



THE ORIGIN OF MULTIPLACOPHORANS – CONVERGENT EVOLUTION IN ACULIFERAN MOLLUSCS

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Abstract: Multiplacophorans are Palaeozoic (Silurian to Permian) stem group polyplacophorans with 17 shell plates in a particular arrangement of single terminal plates separated by three columns of plates forming five transverse rows. Their distinctive morphology has prompted disparate interpretations of their relationship to polyplacophorans. Some features are strikingly similar to crown group polyplacophorans and even to some living families. Here we describe two Devonian forms, *Protobalanus spinicoronatus* sp. nov., a hercolepadid from northeast Ohio, USA, and *Han-*

nestheronia australis gen. et sp. nov., a strobilepid from South Africa. Using the results from a Bayesian relaxed molecular clock to test competing scenarios of the relationship of multiplacophorans to crown group polyplacophorans, we demonstrate that multiplacophorans are stem group polyplacophorans in which certain characters of the crown group evolved convergently.

Key words: Neoloricata, Multiplacophora, Hercolepadida, convergence, mollusc, Aculifera.

CHITONS (Polyplacophora) are a small class of molluscs identified by a longitudinal column of eight shell plates surrounded by a thick leathery mantle or girdle with many small embedded sclerites. Most forms inhabit rocky substrates in tidal to subtidal marine waters, and feed by scraping food off surfaces using a magnetite-impregnated radula (Ernisse and Reynolds 1994; Schwabe and Wanninger 2006). The shell plates are differentiated into a head, a tail and six relatively uniform intermediate plates. The typically tightly interlocked articulated skeleton is flexed by discrete oblique and longitudinal muscles (Wingstrand 1985) and embedded in the underlying tissue by anteriorly directed projections of the medial shell layer (articulamentum) called sutural laminae (Baxter and Jones 1981) (Fig. 1A, B, E). The outermost shell layer is very distinctive among molluscs in having a dense set of branching pores, called aesthetes, which harbour a suite of sensory and secretory cells (Reindl *et al.* 1997; Vinther 2009). Members of the Order Chitonida have lateral extensions of the articulamentum, insertion plates that embed the shell plates firmly in the mantle (Fig. 1A–D).

Many of these features appear late in the fossil record of polyplacophorans and it has been suggested that the crown group, traditionally classified within Neoloricata (Bergenhayn 1955), diverged in the Carboniferous (Sigwart and Sutton 2007; Sigwart 2009) with the widespread appearance of sutural laminae, although these structures are known in Devonian forms (Smith and Hoare 1987). Many late Cambrian to Silurian polyplacophorans (Pojeta *et al.* 2003; Cherns 1998*a, b*, 2004; Vendrasco and Runnegar 2004; Pojeta and DuFoe 2008) that lack the characteristic sutural laminae and the articulamentum, the secondary shell layer from which the sutural laminae originate, are placed in the Order Paleoloricata (Bergenhayn 1955). Members of the Order Chitonida, which falls in the crown group, possess slitted lateral insertion plates (Sirenko 2006) (Fig. 1A, B). The Early Permian taxon *Ochmazochiton* Hoare and Smith, 1984 shows this character in an approximate condition to the crown group, which suggests that it is a stem chitonid.

Another group of polyplacophoran relatives was first recognized by Dzik (1986) as the Order Hercolepadida

