
The Early Cambrian *Halkieria* is a mollusc

JAKOB VINTHER & CLAUS NIELSEN

Accepted: 2 August 2004

Vinther, J. & Nielsen, C. (2005). The Early Cambrian *Halkieria* is a mollusc. — *Zoologica Scripta*, 34, 81–89.

Halkieria evangelista was originally interpreted as a stem-group brachiopod. It was later proposed that the brachiopods evolved from a halkieriid ancestor that curved ventrally, lost the foot and radula, developed a lophophore as a new feeding organ, and modified the sclerites to chaetae. Molluscan affinities have been discussed by a number of authors. We have studied some of the original material of *Halkieria* and found that all the characters that can be observed with certainty are compatible with characters in living molluscs. The combination of characters observed in *Halkieria* does not fit with any of the living classes of molluscs, so we propose placing it in a new class, Diplacophora. Living polyplacophorans have hairs secreted by a number of epithelial cells and containing nerve cells; they are clearly not homologous with annelid chaetae. Thus, there is no support for theories that regard *Halkieria* as belonging to the stem group of either the annelids or brachiopods.

Jakob Vinther, Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen, Denmark. E-mail: vinther@stud.ku.dk

Claus Nielsen, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. E-mail: cnielsen@zmuc.ku.dk

Introduction

The well-known Early Cambrian fossil *Halkieria evangelista* (Conway Morris & Peel 1995; see Figs 1 and 2) was first described in detail from the Sirius Passet Buen Formation in Greenland. Isolated sclerites of closely related forms have subsequently been described from many other parts of the world (e.g. Poulsen 1967; Bengtson 1985; Bengtson *et al.* 1990; Conway Morris & Chapman 1997).

It was initially interpreted as closely related to the Cambrian-age *Wirwaxia* and these forms were in the detailed description (Conway Morris & Peel 1995) hypothesized to be stem-group annelids and brachiopods, with *H. evangelista* placed in the brachiopod stem-group. Molluscan affinities were posited in the preliminary description by Conway Morris & Peel (1990) and by Peel (1991), but subsequently rejected in the detailed discussion by Conway Morris & Peel (1995).

A number of authors have suggested that halkieriids could be molluscs (e.g. Bengtson 1992; Runnegar 1996, 2000; Lindberg & Ponder 1996). Conway Morris (1998: fig. 86) proposed that brachiopods are derived from a halkieriid ancestor, which became short, with the body curved ventrally, developing a lophophore as the feeding organ, and with the calcareous sclerites along the edge of the scleritome evolving into the chitinous chaetae at the margins of the mantle. This view has found some support (Williams & Holmer 2002; Cohen *et al.* 2003; Ushatinskaya 2002).

It appears to us that some of the recent discussions of the phylogenetic position of *Halkieria* have been rather fanciful, with little consideration for actual characters of living animals, for adaptive values of evolutionary changes, and for the function of the proposed intermediate forms. Furthermore, it appears that most previous discussions of the phylogenetic position of *Halkieria* have become muddled by including other fossils (e.g. *Wirwaxia* and tommotiids like *Micrina*) which could possibly be related to halkieriids, instead of dealing exclusively with well-documented characters of *Halkieria* itself. We therefore give a brief redescription of *Halkieria* and make comparisons with morphological characters of living and fossil molluscs, especially polyplacophorans, and those of brachiopods and annelids, to reach a more clear understanding of the phylogenetic position of *Halkieria*.

Materials and methods

Specimens of *H. evangelista* kept at the Geological Museum, Copenhagen (MGUH) and Sedgwick Museum, Cambridge (SM) were examined under the dissecting microscope, with particular attention given to the structure of the different sclerite types. The relationships between the sclerite zones were investigated, in specimens of different sizes, in order to deduce the way the scleritome has grown. The anterior and posterior shell were examined for possible structures such as

