesthetes, which are connected to the shell surface (Text-fig. 5C). The macro-aesthete is bounded to the exterior by an organic apical cap, which is porous, and the micro-aesthete is capped by an unperforated subsidiary cap (Eernisse and Reynolds 1994; Reindl et al. 1997). The macro-aesthete consists of large, elongate secretory cells that probably secrete substances to the shell surface and slender sensory cells with a distal cilium underneath the apical cap (Reindl et al. 1997). In most forms there is a peripheral rhabdomeric photoreceptor complex in the periphery of the macro-aesthete (Text-fig. 5C). The entire aesthete body is bound from the mineralized matrix by lining cells and a cuticle. The micro-aesthetes are so thin that each are occupied by just a single cell, the nucleus of which is situated within the body of a macro-aesthete. The function of the micro-aesthetes remains unresolved. Baxter et al. (1987), studying Callochiton, suggest a secretory function, but the fact that the subsidiary cap is imperforate led Reindl et al. (1997), studying Leptochiton and with a number of other morphological arguments, to suggest a sensory function instead.

Some aesthetes within the Chitonina are very specialized, and larger aesthetes are modified into ocelli with a large calcareous lens at the shell surface and a retina-like organization of rhabdomeric photoreceptors underneath (Boyle 1969; Eernisse and Reynolds 1994).

The incorporation of the aesthetes into the shell plate matrix is described by Blumrich (1891), Haas (1981) and Baxter and Jones (1981). The marginal epithelium secretes the mineralized component, but it also forms the aesthete bodies. The first micro-aesthetes are incorporated in the upper part of the shell-secreting epithelium. As the shell plate continues to grow, the macro-aesthete is gradually incorporated as the area of further incorporation migrates downwards terminating when merging into the basal canal.

A morphological analysis of the aesthete canal system

The morphology of the aesthete canal system was studied in a number of taxa, representing the major clades of modern chitons. The aim was to define the morphological disparity and constraints that define the aesthetical canal system in modern chitons. A great diversity in morphology was observed that would be valuable in a cladistic analysis of modern chitons (Fernandez et al. 2007; Vendrascos et al. 2008), but this is beyond the scope of the paper. Other descriptions of the superficial aesthete canal morphology have been published by Haas and Kriesten (1975), Currie (1992), Fernandez et al. (2007) and Vendrascos et al. (2008) among others.

Table 2 shows a chart of the measured dimensions of the studied species. Plates 3 and 4 give some representative examples of the studied samples. The typical maximum width of a macro-aesthete is between 15–50 μm, but with most forms around 25–30 μm. The larger ocelli in species of Acanthopleura and Lucilina have a thickness of 50–70 μm and numerous surrounding micro-aesthetes of the calcareous lens. Hanleya nagelsa also has large macro-aesthetes of a width about 50–80 μm. The micro-aesthete width is of about 2–10 μm, but is typically less than 5 μm. The number of micro-aesthetes per macro-aesthete (mi/ma) varies (Pl. 3, figs 4, 7; Pl. 4, figs 6, 8): Leptochiton asellus Gmelin, 1791 within the Lepidopleurida has 2–7 mi/ma, whereas the ocelli of Acanthopleura possibly have got more than 50 mi/ma. The Chitonina generally has more micro-aesthetes per macro-aesthete than the Acanthochitonina and the Lepidopleurida. The length of an aesthete varies considerably more than the

### EXPLANATION OF PLATE 4

**Figs 1–2. Schizopelaz brandtii**, Alaska, USA. ZSM Mol 20050464 and YPM IZ 043617. 1, Ventral view, 2, Ventral view, focusing on the slit ray.

**Figs 3–4. Rhysoplaz olivacea**, Island of Rhodes, Greece. 2, ventral view, 3, ventral view. Illustrating zonal variation between the lateral and median or jugal area. Lateral area is in lower left corner of 2 and lower right corner of 4 where most of the connecting basal canals have broken off.

**Figs 5–6. Ischnochiton elizabethensis**, South Africa. ZSM Mol 20050840 and YPM IZ 043622. 5, ventral view showing the distribution of aesthetes according to ribs of dorsal shell surface underneath, 6, lateral view.

**Figs 7–8. Stenochiton longicymba**, Western Australia. ZSM Mol 20041373 and YPM IZ 043623. 7, ventral view, 8, dorsal view. Small aesthetes, note the oblique orientation of the basal canals with respect to the shell margin.