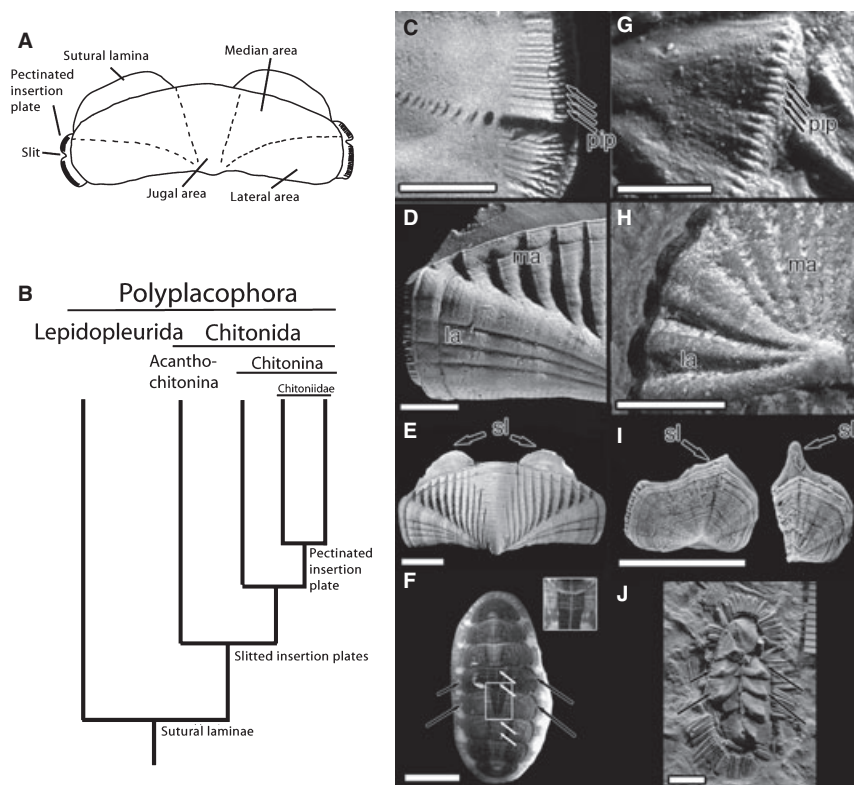


FIG. 1. A, features of chiton shell plates with notable characters depicted. B, a phylogeny with the morphologic classification of crown group Polyplacophora showing the distribution of shell plate traits shown in A. C–J, convergence in multiplacophorans and crown group chitons. C–F, details of modern chitons. G–J, multiplacophoran structures convergent with those in crown group chitons. Pectinated insertion plates in the modern chiton *Rhyssoplax olivacea* (C) and *Protobalanus spinicoronatus* sp. nov. (G). Division of the intermediate shell into a raised lateral (la) and more depressed median area (ma) in *R. olivacea* (D), and the similar condition in *P. spinicoronatus* (H). E, Sutured laminae (sl) in *R. olivacea* and I, *Diadeloplax paragrapsima* Hoare and Mapes, 1995. F, *Schizoplax brandtii*, an acanthochitoninid with intermediate plates divided (black arrows) by an organic ligament (white arrows) (detail) and J, the complete skeleton of *Polysacos vickersianum* Vendrasco *et al.*, 2004. Scale bars represent 1 mm in C–E, G, H; 5 mm in F, I, J.

but they have since become more widely known as multiplacophorans (Hoare and Mapes 1995). These forms have 17 shell plates (Fig. 1J). Single head and tail plates are separated by intermediate plates arranged in three columns and five transverse rows, each row with a symmetric median plate flanked by left/right asymmetric plates (Figs 1J, 2 and 3). This distinctive arrangement is considered diagnostic of a monophyletic group which consists of two families, the Hercolepadidae and the Strobilepidae. The oldest form is *Hercolepas signata* Aurivillius, 1892 from the Silurian (Wenlock) of Sweden (Appendix S1) and the youngest is *Diadeloplax apiculatus* (Hanger *et al.* 2000) from the Permian of Oregon. Vendrasco *et al.* (2004) showed that the multiplacophorans are closely related to polyplacophorans and concluded that they are part of the stem group: the shells, like those of polyplacophorans, have an upper layer harbouring aesthete canals that overlies a medial layer, the articulamentum, which extends laterally and anteriorly. Vendrasco *et al.* (2004) also noted that multiplacophorans possess charac-

ters of the polyplacophoran crown group: sutured laminae and insertion plates. However, given the stratigraphic separation between the multiplacophorans (Silurian) and the oldest suggested crown polyplacophorans (Carboniferous) they argued that some crown group features had evolved in the stem group and placed the multiplacophorans above paleoloricates on the stem lineage to crown polyplacophorans. Puchalski *et al.* (2009), in contrast, placed the multiplacophorans within the Neoloricata and argued that they belong to the polyplacophoran crown group because of the presence of sutured laminae, thereby extending the fossil record of crown group polyplacophorans into the Silurian.

At least part of this conflict we believe is because of the utilization of different nomenclature in the classic Linnean sense and the recent implementation of crown group/stem group distinctions. Invertebrate palaeontologists, in particular, have tended to classify fossil stem groups under the same name as the crown when they resemble them for the most part, which can create conflicts about the definition

