ONTOGENY, MORPHOLOGY AND TAXONOMY OF THE SOFT-BODIED CAMBRIAN ‘MOLLUSC’ WIIWAXIA

by MARTIN R. SMITH1,2,3

1Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, M5S 3G5, Canada
2Palaeobiology Section, Department of Natural History, Royal Ontario Museum, Toronto, Ontario, M5S 2C6, Canada
3Current address: Department of Earth Sciences, University of Cambridge, Cambridge, CB2 3EQ, UK; e-mail: ms609@cam.ac.uk

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Abstract: The soft-bodied Cambrian organism Wiwaxia poses a taxonomic conundrum. Its imbricated dorsal scleritome suggests a relationship with the polychaete annelid worms, whereas its mouthparts and naked ventral surface invite comparison with the molluscan radula and foot. My observations illuminate the diversity within the genus and demonstrate that Wiwaxia did not undergo discrete moult stages; rather, its scleritome developed gradually, with piecewise addition and replacement of individually secreted sclerites. I recognize a digestive tract and creeping foot in Wiwaxia, solidifying its relationship with the contemporary Odontogriphus. Similarities between the scleritomes of Wiwaxia, halkieriids, Polyplacophora and Aplacophora hint that the taxa are related. A molluscan affinity is robustly established, and Wiwaxia provides a good fossil proxy for the ancestral aculiferan – and perhaps molluscan – body plan.

Key words: halwaxiids, scleritomorphs, Aculifera, Mollusca, evolution, Cambrian explosion.
in morphology; they may represent multiple species or ontogenetic stages. Articulated specimens from Kaili, China may belong to *W. corrugata* (Sun et al. 2013) but have been proposed as a separate species, *Wiwaxia taijiangensis* (Zhao et al. 1994).

This study revisits features in *Wiwaxia* and *Odontogriphus* that have previously been contentious, and provides a detailed account of the *Wiwaxia* scleritome. This abundant new material fills a gap in the *Wiwaxia* size distribution, resolving the ontogeny of the scleritome and confirming that smaller specimens are more likely to represent juveniles than separate taxa. Novel observations substantiate *Wiwaxia*’s molluscan affinity, but its position within Mollusca remains unsettled.

**MATERIALS AND METHODS**

I examined 476 *Wiwaxia* and 170 *Odontogriphus* specimens (Table 1 and Table S1), most collected by the Royal Ontario Museum. Backscatter electron micrographs of uncoated specimens were obtained under environmental pressure SEM (Orr et al. 2002), complementing traditional light microscopy and digital interference of images obtained under plane- and cross-polarized light (Bengtson 2000). Scaling relationships were recovered from log-transformed dimension measurements (obtained from digital images) using linear models; sclerite zones were treated separately where this improved the Akaike information criterion.

**SCLERITOME**

**Previous research**

The dorsal and lateral surfaces of *W. corrugata* are covered with imbricating leaf-like sclerites. Conway Morris (1985) found the sclerites to be consistently arranged in seven to nine transverse rows and five distinct regions. From the midline out, he recognized zones of (1) asymmetrical dorsal sclerites; (2) rounded, symmetrical upper-lateral sclerites; (3) more oval-shaped symmetrical lower-lateral sclerites; and (4) sickle-shaped ventrolateral sclerites. A distinct anterior row forms the fifth sclerite zone; sclerites in this row resemble the upper laterals. Eibye-Jacobsen (2004), however, saw a different number of transverse rows in each scleritome zone, reporting 11–14 rows of upper-lateral sclerites in contrast to seven to eight rows of lower-lateral sclerites.

In addition to these ‘body sclerites’, a variable number of elongate spines (7–11) emerge from the dorsal/lateral sclerite zones on each side of larger specimens. Spine length is variable, with spines usually shorter near the front and rear; maximum spine length grows nonlinearly with respect to sagittal length (Conway Morris 1985).