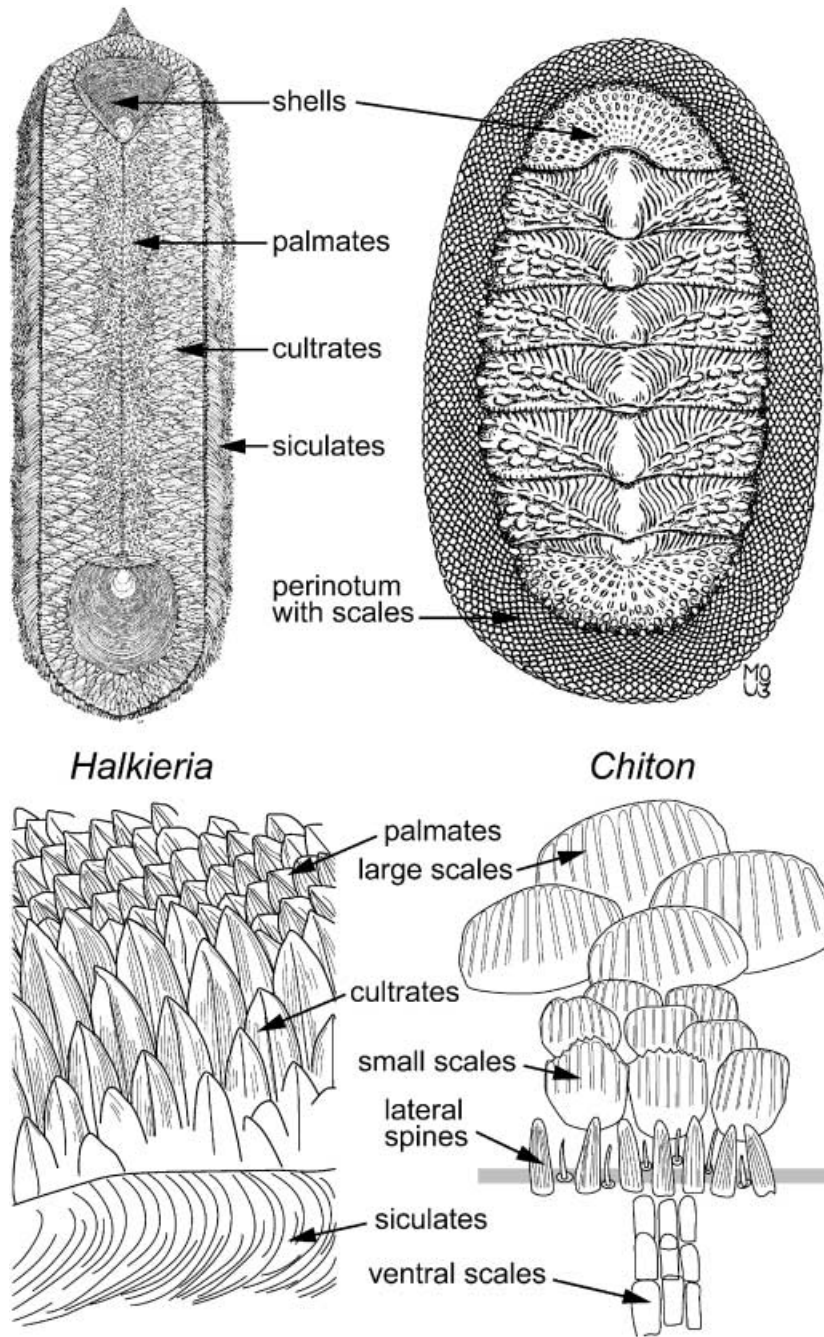


Fig. 1 Upper half: drawings of dorsal aspects of *Halkieria evangelista* (reconstruction, modified from Conway Morris & Peel 1995) and *Chiton tuberculatus* (drawn by M. Unsöld, Zoologische Staatssammlung, Munich, Germany), showing general configuration of shells and zones of sclerites. Lower half: drawing of a portion of the scleritome of *H. evangelista* (SM X24911; see also Fig. 2; anterior to the right) and of sclerites of the perinotum of *Ischnochiton punctulatissimus* (redrawn from Plate 1899); the perinotum of the chiton has been cleaned with potassium hydroxide and unfolded along the grey line so that the scales of the ventral side are also seen.

ornamentation, growth lines, pores and muscle scars. Specimens were coated with a layer of ammonium chloride through sublimation and placed in a unidirectional light source. MGUH specimens were photographed digitally at a resolution of 600 dpi, while SM specimens were photographed using 50 ASA black and white film. Because of the complex state of preservation of the halkieriids, with rods imposed on the palmate and cultrate zones obscuring the view of both, the light

source had to be placed in a variety of positions in order to highlight the different elements (e.g. in Fig. 4).