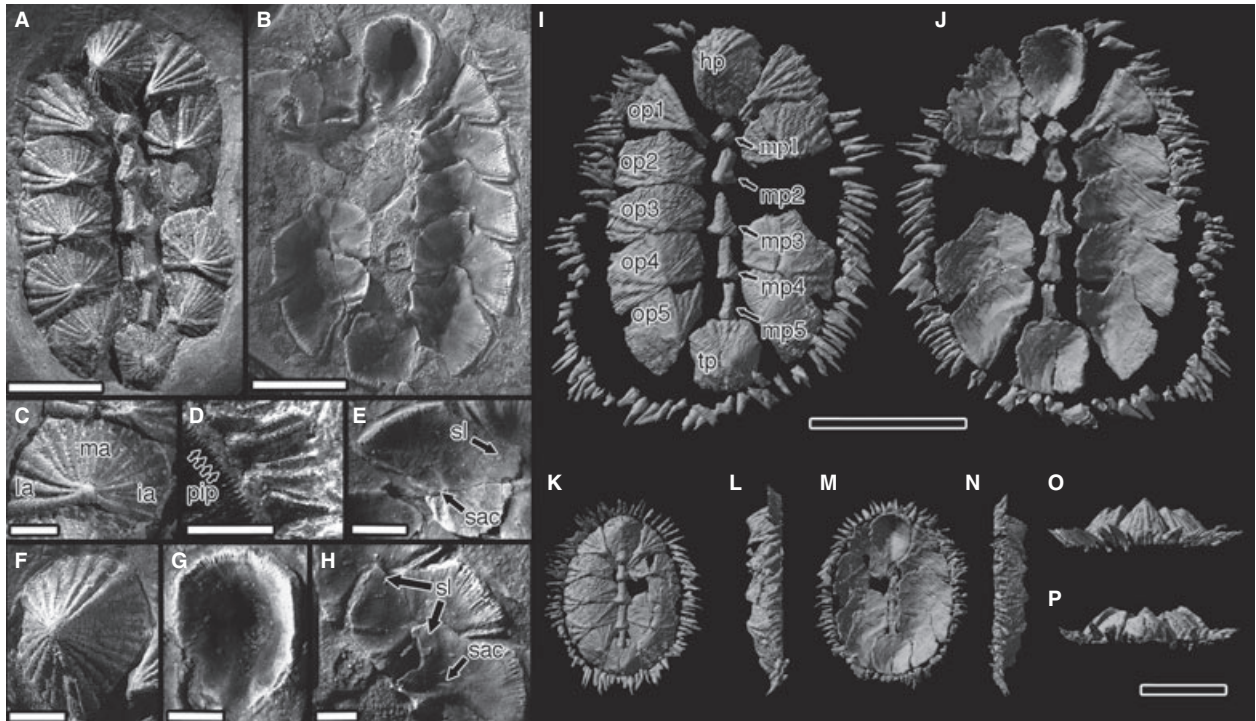


FIG. 2. *Protobalanus spinicoronatus* sp. nov. Holotype CMC 53909. A–H, dorsal and ventral view before embedding ventral surface in resin. I–J, microCT scan. K–P, plates restored to their original positions. A, dorsal view. B, ventral view. C, fourth left outer intermediate plate with the lateral (la), median (ma) and inner (ia) areas denoted. D, detail of the ventral side of the 1st left outer intermediate plate showing the mantle spines and the pectinated insertion plates (pip). E, ventral view of right fifth outer intermediate plate showing a sediment infilled subapical cavity (sac) and an anterior projection of the ventral shell layer similar to a sutural lamina (sl). F, detail of head plate. G, ventral view of head plate. H, ventral view of the 4th and 5th left outer plates showing the sutural laminae and subapical cavities. I, microCT rendering of the dorsal side and the ventral side, J. The restored specimen in dorsal, K; lateral right, L; ventral, M; lateral left, N; anterior, O; and posterior view, P. Scale bars represent 3 mm in A, B; 1 mm in C–H; 5 mm in I, J and 5 mm in K–P.

of the common name and result in arbitrary determinations of what stem taxa are included (De Queiroz and Gauthier 1990; De Queiroz 2007). In this study, we discuss the systematic position of multiplacophorans using the stem vs crown group distinction and define their systematic placement among extant and fossil polyplacophorans.

As stated earlier, some features of multiplacophorans are similar to those in crown group polyplacophorans (Fig. 1). Vendrasco *et al.* (2004) noted, the articulamentum extends further than the tegmental (uppermost) shell layer along most of the shell margin (Fig. 1G, I), like the sutural laminae that define the polyplacophoran crown group (Fig. 1A, B, E) and the insertion plates in the Chitonida (Fig. 1A, C). The plate margins for insertion in multiplacophorans are beset with densely spaced grooves (Figs 1G and 3D) that resemble those of the subgroup Chitonidae (Fig. 1C, D). The shell surface is divided into lateral and median shell areas in most multiplacophorans (Fig. 1H). This division is especially prominent in the Hercolepadidae and resembles the condition in Chitonidae (Fig. 1C, D) and closely related families. Interestingly,

the modern polyplacophoran *Schizoplax brandtii* resembles multiplacophorans in having six intermediate plates divided medially by an organic ligament (Fig. 1F) and single terminal shell plates.