Each sclerite comprises a hollow tubular root that opens out to form a flattened, one-sided blade (Butterfield 1990). The blade is ornamented by a number of longitudinal ribs, of which more are present in larger specimens (Conway Morris 1985). These external ribs are restricted to the upper surface of sclerites and are sometimes accompanied by irregularly scattered pustules (Butterfield 1990). In some sclerites from Mount Cap and Kaili, ribs have two thicknesses: prominent ribs alternate with fainter ones (Butterfield 1994; Harvey et al. 2012).

The full width of each sclerite is striated by finely spaced longitudinal lineations. Parker (1998) argued that these were superficial – although they are not visible on surfaces imaged under SEM and do not exhibit interference under transmitted light, so might be better interpreted as internal channels indicating microvillar secretion (Butterfield 1990).

Butterfield (1990) suggested that sclerites were moulted individually, as in *Halkieria* (Vinther and Nielsen 2005). Conversely, whole-body ecdysis is suggested by a putatively mouling specimen and the absence of specimens in the 15- to 20-mm size range (Conway Morris 1985).

**Sclerite morphology**

In the examined material, sclerites are uniformly ornamented with a single order of ribs that are most prominent in the smallest specimens. The ribs’ number generally increases with the fossils’ sagittal length, reaching 9–15 in

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**TABLE 1.** Details of examined material.

<table>
<thead>
<tr>
<th>Taxon</th>
<th><em>Wiwaxia</em></th>
<th><em>Odontogriphus</em></th>
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</thead>
<tbody>
<tr>
<td>Total specimens studied</td>
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<td>170</td>
</tr>
<tr>
<td>Provenance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walcott Quarry</td>
<td>447</td>
<td>167</td>
</tr>
<tr>
<td>Talus below Walcott Quarry</td>
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<td>1</td>
</tr>
<tr>
<td>Talus below Raymond Quarry</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Tulip Beds (locality S7 on Mount Stephen)</td>
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<td>1</td>
</tr>
<tr>
<td>Status</td>
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<tr>
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<td>160</td>
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<tr>
<td>‘Juvenile’ specimen (≤25 mm in length)</td>
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<tr>
<td>Geological Survey of Canada, Ottawa, Canada</td>
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<td>–</td>
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</table>
adult body sclerites (intercept = 0.88 ± 0.26, exponent = 0.27 ± 0.03, \( R^2 = 0.38 \); \( p < 10^{-7} \)) and 5–12 in spines (intercept = 0.58 ± 0.50, exponent = 0.20 ± 0.06, \( R^2 = 0.16 \), \( p = 0.0037 \)); ventrolateral sclerites are the exception, with no statistically significant increase in rib count (\( p = 0.42 \), 6.7 ± 1.3 ribs, \( n = 11 \)). The ribs’ spacing increases with body sclerites’ length (exponent = 0.68 ± 0.05, \( R^2 = 0.76 \)); ribs are more closely spaced on the spines than on the body sclerites (\( p = 0.048 \); raw measurements listed in Table S2). Pustules (Fig. 1A–B) are only present on body sclerites in specimens shorter than 8 mm (which lack spines); in four such specimens, they are ubiquitous, whereas in two, they are absent on the largest sclerites. Small pustule-bearing sclerites were apparently replaced by larger sclerites that lacked pustules.

The tubular roots of sclerites appear to represent a curled planar surface; in some cases, incomplete curling results in a partly open tube (Fig. 1C). The spines are gently curved in cross section (Fig. 1D).

In six smaller specimens (sclerite length c. 1 mm), sclerites’ fine longitudinal striations (the ‘chambers’ of Butterfield 1990, around 1 \( \mu \)m in width) contain acicular crystals (Fig. 2A–F). Correspondence between the crystals and the striations is indicated by their alignment and identical spacing (Fig. 2B). Some striations are vacant or partially filled; in some cases, many short crystals are present throughout a striation (Fig. 2A–B); in others, part of the striation is occupied by elongate needles (Fig. 2C–F). Crystals are concentrated within the ribs of each sclerite and near the sclerites’ tips and bases. Crystals have a similar width within each sclerite.