Brief description of *Halkieria evangelista*

The original description by Conway Morris & Peel (1995) of articulated specimens is very detailed and complemented by magnificent photographs of this difficult material. In this paper we summarize and discuss published information on important

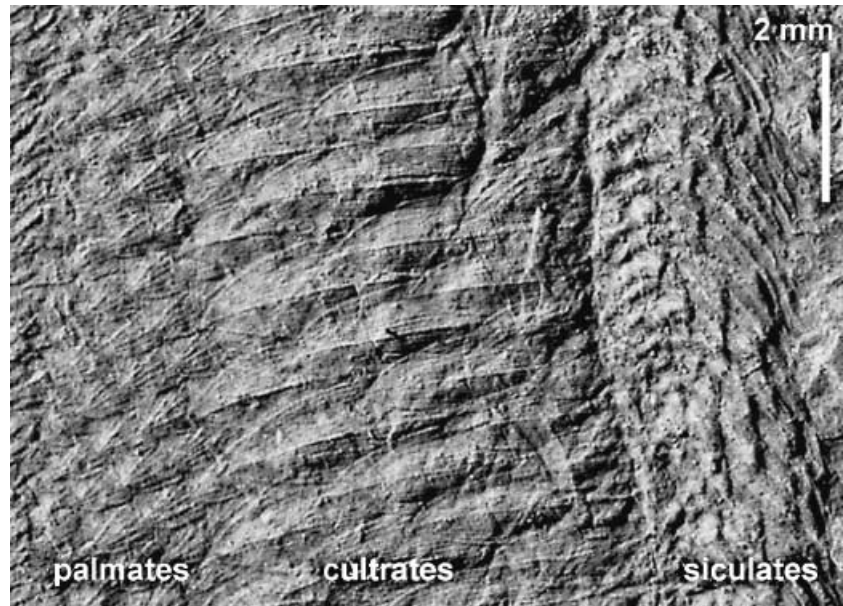


Fig. 2 Part of the scleritome of *Halkieria evangelista* (SM X24911).

characters and add some new observations to create a basis for a discussion of the systematic position of *Halkieria*.

The original specimens from the Sirius Passet Buen Formation are preserved as flat impressions in black shale of an anterior and a posterior dorsal shell and peripheral and dorsal sclerites, together called the scleritome. They are 1.5–8 cm in length. It has been argued, based on the phosphatized, three-dimensionally preserved material from other deposits of the same age, that both the sclerites and the shells were originally calcareous (see below). It appears that the calcareous material dissolved more or less rapidly during the processes of fossilization and compaction.

The lithology and the sparse ichnofauna indicate an anaerobic environment, with acidic conditions promoting organic preservation and early decalcification. Most of the articulated specimens are imprints of the dorsal side of the scleritome with the sclerites pressed together, showing only the compressed shape of the dorsal side (for example the holotype, MGUH 19728; see also Fig. 2). However, a few specimens (for example MGUH 19731) show sclerites that look ‘transparent’ with preserved impressions both of the inner structures and of the underlying sclerites (Fig. 3). Here, we infer that the calcareous material had been dissolved completely, leaving only the cuticle plus

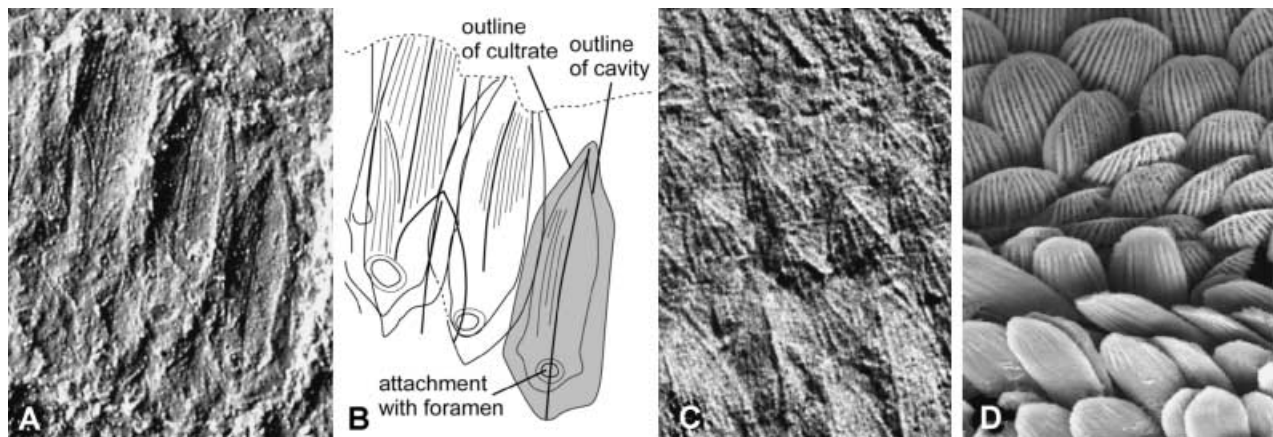


Fig. 3 A–D. —A, B. Photograph and interpretive drawing of isolated ‘transparent’ cultrates of *Halkieria evangelista* (MGUH 19731). —C. Photograph of cultrates and palmates (SM X24911). —D. SEM of perinotum of *Leptochiton compostellanum* Zalvide & Urgorri (Off Mauretania, Meteor 44, stn. 244; SEM by Dr E. Schwabe, Zoologische Staatssammlung, Munich, Germany) showing two dorsal zones of different scales.

an organic matrix of the calcareous parts to become fossilized.