These similarities between multiplacophorans and certain crown group polyplacophorans are chimaeric: the division of the shell into distinct lateral and median areas, and the pectinated insertion plates are features of the Chitonidae in the Chitonina, whereas the laterally divided intermediate shell plates of *Schizoplax* (Fig. 1F) occur in the Acanthochitonina (Sirenko 2006). The presence of structures similar to sutural laminae defines the Neoloricata and the crown group and could be posited to argue for a placement of the Multiplacophora in these.

If multiplacophorans are crown group polyplacophorans with affinities to the Chitonina or Acanthochitonina, the crown group diverged prior to the Silurian when multiplacophorans appeared. On the other hand, if multiplacophorans are stem group polyplacophorans, the divergence should coincide with the first appearance of accepted fossil crown group polyplacophorans, which is

most likely at or after the Carboniferous (Vendrasco *et al.* 2004; Sigwart and Sutton 2007; Sigwart 2009). The Order Chitonida diverged sometime around the early Permian depending on the interpretation of *Ochmazochiton* as stem (Hoare and Smith 1984) or crown Chitonida (Sirenko 2006). To test these hypotheses, we used the results of a recent phylogenetic analysis (Vinther *et al.* 2012) that includes a relaxed molecular divergence estimate of the crown group (Neoloricata) and the Chitonida.

MATERIAL AND METHODS

Two new Devonian species are described: *Protobalanus spinicoronatus* sp. nov. and *Hannestheronia australis* gen. et sp. nov. The holotype of *P. spinicoronatus*, collected from the Silica Formation, Ohio, USA, is held at the Cincinnati Museum of Natural History, Cincinnati Museum Center (CMC) 53909. The Silica Formation has been correlated broadly with similarly fossil-rich Givetian, Hamilton age strata within the epicontinental Appalachian and Michigan basins (Bartholomew and Brett 2007). *P. spinicoronatus* was collected from Arthroacantha-dominated crinoid beds at the base of Unit 9 (Kesling and Chilman 1975). The specimen was exposed from the ventral side upon discovery. This surface was fixed with silicone glue to allow preparation of the dorsal side. However, it was

then decided that the silicone glue should be replaced with a more solid and transparent resin, so the glue was mechanically prepared away to expose the ventral surface again. The dorsal surface was fixed with cyclododecane (Brown and Davidson 2010) to support the delicate shell plates. The ventral surface was coated in ammonium chloride sublimate and photographed (Fig. 2B) before being fixed with ultratransparent epoxy resin HXTAL (NYL-1). Most of the dorsal surface was exposed mechanically; the matrix enclosing the mantle spines and shell margins was left intact. The specimen was subjected to a microCT scan at the Yale Core Center for Musculoskeletal Disorders. The specimen was scanned in water using a UCT-35 scanner (Scanco, Bruttisellen, Switzerland) at an energy of 75 kVp, 500 ms integration time, and an isometric voxel size of 18.5 μm . Enough contrast between the fossil and the matrix was available to allow the plates and spines to be separated from the matrix manually using the software Avizo 6. The position of faceted or curved edges of individual plates indicates where they were juxtaposed. The shell plates and spines were restored to their original relative positions with the software Maya 2010 by Autodesk, Inc. A video of the microCT scanned specimen, before and after segmentation and restoration, is included in the supporting information (Appendix S2).

Geological Survey of South Africa specimen C730, the holotype of *Hannestheronia australis* gen. et sp. nov., is a