The relative abundance of Fe and S in the crystals’ EDS spectra is similar to co-occurring pyrite frambooids, indicating that the crystals are iron sulphides. Because iron sulphides do not freely take an acicular form, the crystals

**FIG. 1.** Details of *Wiwaxia corrugata* sclerites. A–B, NMNH 229901, the smallest known specimen; relative to body length, dorsal sclerites are vast; B, enlargement highlights pustules on sclerites. C, NMNH 199953; tube in sclerite stalk is partially open. D, ROM 62270, kink emphasizes curved cross section of spines. Scale bars represent 1 mm (A, C, D) and 100 \( \mu \)m (B).
must have formed within enclosed spaces – further evidence that the striations represent internal chambers rather than surface features. The crystals formed early in diagenesis: they are deflected by later growths of rhombic pyrite and are truncated by cracks in the carbon film. Their tapering ends indicate that they grew into space (rather than originally occupying the full length of the sclerite and later being eroded away). As no other mineral phase is ever present within the striations, the crystals cannot represent replacement products of a prior mineral phase. The crystals’ concentration in regions that were more resistant to compaction (i.e. ribs and sclerite apices) presumably reflects the delayed collapse of chambers in these areas.

In contrast, I did not observe acicular crystals in chaetae of the Burgess Shale annelids *Canadia* or *Burgessochaeta-.  

**FIG. 2.** Acicular crystals within sclerites of *Wiwaxia corrugata* and in chaetae of *Burgessochaeta*. A–F, *W. corrugata*, NMNH 198674; sagittal length 4 mm. A–B, pyrite crystals are concentrated in ribs (arrowheads) and near tip of sclerite; enlargement shows striations (str) running parallel to incipient needles, and cracks (crack) cutting through carbon film and crystals; C–D, crystals preserved in overlapping sclerites (topmost sclerite’s margins highlighted with dotted lines in C); needles attain greater lengths within ribs; E, needles most pronounced near the tip of sclerite and in ribs (arrowheads); F, densely packed needles occupying adjacent lineations, interrupted by cracks. G–H, *Burgessochaeta setigera* (Annelida), NMNH 198634; pyrite frambooids (not needles) within chaetae. Scale bars represent 20 µm (A–F) and 200 µm (G–H).
ta, despite their comparable internal microstructure (Butterfield 1990). When present, pyrite formed framboids in longitudinal series (Fig. 2G–H). Apparently the chambers within annelid chaetae were less robust than Wiwaxia’s and were unable to constrain the growth of pyrite crystals.

Sclerite growth

Whereas the ventrolateral sclerites and the spines each follow their own growth trajectory, there is no statistical distinction between the growth of dorsal, upper-lateral and lower-lateral sclerites, and these latter body sclerites can be considered together. Their width, length and rib count scale linearly with total body length (log–log gradient = 1, p < 10⁻⁶; R² = 0.88, 0.93 and 0.38, respectively; intercepts = −1.1 ± 0.3, −1.6 ± 0.3 and 0.88 ± 0.26), and they are around twice as long as its width at all stages of growth (R² = 0.92). Ventrolateral sclerites become long and angular in adults, but are relatively rounded at their inception (Fig. 3A, E–F, I); their length increases faster than body length (exponent = 1.14, intercept = −2.5, R² = 0.97), and although their width increases at the same rate as the dorsal/lateral sclerites, they are significantly narrower (p < 10⁻⁴). Spines begin to develop when specimens are 8–16 mm in length (Fig. 3C–E); they comprise a root