As already mentioned, it has been argued that the original mineralogy was calcareous (Bengtson & Missarzhevsky 1981; Bengtson & Conway Morris 1984; Bengtson *et al.* 1990). The sclerites are either preserved as internal moulds (steinkerns) of amorphous phosphate or external moulds in phosphatic concretions. Original phosphatic fossils, such as nonarticulated brachiopods and tomotiids, are usually preserved with primary mineralogy and ultrastructure in these deposits, whereas calcareous shells like molluscs are preserved as steinkerns of secondary phosphates like the halkieriids and other so-called coelosclerithophorans. This indicates a probable calcareous origin for the halkieriids. Bengtson & Conway Morris (1984) argued that an organic composition seems improbable because the three-dimensional preservation shows that they were resistant to early decay and deformation.

Ushatinskaya (2002) suggested that halkieriid sclerites could have been noncarbonate, based on the fact that some other types of shells and sclerites are sometimes preserved with thin sheets of calcite while halkieriids are never preserved in this manner. This could also be explained by different original calcareous mineralogies. Various molluscs use calcite, aragonite or both. It might be that fossil shells and sclerites preserved as partly calcite sheets were originally calcitic or were a mixture, whereas halkieriids were exclusively aragonitic. The suggestion that halkieriids were wholly organic [Ushatinskaya (2002)] is supported by the mode of preservation in Sirius Passet described in this paper and by Conway Morris & Peel (1995), where fossils with organic cuticles and exoskeletons tend to be preserved as thin films with no significant relief. Halkieriids tend to have a relief similar to that seen in trilobites and hyoliths that are typically preserved as decalcified moulds.

The anterior end of several of the specimens is similarly curved in the horizontal plane. This indicates that the musculature associated with the scleritome was still present at the time of burial. Nothing has remained of the soft parts, but phosphatic concretions in the middle and posterior regions of several specimens probably represent diagenetically altered gut contents (MGUH 19731) (Conway Morris & Peel 1995). Both shells are comparatively thin, dorsally convex and possess prominent growth lines and a less marked radial ornamentation. No other structures, such as traces of pores or indications of shell ultrastructure, have been recognized in the imprints. The mineralogy of the shells is dubious, but may have been calcareous, as indicated in steinkerns of putative disarticulated halkieriid shells from elsewhere (Bengtson 1992; Conway Morris & Chapman 1997).

The entire margin of the scleritome is formed by a rather narrow zone of curved spines, called sicutates, arranged in dorso-ventrally imbricating rows, and it is surmised that the spines curve backwards, indicating the anterior-posterior

orientation of the fossils. Observations on isolated sicutates from other localities (Conway Morris & Chapman 1997; Conway Morris, pers. comm.) indicate that they were hollow. Conway Morris & Peel (1995) interpreted some structures in SM X24926 as traces of a radula, which seems possible. However, the edge of the scleritome is folded and it cannot be excluded that the putative radula could be a group of dislocated sicutates.

A wide band of larger, flattened, lanceolate scales, called cultrates, with a prominent, median, longitudinal keel and weaker, lateral keels, cover the lateral, anterior and posterior regions of the scleritome in a quincunx pattern. The cultrates increase in size and imbricate towards the median zone and the shells; they superimpose slightly both on the outer edges of the shells and on the lateral parts of the zone of palmates and 'rods' (see below and Fig. 4). Observations on phosphatized specimens (Bengtson & Conway Morris 1984; Bengtson 1985) from other deposits show that the cultrates were hollow with a basal foramen for attachment on the basal side.