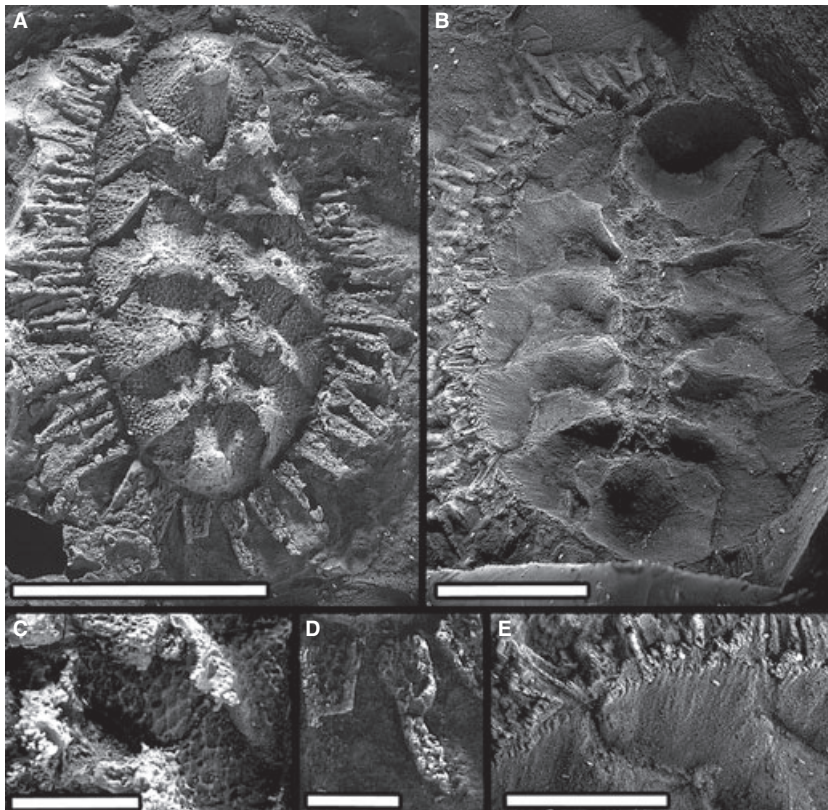


FIG. 3. *Hannestheronia australis* gen. et sp. nov. A, C, D, holotype C730. B, E, paratype C0601. C, D, detail of reticulate ornamentation on plates and spines. E, Detail of the ventral side of the 4th and 5th outer right plate showing the pectinated insertion plates. Scale bars represent 5 mm in A and B; 1 mm in C and D and 3 mm in E.

decalcified external mould. It was studied from a black latex cast that shows the dorsal surface but, because of the lacquer applied to the mould, the details are compromised in several areas. The paratype C0601 is an internal mould. The blackened latex moulds of the holotype and paratype of the species were photographed after coating with ammonium chloride sublimate.

The time calibrated tree in Figure 4 is derived from a molecular clock analysis (Vinther *et al.* 2012) using the inferred optimal substitution model (GTR + CAT + Γ^4) and molecular clock (CIR), with soft bounds under the default setting in Phylobayes 3.3b. Eleven calibrations were used, all of which lie in outgroups with respect to the Aculifera.