Scale bars represent 1 mm in 1, 3 and 4, 500 μm in 2, 5 and 7, 50 μm in 6 and 8.
VINOTHER, extant chitions
width: From being short and almost spherical in *Leptocho- 
ton* and *Hanleya* in the Lepidopleurida to elongate and 
cylindrical in most other forms. Many forms display zonal 
variation: *Rhysopax olivacea* and *Callotochiton euplaca* 
have more elongate aesthetes in the lateral area of the 
intermediate shell plate where the tegumentum is thicker 
than the median or jugal area where the aesthetic is 
shorter (Pl. 3, fig. 1; Pl. 4, figs 3, 4), but the width is 
similar in both areas.

The thickness of the basal canals, which connect the 
aesthetes to the marginal or basal epithelium, varies. The 
typical size range is between 10–30 μm with the canals 
projecting to the shell margin in multiple layers (Pl. 3, 
fig. 1). Some forms, like the families Tonicellidae and 
Schizoplasticidae (both might have to be considered part of 
Mopaliidae sensu Eernisse et al. 2007) have significantly 
thicker basal canal systems (between 30–80 μm) and the 
basal canals in a single layer (Pl. 4, figs 1–2).

The aesthetic canals has not been described in any detail 
in fossil chitons, but Hoare (2000) noted the diameter in 
nine Carboniferous chiton species to be between 19.3 μm 
and 31.2 μm, consistent with size distribution seen in the 
material studied here.

*Constraints on the chiton aesthete canal system*

The aesthetic canals are a sensory and secretory system 
that requires an intimate connection with the underlying 
mantle epithelium to receive nutrients and to transmit 
nervous input from the sensory cells. The size of the canal 
system is quite variable with a macro-aesthete and 
micro-aesthetes having a regular thickness, but much 
more variable in length in different shell areas or different 
species with variable shell thickness. Thus, the aesthetic is 
dependent primarily on the thickness rather than its 
length and coordinates its morphology to the accommo-
dation space as the thickness of the shell plate and local 
surface variability have such a clear influence on the aest-
the cortex morphology. This is also exemplified in forms with 
shell ornamentation, like nodules or ribs. In these, the 
aesthetes are distributed according to the ornamentation, 
so that they primarily emerge on a rib or a nodule, which 
provides local variability in accommodation space. The 
basal canals vary according to the amount and style of 
aesthetes connecting to it and can be slender or thick 
depending on which group is studied.

*Shell pores in other molluscs and Lophotrochozoans*

A number of lophotrochozoans and especially molluscs 
have canals within a mineralized shell matrix. The fissur-
eliid limpets (Vetigastropoda) are one example. In these 
molluscs, pores are incorporated into the shell matrix 
during the marginal accretion and have a similar organic 
porous cap to those in chitons. They do, however, seem 
to be ultra-structurally different to the aesthetes with 
other cell types (Reindl and Haszprunar 1994). Some 
bivalves have shell pores, but these are etched into the 
shell from the underlying mantle and bear no similarity 
to the aesthetes (Reindl and Haszprunar 1996). Extant 
monoplacophorans in some cases also have regular pits 
that might be shell pores (e.g. Wagen and Gofas 1996), 
but nothing is known about their nature. Similar shell 
pores have been observed in fossil monoplacophoran-like 
molluscs from the Lower Cambrian (Parkhaev 2006; Feng 
and Sun 2006).

Bryozoans have small so-called punctae that house a 
single cell bounded to the exterior by a coffee bean-
shaped organic cap with a slit. The base of the cell is sur-
rounded by a few other cells (Nielsen and Pedersen 
1979). The exact function of these is unknown but 
Nielsen and Pedersen (1979) have suggested a secretory 
function.

Articulate brachiopods have unbranching shell pores 
called caecae (Owen and Williams 1969; Reindl et al. 
1995). These are very similar in cellular organization to 
the aesthetes with large secretory cells and a sensory cell 
with a distal cilium. The caecum is bounded to the exter-
ior by a porous organic cap. Reindl and Haszprunar 
(1996) ascribed this similarity as being a remarkable case 
of polyphyly since brachiopods were generally regarded as 
deuterostomes at the time of publication. With recent 
molecular evidence grouping the spiralian and lophoph-
orates in Lophotrochozoa, the polyphyletic interpretation 
is much less obvious. The morphological diversity of shell 
pores in brachiopods is nevertheless much more diverse 
than observed in the aesthetes of chitons and halkieriids 
and there are no obvious arguments to suggest close 
affinities between halkieriids and brachiopods, as sug-
gested by Conway Morris and Peel (1995). Cranian brachiopods 
have been shown to possess branching 
caecae, a feature still not fully understood (Reindl and Haszprunar 1996). However, these canals are much 
smaller (Williams et al. 1997) than in the branching 
aesthete complex in modern chitons.