This can also be seen in the material studied here (Fig. 3). In one specimen (MGUH 19733) the cavities of some cultrates in the right side are filled with a matrix (possibly of limonite or goethite), which reveals the presence of putative lateral canals from the central cavity (Conway Morris & Peel 1995: fig. 22b). This is also observed in disarticulated phosphatized halkieriid sclerites (e.g. Conway Morris & Chapman 1997). The attachment of the cultrates seems to be at the foramen on the basal part of the interior side of the sclerites by a short attachment stalk. It seems to us that the long basal

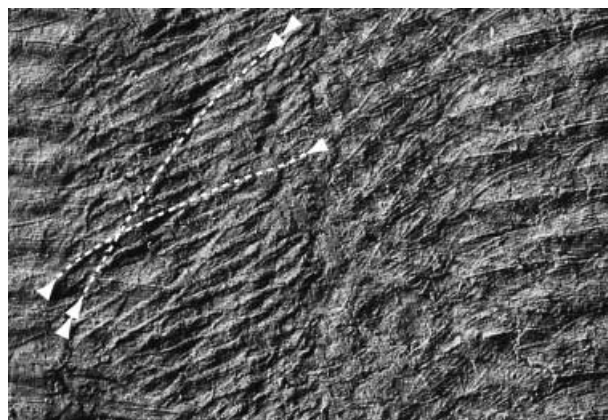


Fig. 4 Photograph of *Halkieria* scleritome in oblique light showing two types of linear structures. The first, indicated by a white dotted line between single arrowheads, represents the structure called 'rods' by Conway Morris & Peel (1995). The second, indicated by a white dotted line between double arrowheads, represents another structure, which follows the rows of palmates. Note that the tips of the cultrates cover the lateral zone of both types of structures (and the palmates) (SM X24911).

stalk described by Conway Morris & Peel (1995: figs 11, 39o, 42o) (MGUH 19731 and SM X24926) is a misinterpretation of a median keel of a neighbouring cultrate. The quincunx pattern makes oblique rows of cultrates quite conspicuous in many specimens. In specimens longer than about 2.5 cm, each oblique row consists of 6–7 sclerites, irrespective of the size of the specimen. The number of rows between the two shells is also rather constant, viz. about 23; the number of cultrate rows in smaller specimens could not be ascertained.

The median zone, a band between the two shells, is covered by shorter scales called palmates; they imbricate posterior–adaxially from each lateral side, meeting each other at the dorsal midline that shows a prominent groove. The palmates have more pronounced ribs than the cultrates and increase slightly in size towards the lateral margins of the zone. In specimens smaller than about 3 cm, the palmate zone is quite narrow and sclerites have not been observed. This may indicate that the palmates do not develop until the animals have reached a certain size.

The morphology of the sclerites — with an extensive cavity and the basal restriction with the attachment foramen — indicates that the sclerites have grown to a finite size (Bengtson & Conway Morris 1984). The constant number of cultrate sclerites in the oblique rows in specimens of varying sizes indicates that sclerites have not been added from a growth zone, but have been lost and replaced with larger sclerites in the same place in a continuous process during the growth of the animal. Bengtson & Conway Morris (1984) speculated that the sclerites were ‘moulted’, and proposed that the internal organic tissue was withdrawn before the shedding of the calcified part of the sclerite. The organic tissue should then have expanded again and secreted the new sclerite, as in a moulting arthropod. This is not supported by the structure of the isolated sclerites described by Bengtson & Conway Morris (1984: fig. 5), which clearly show transverse growth lines.

Most of the specimens show a tight pattern of chevron-shaped ribs with the tips pointing anteriorly (Fig. 4) imposed on the sclerites. The angle between the rows of the two sides varies between 90° and 140°, which indicates a flexibility of the scleritome. Conway Morris & Peel (1995) describe them as internal rods. They may be ribs on the organic cuticle that holds the sclerites. There is actually a second, less dense and less conspicuous system of such ribs (Conway Morris & Peel 1995: fig. 27f), meeting in a more acute anterior angle (viz. 40–60°) and following the rows of palmate sclerites. Both systems of ribs can be recognized underneath the overlapping cultrates. A few specimens display what is interpreted as an anterior cone (Fig. 1).

Characters of molluscs, especially polyplacophorans

Both living and fossil polyplacophorans are characterized by a mantle with a number of dorsal shell plates and a surrounding

perinotum with spines, scales and hairs of varying types set in a thick organic matrix (Fig. 1). All living and most fossil polyplacophorans, including the Ordovician *Echinobiton* (Pojeta *et al.* 2003) have eight shells, but the newly described Carboniferous *Polysacos* (Vendrasco *et al.* 2004) shows that the Devonian to Permian multiplacophorans with higher numbers of shell plates, partially in two rows, were also polyplacophorans. Both shells and scales consist of calcium carbonate, aragonite, secreted into an organic matrix and surrounded by a periostracum (Eernisse & Reynolds 1994). The surface of the shells is covered by a very thin ‘properiostracum’, which is difficult to distinguish and has often worn off in larger specimens. There is no well-defined shell gland as in the conchiferans, and both structure and shell deposition indicate that the shells of polyplacophorans and conchiferans may not be homologous (Scheltema 1988). The ventral side is dominated by a wide, ciliated, muscular foot, which is used in locomotion. All species have a strong radula.