SYSTEMATIC PALAEOONTOLOGY

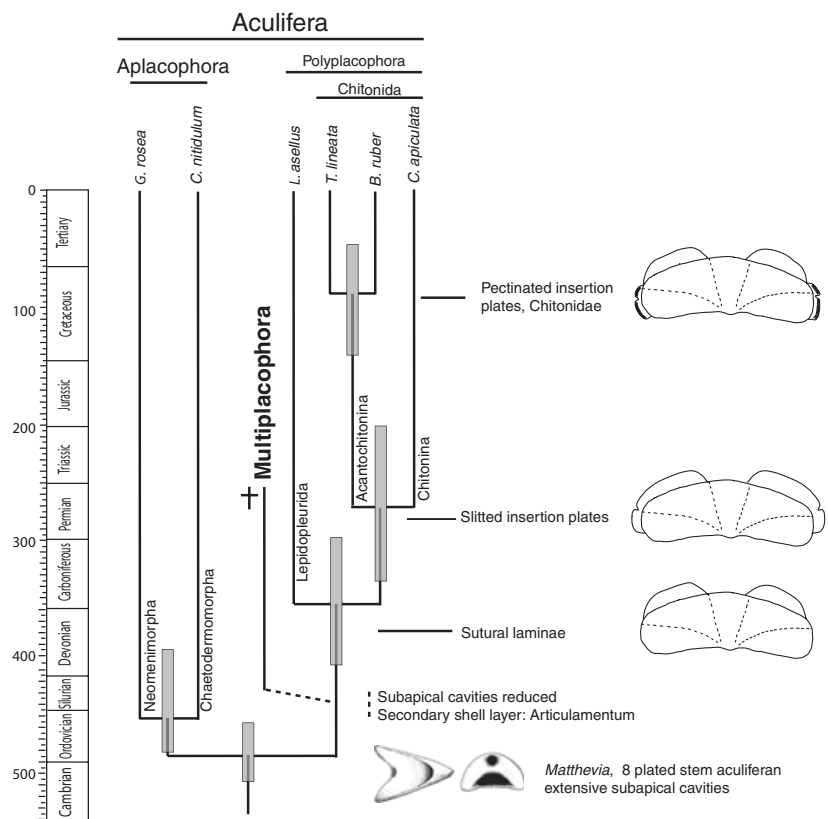
Crown group ACULIFERA Hatchek, 1891

Remarks. Several workers have advocated the use of crown, total and stem group in classifications that incorporate fossils (Jefferies 1979; Donoghue 2005; De Queiroz 2007) to minimize ambiguity regarding the position of extinct forms. We use such an approach here to clarify our use of higher taxonomic names that refer to different molluscan groups. Molecular studies (Kocot *et al.* 2011;

Smith *et al.* 2011; Vinther *et al.* 2012) showed that polyplacophorans and aplacophorans are sister taxa, together constituting the clade Aculifera (Scheltema 1993). The classification of crown Polyplacophora is based on Sirenko (2006) (Fig. 4).

The traditional classification of polyplacophorans (Bergenhayn 1955) does not translate readily to a cladistic scheme that distinguishes between stem and crown group taxa. Bergenhayn (1955) erected Neoloricata for polyplacophorans with an articulamentum forming sutural laminae (Fig. 1A) and Paleoloricata for fossil polyplacophorans lacking these features. The Neoloricata includes all living polyplacophorans together with fossil forms on the stem lineage with sutural laminae. Some Early Palaeozoic Paleoloricata are stem group polyplacophorans, but some are most likely stem aplacophorans or stem aculiferans (Sigwart and Sutton 2007; Vinther, *et al.* 2012). Paleoloricata is therefore paraphyletic towards the two extant groups Aplacophora and Polyplacophora and should be abandoned as a formal taxon (but see Pojeta *et al.* (2010) for an alternative view of the affinities of *Acaenoplax* and the paleoloricates as stem polyplacophorans). Neoloricata is often equated to crown group Polyplacophora (Puchalski *et al.* 2009) even though it is an apomorphy-based clade that includes fossil forms that lie on the stem lineage. Multiplacophorans form a monophyletic clade on the polyplacophoran stem lineage. Clades above family level are unranked.

FIG. 4. A chronogram of aculiferans from Vinther *et al.* (2012) with indication of fossil appearances of certain characters. The estimated molecular divergence times of crown chitons are congruent with the fossil record, suggesting an early Carboniferous appearance. The multiplacophorans are tentatively placed on the chiton stem lineage with a dotted line to the earliest appearance in the Silurian. The first known fossil appearance of certain key features in crown group polyplacophorans is shown. The appearance of sutural laminae is indicated (Devonian) as well as slitted insertion plates present in *Ochmazochiton* (Hoare and Smith 1984), a putative stem group chitonid. The oldest known fossil appearance of pectinated insertion plates is in the Upper Cretaceous *Chiton rossii* (Smith 1973). The drawings of plates of the proposed stem aculiferan *Matthevia* are modified from Vendrasco *et al.* (2004).



Total group POLYPLACOPHORA De Blainville, 1816

Order MULTIPLACOPHORA Hoare and Mapes, 1995

Amended diagnosis. The Order Multiplacophora is defined by seven transverse shell rows. Single head and tail plates are separated by five intervening rows, each consisting of a larger left and right outer plate and a smaller median plate arranged in three longitudinal columns (Fig. 2I). The first outer shell plate overlaps both the head plate and the second outer shell plate. Outer plates 2–5 overlap posteriorly. Aesthete canals are present in the uppermost shell layer. The underlying shell layer forms projections on the outer margins reminiscent of insertion plates in Chitonida, and sutural laminae on outer shell plates 2–5 as well as the tail plates. The projections on the outer margins are densely pectinated by evenly spaced furrows. (After previous authors: Hoare and Mapes 1995; Vendrasco *et al.* 2004; Puchalski *et al.* 2009.)

Included families. Hercolepadidae Dzik, 1986, Strobilepidae (Hoare and Mapes 1995).

Remarks. We follow Vendrasco *et al.* (2004) in using Multiplacophora Hoare and Mapes, 1995 in preference to Hercolepadida Dzik, 1986 as this name is more widely used in the literature (Hoare and Mapes 1995; Vendrasco, *et al.* 2004; Larsson *et al.* 2009; Puchalski *et al.* 2009).