**HOMOLOGY OF THE CANAL SYSTEMS 
IN SACHITIDS AND CHITONS**

The morphology of both canal systems seems to be con-
strained by one parameter: the morphology and extent of 
accommodation space. Both canal systems show difference 
in length of a macro-aesthete/lateral canal, but at 
the same time they are conservative regarding transverse 
thickness. It can be inferred that the canal system of
Sinosaechites was organized so that it had been connected to the basal epithelium of the animal body through the basal foramen. The lateral canals were connected to the exterior through the perforating tubules. This kind of connectivity and morphology are directly comparable to the aesthete system.

The step from interpreting an aesthete function of a canal system within the sclerite of a supposed stem-aculiferan, seems to involve dramatic evolutionary or transitional steps. However, the histology of the aesthetes in extant echinoids shows that it corresponds in morphology to the epithelial papillae in the mantle of both aplacophorans and polyplacophorans (Blumrich 1891; Hoffmann 1949; Haas and Kriesten 1977; Fischer et al. 1980; Scheltema 1994). The function of the epithelial papillae in polyplacophorans is to secrete sclerites and other sensory structures like chitinous bristles. Sinosaechites and the other saccopods are related to the aculiferans (Bengtson 1992; Vendrasco et al. 2004; Vinther and Nielsen 2005) and it could be expected that a similar epithelial organization was present in their integument. At the least, it can be envisaged that a chiton incorporating cells of the epidermal papillae into the sclerite at secretion and thereby would be incorporating an aesthete system. This is thought to have occurred in a putatively derived group of Upper Palaeozoic polyplacophorans, the multiplacophorans (Hoare and Mapes 1995; Vendrasco et al. 2004; see below).

EVOlUTION OF THE AESTHete CANAL SYSTEM

There is no evidence for pores in the shell plates of Halkieriidae in view of its preservation of delicate radial ornamentation, although it cannot be excluded that the lack is due to coarseness of preservation. There seems to be a reverse organization of aesthecan canals in halkieriids, with solid shell plates and aesthetes in the sclerites and the opposite configuration in modern chitons. No extant chitons are known with aesthetes in their sclerites, which consist of a solid body of aragonite with an external organic cuticle attached by an organic stalk, except for continuously growing spines. It is known that the earliest articulated chiton fossil from the Ordovician, Echinocladus dafnei Pojeta et al. (2003), had large hollow sclerites, in contrast to the condition in extant chitons, but the state of mouldic preservation in a dolomitic limestone does not provide for a delicate canal system like the aesthetes to be preserved if present. The Upper Palaeozoic group called multiplacophorans (Hoare and Mapes 1995) belongs to the polyplacophorans, but is characterized by a shell plate configuration distinct from modern chitons. The articulated multiplacophoran Polysacoidea vickersianum Vendrasco et al. (2004) has 17 shell plates arranged in seven transverse bands with single anterior and posterior shell plates, and five intermediate areas with three shell plates in each. These forms have long spinose marginal sclerites (Text-fig. 6C–E) that were embedded in the perinotum. Furthermore, the sclerites possess an internal canal system similar in morphology to the aesthetic canal system that is also seen in the shell plates (Text-fig. 6A–B, F) of the same fossils (Hoare and Mapes, 1995; Vendrasco et al. 2004). This indicates that the polyplacophorans have the ability to form an aesthetic canal system within their sclerites in the perinotum. It has been suggested that the multiplacophoran sclerites should have been derived from the shell plates (Vendrasco et al. 2004; Conway Morris 2006) primarily because of their possession of an aesthetic canal system. However, there does not seem to be that much derivational difference between sclerites and shell plates since it is the same epithelium secreting both structures and the fact that they are compositionally and microstructurally similar. There is evidence that shell plates evolved from sclerites that merged together in the aculiferans (Bengtson 1992) in the sachtiid genus Siphogonouchites. So the shell plates are in fact a modification of the same epithelium that secretes sclerites. Bengtson (1992) drew attention to the fact that the aesthetes are modified from the epidermal papillae, which also secrete the sclerites (Haas and Kriesten 1977; Fischer et al. 1980), and so the merging of sclerites may be closely linked to the formation of the aesthetic canal system.