Aplacophorans (i.e. solenogasters and caudofoveates) have a mantle with calcareous spines, but more scale-like sclerites, resembling the cultrates of *Halkieria*, are found in the solenogaster *Teuglaberpia tasmanica* (Scheltema 1999). There are no shells and the foot is strongly reduced or absent in association with the approaching or complete fusion of the lateral mantle edges along the ventral side. The Silurian *Acaenoplax* (Sutton *et al.* 2001), which has a body almost completely covered with spicules and a row of shells, could be interpreted as an ‘aplacophoran with shells’ (see also Vendrasco *et al.* 2004), but we believe that the information at hand will not support deeper phylogenetic analysis.

The shells of the polyplacophorans cover most of the dorsal surface in most species, but are rather small in *Katharina*, reduced to a row of oval plates surrounded by the extended perinotum in *Cryptoplax*, and completely overgrown by the perinotum in *Cryptochiton*; however, they are always present. Each shell consists of an outer layer, the tegmentum, and an inner layer, the articulamentum. The tegmentum is pierced by branching canals with epithelial cells and nerves, whereas the articulamentum is composed of solid aragonite (Eernisse & Reynolds 1994). The tegmentum of the fossil multiplacophorans clearly shows the canals and their openings (Vendrasco *et al.* 2004). Conchiferan shells lack the tegmentum and are usually covered by a well-defined periostracum.

The polyplacophoran perinotum carries numerous sclerites, variously described as scales, spines, hairs, clappers, and spicules, on the dorsal side and in some species also at the peripheral zone of the ventral side (Eernisse & Reynolds 1994). These structures are arranged in characteristic patterns of considerable systematic importance and parallel zones of various types are seen in many species; some species have flat sclerites along the ventral mantle edge (Fig. 1). Spines are simple, calcified structures which are secreted

from a large number of cells and continue growing over a long period (Fischer *et al.* 1980). Scales, spicules and clappers are stalked structures of organic material containing a smaller or larger calcified body; sensory cells may be associated with them (Fischer *et al.* 1988; Leise 1988).

Many species, for example of the genus *Ischnochiton* (Kaas & Van Belle 1990), show a robust perinotum with large scales in a regular quincunx pattern. The number of oblique rows in the perinotum increases only slightly during growth. A 1.8 cm long specimen of *Chiton granosus* Broderip had about 18 oblique rows of scales along the six middle shells with about 15 scales in each row, and a 5.0 cm specimen had about 25 rows each with about 15 scales [both from Valparaiso, Chile, in Zoological Museum, University of Copenhagen (ZMUC)]. Scales and spicules continuously develop from small epithelial papillae, grow until a certain size where the basal part of the calcified sclerite becomes lined with a cup-shaped thickening of the periostracum that makes further mineral secretion impossible. The spicules remain attached to the mantle by a short organic stalk, and are shed when a new structure pushes the old one out (Reinke 1868; Blumrich 1891; see also Fig. 5). Scales resembling sclerites of *Halkieria* in a similar pattern have been described from species of several genera (Kaas & Van Belle 1990; Fig. 3). Hairs are slender sensory structures found in many species. They typically consist of a long, grooved cuticular structure secreted by many cells, and house a nerve, sensory cells each with a stiff rod, and other structures (Leise 1988). They bear no resemblance to annelid or brachiopod chaetae (see below).

Living polyplacophorans and the aplacophoran postlarva described by Scheltema & Ivanov (2002) have compact scales or spines (Eernisse & Reynolds 1994; Scheltema *et al.* 1994). Adult solenogasters have hollow spines (Hoffman 1949; Scheltema & Schander 2000), and this is also the case for the newly described Ordovician *Echinochiton* (Pojeta *et al.* 2003), which unquestionably is a polyplacophoran with eight shells and a pair of large, hollow spines at the perinotum lateral to each of the shells. The hollow spines of *Proneomenia* are secreted by one cell, which does not extend into the spicule. When the spicule has reached full size, the canal closes and a basal periostracum cup, like that of the chitons (see Fig. 5), is formed before the spicule is shed (Hoffman 1949).