Family HERCOLEPADIDAE Dzik, 1986

Amended diagnosis. Radial ornament on shell plates distinctive. Outer intermediate plates 2–5 with a distinct raised lateral area bearing three radial ribs in contrast to

more delicate radial and concentric ornamentation in the median area. First outer intermediate plate with more ribs (five in *Protobalanus spinicoronatus* sp. nov. and seven in *P. hamiltonensis*). Girdle spines shorter than in Strobilepidae (after Dzik 1986).

Included genera. *Hercolepas* Aurivillius, 1892 and *Protobalanus* Hall and Clarke, 1888 (Appendix S1). *Aenigmatectus* Hoare and Mapes, 1996 is excluded as it does not possess key hercolepadid characters.

Protobalanus spinicoronatus sp. nov.

Figures 1G, 2

Derivation of name. From the Latin *spina* (spine) and *corona* (crown), for its resemblance to a thorny crown.

Type specimen. Holotype CMC 53909 (Fig. 2), a complete, partially disarticulated specimen from the Devonian (early Givetian) Silica Formation of Lucas County, Ohio.

Diagnosis. Head and tail plates of subequal width; first outer shell plate with five radial ribs on the lateral area.

Description. This specimen is preserved complete and partially disarticulated. The right outer plate number 3 (Fig. 2) is displaced underneath the first and second outer plate, and the spines are splayed out from the body, except in the anterior left portion.

The reconstruction, based on the microCT scan, indicates that the body was about 8 mm long and 6 mm wide excluding the spines. The dimensions of the individual plates are shown in Table 1.

Radial ribs are present on the dorsal surface of all plates. The outer areas show more prominent ribs. The head plate is sub-oval with a median umbo (Fig. 2F, G) and a flatter anterior

TABLE 1. Dimensions of individual plates, measured with a caliper on the specimen or latex peel.

<i>Protobalanus spinicoronatus</i>	Length/mm	Width/mm	<i>Hannestheronia australis</i>	Length/mm	Width/mm
Head plate	2.9	2.2	Head plate	2.52	2.27
Tail plate	2.18	2.3	Tail plate	2.02	2.08
1st out. int.	2.33	2.73	1st out. int.	1.74	2.23
2nd out. int.	1.74 (2.16)	3.1	2nd out. int.	1.6	1.99
3rd out. int.	1.97 (2.31)	3.27	3rd out. int.	1.86	2.38
4th out. int.	1.96 (2.30)	3.39	4th out. int.	1.61	2.48
5th out. int.	1.91 (2.24)	2.88	5th out. int.	1.63	2.03
1st med. int.	0.78	0.86	1st med. int.	c. 0.28	c. 0.3
2nd med. int.	1.18	0.8	2nd med. int.	NA	NA
3rd med. int.	1.43	0.82	3rd med. int.	NA	NA
4th med. int.	1.41	0.65	4th med. int.	c. 0.92	c. 0.47
5th med. int.	1.27	0.43	5th med. int.	c. 0.78	c. 0.47

Measurements in parentheses are the length of the intermediate plate including apophysis/sutural laminae. The lengths of outer intermediate plates (out. int.) 2–5 in *H. australis* holotype PRV730, are concealed by strong overlap, and the median intermediate plates (med. int.) are not present or poorly preserved, which prevents detailed measurement.

area with eight radial ribs. Posteriorly, two ribs form a raised narrow transverse area on the head plate that abuts the first median intermediate plate (Fig. 2F, bottom). The tail plate is subquadrate with a posteriorly positioned umbo. Six more or less pronounced ribs are present in the anterior area. The rest of the tail plate is poorly preserved or concealed by matrix but the left lateral area reveals about six less pronounced ribs with pits concentrically arranged in the furrows. The first median intermediate plate is equidimensional, whereas the following four are elongate, increasing in size to the third (Fig. 2A, I, J). The lateral margins are notched and the plates widen markedly beyond this. The first outer plate overlaps both the head and the second lateral plate. Five radial ribs are present in the outer area and two in the inward-facing area. Three ribs are present on the raised lateral area of outer plates 2–5, although one rib on left lateral plate 4 is subdivided (Fig. 2C). The ribs on the raised inward-facing area of outer plates 3–4 are less prominent. The anteriorly facing area of the outer intermediate plates (referred to as the median area in Fig. 1H) shows 10–12 less pronounced ribs with pits in the furrows that separate them. Outer intermediate plates possess a distinct subapical cavity (Fig. 2E, H).

The outer margins are pectinate with dense furrows on the underside of all plates except the median intermediate plates (Fig. 2B, D, E, H). A projection of the underlying shell layer (sutural lamina) occurs at the most elevated central part of lateral plates 2–5 (Fig. 2E, H).