**FIG. 3.** Ontogeny of *Wiwaxia corrugata*. Specimen size, and thus ontogenetic stage, increases from A→I. A, dorsal surface of ROM 57195, spines absent. B, ROM 61512, partially enrolled specimen with clear transverse banding; spines absent. Interference imaging. C, ROM 62271, exhibiting short incipient spines. D, ROM 61699, anterolateral view; incipient spines increasing in length. E, NMNH 198675, exhibiting full-length spines. Relatively short ventrolateral sclerites visible at body margin. Interference imaging. F, ROM 62272, spines and ventrolateral spines are progressively longer and narrower as body size increases. G–H, ROM 61511, mature specimen with a full complement of spines; incipient spines (inc) resemble the distal portion of mature spines (mat). I, ROM 62273, dorsal view, note long and slender ventral sclerites arranged in bunches. Scale bars represent 5 mm.
akin to other sclerites, an approximately parallel-sided proximal section, and a tapering distal end that culminates in a c. 20° point. Incipient spines are triangular and lack the parallel-sided section seen in mature spines (Fig. 3E–G); this indicates growth by basal accretion. The length of mature spines increases with body length, but only up to a point; their size is well described by a logistic or asymptotic model, tending to a 22-mm asymptote (Fig. 4). In contrast, spine width scales linearly with body length, so spines cannot have grown by isometric inflation (i.e. enlargement without change in shape). To achieve wider spines with more ribs, spines must have been periodically sloughed and replaced – accounting for the presence of incipient spines in mature specimens (Fig. 3H).

**Scleritome morphology and development**

Sclerites remain in transverse rows as specimens begin to disintegrate (Fig. 5A), suggesting that rows were underlain by robust decay-resistant connective tissue. NMNH 199953 (Fig. 5B) seems to represent a partial, isolated transverse row; each sclerite emerges from an underlying fibrous entity. Within each row, sclerites are bunched into bundles, with their roots tightly packed (Figs 3I, 5A–C); these bundles perhaps correspond to Conway Morris’ zones. In complete specimens, the bundles overlap and rotate, often disguising the true number of transverse rows; where the number of rows is unambiguous, there are always eight.

The new ROM material contains 13 specimens in the 15- to 20-mm size range, bridging the apparent size gap reported by Conway Morris (1985). These specimens are poorly preserved, suggesting that different taphonomic processes are active at this scale.

*Wiwaxia* specimens longer than 25 mm have limited morphological disparity. Aside from variations in the number and position of spines, the overall body proportions and sclerite distribution are broadly consistent; there are typically around five ventrolateral sclerites, one lower-lateral, c. four upper-lateral and three dorsal sclerites per half-row. ‘Juvenile’ specimens – measuring 2.1–25 mm – have fewer sclerites in each zone (Figs 1, 3): in the smallest specimens, each zone is represented by a single
large sclerite per half-row, whereas at 7 mm, specimens bear around two dorsal sclerites per half-row and five sclerites in their upper-lateral zones. Body sclerite length scales linearly with sagittal body length (exponent $=1.02 \pm 0.04$, $R^2 = 0.92$, $n = 65$), consistent with the fixed number of transverse rows. Although sclerite width scales more slowly than body length (exponent $=0.85 \pm 0.05$, $R^2 = 0.84$, $n = 65$), the addition of sclerites during growth means that the cumulative surface area of sclerites increases faster than body area (exponent with respect to body length $=2.34 \pm 0.12 > 2$). This indicates a greater degree of overlap in larger specimens, consistent with their deeper scleritome (Fig. 5C).

**Reconstruction**

The sclerites of *W. corrugata* were arranged in eight transverse rows, each held together by connective tissue. The body sclerites grew to a fixed size by basal accretion and were periodically shed. The smallest sclerites bore an irregular tubercular ornament that is absent in larger sclerites. The sclerites bore a single order of equally spaced ribs; these presumably served a structural function, as they are more closely spaced on spines than on the shorter body sclerites. Although the spines have the same ultrastructure as the body sclerites, their growth proceeds differently, and they were only incorporated into the scleritome once body length exceeded 8–16 mm (Fig. 6).