Characters of brachiopods

Both living and fossil brachiopods are characterized by the presence of two shells which have been called dorsal and ventral, but which are probably anterodorsal and posterodorsal (Nielsen 1991; Cohen *et al.* 2003). A ciliated lophophore is attached to the anterodorsal shell, and chaetae formed from single chaetoblasts are found in groups on the larvae and along the margins of the mantle in adults (Williams 1997). The chaetae

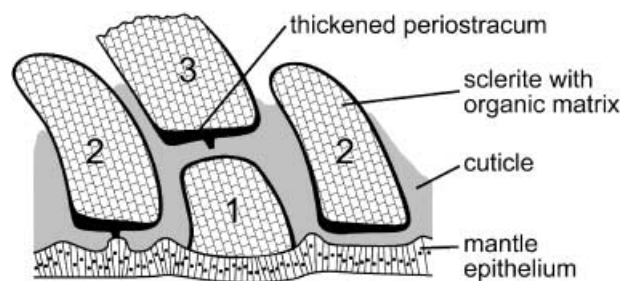


Fig. 5 Diagram of the replacement of scales in the perinotum of *Chiton* sp. based on Blumrich (1891). The scale marked 1 is developing; the scales marked 2 are fully formed, and the scale marked 3 is being shed.

show a high degree of resemblance to annelid chaetae, but none to structures found in polyplacophorans or *Halkieria*.

The brachiopod shells are of two types, calcitic and phosphatic. The shells of all living brachiopods (except the rhynchonellids) are pierced by perforations, either narrow cylindroids or wider punctae, which are occupied by epithelial cells (Williams 1997).

The only character that could indicate a closer relationship between *Halkieria* and brachiopods appears to be the presence of two median shells. Unfortunately, the structure of both living and fossil brachiopods is highly diverse and nothing is known about the shell structure in *Halkieria*, so this character does not reveal anything about mutual relationships.

Characters of annelids

Annelids have a segmented body with smaller or larger parapodia with chaetae each formed by one chaetoblast with microvilli; other cells lateral to the basal part of the chaeta may secrete additional material onto the chaeta (Jamieson 1992). The chaetae consist of β -chitin and proteins, which become consolidated by proteins tanned by a quinone-based process (Schroeder 1984). Amphinomidids have chaetae that are incrustated with calcium carbonate, and possibly also have carbonate inside the chitinous structure (Gustafson 1930). This report has been questioned, but the presence of calcium, although not its quantity, has been ascertained (Fredrik Pleijel, pers. comm.). Calcareous dorsal shells are not found; the shield on the posterior, ventral part of the highly specialized *Sternaspis* consists of organic material, apparently impregnated with iron (Bartolomaeus 1992).

Thus, there seems to be no single character that indicates a closer relationship between *Halkieria* and annelids.

Conclusions

A comparison of the morphological characters of *Halkieria*, molluscs (especially polyplacophorans and aplacophorans), brachiopods, and annelids unequivocally supports the interpretation of *Halkieria* as a crown-group mollusc (see also

Bengtson 1992). The two shells resemble shells of conchiferan molluscs due to the lack of any trace of canals and pores seen in the tegmentum of polyplacophorans; the sclerites resemble those of living polyplacophorans, but are hollow, like those of adult solenogasters and of the Ordovician polyplacophoran *Echinochiton*.

No characters indicate a sister-group relationship with either of the other two phyla. This implies that there is no support for the theory of the evolution of brachiopods from a *Halkieria*-like ancestor, as proposed by Conway Morris & Peel (1995) and Conway Morris (1998). The recent discussion of a link between halkieriids and tommotids and thereby to brachiopods (e.g. Williams & Holmer 2002 and Ushatinskaya 2002) is based on few characters, the main one being that the shells of *Halkieria* superficially resemble assemblages of disarticulated shells of tomotoids, especially the tannuoliniids. This group of apatophosphatic mineralized shells are similar in ultrastructure to the Cambrian *Mickwitzia*, which is interpreted as being a stemgroup brachiopod. This however, is not indicative of a halkieriid relationship with brachiopods, since neither the mineral composition nor the ultrastructure of halkieriid shells have been described.