To suggest a functional reason for the evolutionary transition to a reverse organization of the aesthetic canal system, one can look at the dorsal aspects of the articulated H. evagelista and a typical chiton. About 5/6 of the dorsal surface of Halkieriidae is covered by sclerites and 1/6 by shell plates. Sinosaechites belongs to the same family (Halkieriidae), but it is not known whether it had any shell plates or not. The recently described sachtiiid Orthozancus Conway Morris and Caron, 2007 possess only one anterior shell and there is only one type of shell plate known from Siphogonouchites (Maithanella; see Bengtson 1992). The sachtiiids probably all had a low proportion of their dorsal side covered by shell plates. Therefore, having an aesthetic system in the sclerites was probably sufficient for it to perceive and interact with the surrounding environment, which was possibly necessary due to the heavy sclerome. Most modern chitons are primarily covered by shell plates, up to 8/10 of the dorsal surface in most taxa. If they had the sensory and secretory system in their sclerites or the girdle (perinotum) only, they would have a limited perception of their surroundings. It can therefore be suggested that the transition is caused by a change in aspect of the dorsal sclerome to a predominantly shell-covered dorsal surface, a more tough and interlocked armour, which would be related to the increased predator/prey interactions throughout the Phanerozoic
and a lifestyle in the energetic intertidal habitat typical of many chitons.

CONCLUSIONS

Sachitids are a group of lepidote bilaterians having hollow sclerites that were mineralized and composed of longitudinal aragonitic fibres secreted by a basal epithelium. The sclerites were arranged on the dorsal surface and, in most taxa, organized into morphological zones. Sclerite replacement occurred during animal growth, larger replacing sclerites was secreted by the underlying epithelium. All these features indicate an aculiferan affinity of the group and is congruent at both macroscopic, microscopic and microstructural level of morphology.

The internal canal system in halkieriid sclerites is morphologically similar to the aesthetes canal system in chiton shell plates. This is demonstrated by the morphologic analysis of the extant chitons, which shows that the canal systems change their morphology according to accommodation space and develop their morphology within certain constraints. The aesthetes morphology between species and in different areas of the shell plate with different thickness vary in aspect primarily by length of the macro-aesthete, whereas the thickness is relatively stable, between 25 and 35 μm in diameter in most species. The analysis of the sclerite canal system in Sinonachites delicatus (Jell, 1981) indicates that it is constrained according to the accommodation space as well having the width relatively constant at about 20–40 μm, coinciding with the size interval of aesthetes in chitons. Other halkieriid species preserved with an internal canal system show a different configuration of the canal system, but the same size intervals of thickness of the lateral canals interpreted as a different compromise to accommodation space.

Sachitids are arguably related to Polyplacophora, which have epithelial papillae homologous to the aesthetes that also secrete the sclerites. Formation of a canal system within an aculiferan sclerite that seems to function like aesthetes perhaps indicates that epidermal papillae were incorporated during formation of the sclerite. The Upper Palaeozoic multiplacophorans possess an aesthetic canal system in both their spinose sclerites and shell plates (Hoare and Mapes 1995) and are closely related to, or perhaps belong to crown polyplacophorans (Vendrasco et al. 2004). Thus, multiplacophorans are a functional intermediate (probably not phylogenetically) between the sachitids and the chitons.

Future molecular analyses will eventually be able to test and polarize morphological and evolutionary scenarios along with new fossil finds and molluscan developmental studies. Currently, it is not possible to argue whether sachitids are stem or crown group molluscs. There is no
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REFERENCES


MISSARZHEVSKY, V. V. 1989. [The oldest skeletal fossils and stratigraphy of the Precambrian-Cambrian boundary beds]. Trudy Geologicheskogo Instituta AN SSSR, 443, 1–237. [In Russian].


hayae from the Herefordshire Lagerstätte (Silurian, England), and implications for molluscan phylogeny. Palaeontology, 47, 293–318.


WALCOTT, C. D. 1911. Cambrian geology and paleontology. II. Middle Cambrian annelids. Smithsonian Miscellaneous Collections, 57, 251–304.