The sclerites’ lineations represent internal chambers, not superficial grooves. Presuming that the crystals occupy the chambers’ original width – as inferred from their accicular habit – then the chambers were smooth walled, uniformly sized and occupied a single tier within the sclerite. A planar system of canals is evident in the sclerites of the Cambrian halkieriid *Sinosachites*, although – like the aesthete canals found in chiton valves – these form a higher-order pattern, are perpendicular to the valve surface and are an order of magnitude wider than the micrometre-sized surface-parallel chambers in *Wiwaxia* (Vendrasco *et al.* 2008; Vinther 2009). Rather, the
chambers seem to denote the longitudinal fabric seen in lophotrochozoan sclerites that are secreted by microvilli.

DIGESTIVE TRACT

The gut of Wiwaxia was originally described based on a specimen (ROM 32569: Conway Morris 1985, figs 157–161) that, based on its mouthparts and lack of sclerites, can now be recognized as Odontogriphus. The Wiwaxia gut (Fig. 7A–B), like that of Odontogriphus, represents a straight, bilaterally symmetrical tube that runs along the body axis. The identification of the gut allows Conway Morris’s ‘moulting’ specimen (Fig. 7A; Conway Morris 1985, figs 17–19, 27) to be reinterpreted as a single, enrolled, partly decayed individual. It contains just one (damaged) set of mouthparts, and a gut can be traced along its length. In Odontogriphus (Fig. 7C–E), the alimentary tract is ventral to the gills and consists of a narrow tube that continues to the subterminal anus. Ventral to the tube is a broad, originally cylindrical organ that appears to be connected to the tube by a series of lateral ducts to merge into the tract at its posterior end. This organ is darkly stained and is often associated with pyrite or aluminosilicate minerals; it perhaps represents a digestive gland.

FOOT

The margin of a locomotory foot, usually concealed by sclerites, is visible on six suitably preserved specimens (Fig. 8A–B). It preserves in a similar fashion to the Odontogriphus foot and occupies most of the ventral surface. Although Butterfield (2006) suggested that transverse lineations in the Odontogriphus foot represent segment boundaries, these features bifurcate (Fig. 8C) and do not align exactly with gills. As such, there is no clear evidence for segmentation in either taxon (Eibye-Jacobsen 2004). The transverse lineations’ distribution resembles that of chitons’ dorsoventral musculature, which overlies the foot (Wanninger and Haszprunar 2002). Other specimens preserve blocks of longitudinal striations running parallel to the midline of the foot (Fig. 8D, F), reminiscent of chitons’ more dorsally positioned rectal muscles (Wanninger and Haszprunar 2002), and radial lineations in the head region (Fig. 8E), reminiscent of chitons’ buccal muscles (Wanninger and Haszprunar 2002).