Recent discussion has tended to be based on the halkieriid–wixioid–annelid–brachiopod model suggested by Conway Morris & Peel (1995) rather than on actually observed, possibly homologous characters. Brachiopods have in all probability evolved from ancestors with a straight main body axis which then became curved ventrally (whereas the phoronids are curved dorsally). However, there seems to be nothing to indicate that the ancestor was *Halkieria*-like. The structure of hairs on the perinotum of some living polyplacophorans is very different from that of annelid and brachiopod chaetae. The scenario, proposed by Conway Morris (1998), of a brachiopod evolving from either *Halkieria* or a polyplacophoran, with loss of radula and evolution of a lophophore, appears to lack the necessary structural/functional continuity and adaptational considerations.

Molecular studies, mostly based on 18S rDNA, generally show groups of annelids, molluscs, brachiopods, phoronids, bryozoans and other ‘lophotrochozoans’ in a chaotic and inconsistent pattern (e.g. Peterson & Eernisse 2001; Jondelius *et al.* 2002; Maxmen *et al.* 2003). This cannot be taken as an indication that *Halkieria* could have a place in the stem lineage of annelids and brachiopods, as indicated by Conway Morris & Peel (1995).

It seems impossible to include *Halkieria* in any of the molluscan classes as presently defined. The wide, flat body shape and the scaly perinotum strongly resemble those of some polyplacophorans by having sclerites arranged in zones growing to a finite size and replaced during animal growth. However, the shell structure, where the tegmental layer is missing, is more reminiscent of conchiferan shells. It seems necessary

to place *Halkieria* in a new class, which could appropriately be named after the two shells. Animals bearing hollow sclerites have been assigned to a separate class, Coeloscleritophora (Bengtson & Missarzhevsky 1981), but with the description of the unquestionable polyplacophoran *Echinochiton* (Pojeta *et al.* 2003), which has hollow lateral spines, and of hollow spines in adult solenogasters (Scheltema & Schander 2000), the Coeloscleritophora has become polyphyletic and cannot be retained.

Systematics

Phylum Mollusca Cuvier, 1797

Class Diplacophora classis nov.

Molluscs with an anterior and a posterior shell separated by an elongate zone of scale-like sclerites, together surrounded by zones with other types of sclerites. The shells grew by marginal accretion and the sclerites were shed and replaced by larger sclerites during growth.

The articulated fossils indicate that the animals were rather flat and had a ventral foot, distinguishing them from the aplacophorans. They resemble polyplacophorans especially in the presence of sclerites, which apparently did not grow but were replaced during the growth of the animal (nothing is known about the growth of the mantle sclerites of the aplacophorans). The moulds of the shells of *Halkieria* do not reveal internal structures, but there is no trace of a tegmentum layer with pores like that found in the polyplacophorans. The basal molluscan radiation seems unresolved at this point, and we now recognize four groups: Aplacophora, Diplacophora, Polyplacophora, and Conchifera in a polytomy. However, the general morphology of *Halkieria* may indicate a sister-group relationship with Polyplacophora.

Halkieriidae Poulsen, 1967

Halkieria Poulsen, 1967

Type species: Halkieria obliqua Poulsen, 1967

Halkieria evangeslista Conway Morris & Peel, 1995

Holotype: MGUH 19728, in the Geological Museum, Copenhagen.

Note added in proof

After submission of this manuscript a description of Middle Cambrian halkieriid sclerites from Australia has been published (Porter 2004). The sclerites, replaced with phosphate, display an ultrastructure of longitudinally oriented fibres interpreted as originally fibrous aragonite. The cavity of the sclerites is suggested to have housed sensory structures like the aesthetes of living polyplacophorans. These observations and the discussion support our view that the halkieriids were molluscs.

Further, Li & Xiao (2004) described new material of sclerites of *Tannuolina* and *Micrina* and speculated that these

forms could be ancestral to linguliform brachiopods, whereas *Halkieria* could be ancestral to the calcareous brachiopods. However, they do not add any new argument supporting a link between *Halkieria* and the brachiopods.

Acknowledgements

Support from the Danish Natural Science Research Council, grant no. 51-00-0278 to C. N., and from MGUH to J. V. is gratefully acknowledged. Thanks also to Dr S. Conway Morris, Cambridge, for hospitality and detailed criticism, to Dr S. Bengtsson, Uppsala, for useful comments, and to Drs D. Harper, E. Håkansson and D. Eibye-Jacobsen, Copenhagen, for discussions. B. Rubæk (ZMUC) helped with drawings, and D. Simons (Department Earth Sciences, Cambridge), S. Lennart Jakobsen (MGUH), and G. Brovad (ZMUC) helped with the photographs.

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