DIVERSITY

Articulated Wiwaxia specimens are known from the Burgess Shale and the Kaili biota, with isolated sclerites obtained from these and other early-to-middle Cambrian deposits (Butterfield 1990, 1994; Porter 2004; Fatka et al. 2011; Harvey and Butterfield 2011; Butterfield and Harvey 2012; Harvey et al. 2012). Although the Kaili material awaits a detailed description (Steiner et al. 2005), its sclerites have been assigned to a separate species, W. taijiangensis, based on the details of their shape and the presence of small and large ribs (Zhao et al. 1994). Sclerites from the Mount Cap Formation (Canada) with transverse rows...
of pustules and a single, diminutive rib size have been proposed as a further species (Butterfield 1994). The second order of fainter ribs present in the Kaili and some Mount Cap body sclerites are not present in any of the **W. corrugata** sclerites recovered from the Burgess Shale by acid maceration (Butterfield 1990), nor in the bedding-surface fossils examined herein; they seem to denote a separate species. This is supported by the pustules that adorn the surface and edges of Kaili spines: in **W. corrugata**, pustules are not present in specimens that are large enough to have spines. Furthermore, the largest Kaili spine (Harvey et al. 2012, fig. 3P), which based on its profile is almost complete and fully grown, measures just 0.6 mm long and 80 μm wide – an order of magnitude
smaller than the shortest complete *W. corrugata* spine (3.5 mm × 600 μm). If, as seems likely, these spines and the co-occurring body sclerites belong to the same organism, *W. taijiangensis* had a distinct ribbing pattern on its sclerites and bore spines from an early ontogenetic stage. The transverse rows of tubercles present in the Mount Cap sclerite morph – also present on sclerites from the early Cambrian Mahto formation, the middle Cambrian Monastery Creek Formation and the late middle Cambrian Earlie Formation (Porter 2004; Butterfield and Harvey 2012) – are absent in *W. taijiangensis* and *W. corrugata*, supporting Butterfield’s (1994) recognition of these sclerites as a probable third species.

**RELATIONSHIP TO HALKIERIIDS**

In terms of sclerite shape and arrangement, the *Wiwaxia* scleritome resembles the halkieriids’ (Jell 1981; Bengtson and Conway Morris 1984; Conway Morris and Peel 1995; Conway Morris and Caron 2007). In both *Halkieria* and *Wiwaxia*, sclerites are arranged in regular transverse rows. Distinct sclerite zones are evident in each taxon and arise through the bundling of sclerites into ‘bunches’. Sclerites are a similar shape in both taxa and can (but do not always) bear a range of ornaments including pustules, transverse lineations and longitudinal ribs (Butterfield 1994; Conway Morris and Chapman 1997).
On the other hand, the sclerites’ homology has been questioned based on differences in their mineralogy and topology (Butterfield 2003). *Wiwaxia*’s sclerites lack the aragonitic component present in *Halkieria*; and whereas *Wiwaxia*’s sclerites were flat and solid, halkieriids’ contained a longitudinal cavity – most evident in *Sinosachites*, which contains secondary lateral chambers attached to the central cavity by small pores (Vinther 2009).

I argue that these similarities and differences carry little taxonomic information. Shape and ornament are prone to convergence (Sigwart 2009) and can vary during ontogeny (Todt and Wanninger 2010). Sclerites commonly have hollow and filled forms within a species or even within an organism (Okusu 2002; Kingsley et al. 2013). Polychaete chaetae can be hollow or filled (Glasby et al. 2000); some, like those of *Wiwaxia*, are solid in their distal component and have a hollow shaft (Gustus and Cloney 1973); others, like *Sinosachites*, feature a complex arrangement of internal chambers (Westheide and Watson Russell 1992; Pleijel and Gustavsson 2010). And there are several examples of microvillar ‘sclerites’ that occur in mineralized and nonmineralized variants (e.g. chiton girdle elements, Fischer et al. 1980; Leise and Cloney 1982; molluscan radulae, Kim et al. 1989; annelid chaetae, Rouse and Pleijel 2001); most strikingly, the Cambrian fossil *Orthrozanclus* seems to represent a halkieriid with a nonmineralized scleritome (Conway Morris and Caron 2007).

The mode of sclerite secretion is a more fundamental character and may have more taxonomic weight. I suggest that, as in *Halkieria* (Vinther and Nielsen 2005; Vinther 2009), *Wiwaxia*’s sclerites grew by basal secretion and were periodically replaced. On this view, the *Wiwaxia* sclerite would be homologous with the (apparently) organic layer on the surface of halkieriid sclerites (Porter 2008). The construction of scleritome zones from bundles of sclerites also seems to genuinely support the relationship between the taxa. On this basis, I tentatively support the parsimony-derived hypothesis of a close relationship between *Halkieria*, *Wiwaxia* and (based on its mouthparts) *Odontogriphus* (Sigwart and Sutton 2007; Vinther et al. 2008) – whether as a clade or a grade.

**AFFINITY**

*Wiwaxia* is not easy to place on the tree of life. Its ventral foot (which was presumably surrounded by gills, as in *Odontogriphus*) seems to signal a molluscan affinity – but the ciliated sole present in many lophotrochozoan larvae hints that a ‘foot’ of some form might have been present in the ancestral lophotrochozoan (Wingstrand 1985). Taking microvillus-secreted sclerites to be a lophotrochozoan symplesiomorphy (Butterfield 2008; Giribet et al. 2009), *Wiwaxia* could conceivably sit anywhere in the lophotrochozoan crown or stem. Here I explore the implications of some possible phylogenetic placements.

### Wiwaxia as a sister group to multiple Lophotrochozoan phyla

Given the uncertain relationships between the Lophotrochozoan phyla, the case for a deep phylogenetic position (Fig. 9A) is difficult to substantiate. Such a placement was originally proposed (Butterfield 2006) based on the interpretations that have since been overturned: *Wiwaxia*’s mouthparts do not resemble annelid jaws (Smith 2012); ctenidia can be preserved in the Burgess Shale (Smith 2013); and ‘segment boundaries’ in *Odontogriphus* are here reinterpreted as internal tissue. Stratigraphically, a deep position raises few problems: ‘halwaxiid’ sclerites appear in the fossil record at the same time as the earliest Lophotrochozoa (Kouchinsky et al. 2012), and the paucity of carbonaceous preservation in the earliest Cambrian (Terreneuvian) leaves scope for earlier wiwaxiids.

The form of pyrite crystals – which are acicular in *Wiwaxia* but framboidal in annelids – suggests that *Wiwaxia* sclerites may share less in common with annelid chaetae than first anticipated. It is notable that sclerites’ microvillar fabric is different in annelids and brachiopods, where chambers near the surface of the sclerite are...
generally narrower (Orrhage 1971; Gustus and Cloney 1972; Hausen 2005), to in chitons, octopus and bryozoans, where the chambers are of equal size throughout each sclerite (Brocco et al. 1974; Gordon 1975; Fischer et al. 1980; Leise and Cloney 1982). If these patterns are phylogenetically informative, they would place Wiwaxia among Mollusca + Bryozoa.

Nevertheless, Wiwaxia’s mouthparts are difficult to reconcile with a deep phylogenetic position. If a radula-like mouthpart was present in the last common ancestor of molluscs and their sister group (bryozoans – or annelids?), then it was lost in this sister group and replaced by a separate feeding apparatus. If not, then the resemblance to the molluscan radula indicates profound parallel evolution. On this basis, a deep phylogenetic position is not parsimonious.

Wiwaxia as an aplacophoran

At the other extreme, one could attempt to shoehorn Wiwaxia into Aplacophora (Fig. 9B). Aplacophorans exhibit a wide range of radular morphologies, including polystichous forms from which the Wiwaxia exhibit a wide range of radular morphologies, including Wiwaxia as an aplacophoran

At the other extreme, one could attempt to shoehorn Wiwaxia into Aplacophora (Fig. 9B). Aplacophorans exhibit a wide range of radular morphologies, including polystichous forms from which the Wiwaxia mouthparts could easily be derived (Scheltema et al. 2003). There are also similarities between Wiwaxia’s sclerites and aplacophoran spicules. The chambers within Wiwaxia sclerites seem to lie within a single plane, which suggests a comparison with the organic pellicle that coats many aculiferan spicules (Fischer et al. 1980; Haas 1981); in other lophotrochozoan sclerites, the full cross section of each sclerite is occupied by a honeycomb-like array of microvillar chambers. As in modern Aculifera (Haas 1981; Vinther 2009), sclerites of Wiwaxia grow to a fixed size, are secreted by basal microvilli, attach to the integument with a chitinous stalk and are periodically replaced on an individual basis. Like in many solenogaster aplacophorans (Todt and Wanninger 2010), sclerites are large relative to body size in young individuals, becoming relatively smaller during ontogeny. The hollow tubes that constitute the basal portion of Wiwaxia sclerites represent a rolled planar surface – and the solenogaster Dondersia generates hollow structures in the same fashion (Scheltema et al. 2012). Spinose elements are interspersed with flat sclerites in the solenogaster Meiomenia (Morse and Norenburg 1992), bringing to mind Wiwaxia’s spines; in another solenogaster, Epimenia, the scleritome comprises discrete zones of sclerites with different morphologies (Okusu 2002), albeit arising in a different fashion to Wiwaxia. Vestigial shell fields sometimes divide the solenogaster scleritome into eight transverse regions, and in other solenogasters and caudovoeates, sclerites are arranged in transverse rows (Scheltema and Ivanov 2002; Nielsen et al. 2007).

At first blush, these shape-based similarities seem to indicate an affinity with the solenogasters. But the Wiwaxia-like characteristics occur in isolation across the solenogaster tree; wherever Wiwaxia is placed, most of the above comparisons would represent parallel evolution. What is more, a derived position for Wiwaxia indicates an early origin of the Aplacophora. Aplacophora seem to have derived from mineralizing chiton-like ancestors, and ‘intermediate forms’ exist from the Ordovician and Silurian (Sutton and Sigwart 2012; Sutton et al. 2012). If this transition pre-dated the earliest (early Cambrian) Wiwaxia fossils, then many mineralizing aculiferans have extensive ghost lineages.

Wiwaxia as an aculiferan

This stratigraphic difficulty disappears if Wiwaxia is interpreted more basally among the Aculifera (Fig. 9C). Wiwaxia’s mouthparts, sclerites and scleritome could then resemble an ancestral Aculiferan form, which would be consistent with both morphology and the fossil record. Because Aculifera (which bear sclerites) are the sister taxon to Conchifera (which do not; Kocot et al. 2011; Smith et al. 2011; Sutton et al. 2012), the presence of sclerites in the ancestral mollusc can only be inferred by reference to the nearest outgroup. If the earliest representatives of this outgroup had a scleritome (Skovsted et al. 2008; Zhang et al. 2013), then a scleritome would be primitive for all Mollusca, and other scleritomous fossils (such as the conch-bearing Halkieria) could sit in the stem lineage of Mollusca, Aculifera or Conchifera.

Wiwaxia as a stem-group mollusc

Wiwaxia could equally be accommodated in the molluscan stem-group (Fig. 9D). In this interpretation, its mouthparts could represent the ancestral molluscan condition or a unique modification to the radular blueprint. Its scleritome is most simply interpreted as an inheritance from a sclerite-bearing lophotrochozoan ancestor that was retained by Aculifera and lost secondarily by Conchifera (unless the conchiferan shell represents a fused scleritome; cf. Bengtson 1992). The occurrence of sclerite-like elements in derived conchiferans (Brocco et al. 1974; Warén et al. 2003) could represent the reactivation of the underlying genetic machinery.

EVALUATION

Taken together, Wiwaxia’s mouthparts, foot and scleritome indicate a molluscan affinity, whether among the
aculiferans or in the molluscan stem. The deep origin of a scleritome-bearing body plan in Mollusca suggests that sclerites emerged at an early stage in lophotrochozoan evolution and that conchiferan molluscs bore a scleritome before they evolved a shell.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of examined specimens from the Royal Ontario Museum (specimens from other institutions are detailed in Conway Morris, 1985).

Appendix S2. Sclerite dimensions (mm), measured from 90 Wiwaxia specimens.

Appendix S3. High-resolution colour images of the figured specimens and images of other fossils studied in this analysis. Available from the Data Dryad repository, doi: 10.5061/dryad.868sm.

REFERENCES