Additional elements of the skeleton of *P. spinicoronatus* are evident in the microCT scan among the spines. An area surrounding the base of the spines in the anterior left region (Fig. 2I), where the spines are preserved in their original position relative to the shell plates, is similar in density to the shell and consistent in position with the outline of the mantle in modern polyplacophorans. Some of this area is made up of distinct spinose elements, but much of it consists of sclerites too minute to be distinguished.

Discussion. *P. spinicoronatus* is distinguished from *P. hamiltonensis* Hall and Clark, 1888 by the near equal size of the head and tail plates and the fewer radial ribs on the lateral area of the first outer shell plate (five vs seven). The number of ribs on the anterior margin of the head plate is approximately the same (seven or eight). Both specimens of *P. hamiltonensis* are incomplete (Van Name 1926) which prevents further comparison of shell morphology.

The reconstruction of *P. spinicoronatus* (Fig. 2K–P, Appendix S2) shows an oval body outline similar to that in *P. hamiltonensis* (Van Name 1925, 1926) and *Hannestheronia* herein (Appendix S1). The outer edges of the plates form a continuous margin around which the marginal spines have been repositioned. The original specimen (Fig. 2I, J) shows that, although they retained their relative positions, the spines became detached and lost in the anterior right area. They may still have been embedded in a decay-resistant sclerite-bearing mantle

(perinotum), as observed in modern polyplacophorans, which held together the sclerites during decay and burial.

Family STROBILEPIDAE Hoare and Mapes, 1995

Amended diagnosis. Body usually elongate and suboval to oblong. Head plate large, about 1/2 to 2/3 of maximum body width excluding the spines. Outer intermediate plates not distinctly separated into lateral and median areas. Ribs weak or absent. Spines longer and more robust than in Hercolepadidae.

Included genera. *Aenigmatectus* Hoare and Mapes, 1996; *Deltap-lax* Puchalski, Johnson, Kauffman and Eernisse, 2009; *Diadelop-lax* Hoare and Mapes, 1995; *Hannestheronia* herein; *Polysacos* Vendrasco and Runnegar, 2004; *Strobilepis* Clarke in Hall and Clarke, 1988.

Genus HANNESTHERONIA gen. nov.

Derivation of name. For Dr Hannes Theron of the South African Geological Survey, Capetown, in recognition of his contribution to our knowledge of the Devonian of South Africa.

Diagnosis. Strobilepid with a distinct reticulate ornament on all dorsal plate surfaces.

Discussion. The reticulate ornamentation makes this form distinctive from any other described strobilepid or multiplacophoran.

Hannestheronia australis sp. nov.

Figure 3

Derivation of name. Latin *australis* (southern); the first Southern Hemisphere multiplacophoran.

Holotype. C730 (Fig. 3A, C, D) an external mould from the Devonian (Eifelian) Waboomberg Shale near the middle of the Bokkeveld Group of Klein Tafelberg, western Cape Province, South Africa.

Paratype. C0601 (Fig. 3B, E) an internal mould from the same locality, tentatively assigned to the same species.

Diagnosis. As for genus.

Description. The holotype is fully articulated concealing the outlines of the plates (Fig. 3A, C, D). The head plate is almost pentagonal with an arcuate anterior area and straighter lateral areas. The tail plate is similar in outline, defined by an arcuate posterior area and four facets: left and right lateral flanking an anterior area with

two facets separated by a median keel. The umbo is posteriorly positioned. Lateral intermediate plates 2–5 are divided into a raised lateral and inner area with almost straight margins and a depressed median area with an arcuate anteriorly convex margin. There appears to have been a row of median intermediate shell plates along the midline. An imperfect impression of this plate is evident in rows 1 and 3–5 (Fig. 3A). A central raised triangular structure similar to the median plate in other multiplacophorans is particularly evident in row 4.

The upper surface of all shell plates and spines is covered by a distinctive reticulate, rhombic pattern of fine ridges (Fig. 3A, C, D). The shell plates show densely pectinated margins in many places (Fig. 3E).

The most anterior preserved spine, which is almost complete, is shorter than those behind it, indicating that spine length may increase posteriorly. The marginal spines (Fig. 3) have a median dorsal groove as in *Hercolepas* (Appendix S1) and other strobilipids.

Dimensions. Holotype: body without spines: 9.2 mm long, 4.4 mm wide; including spines: 10.9 mm long, 7.9 mm wide. The dimensions of individual plates are shown in Table 1. Paratype C0601 (Fig. 3B, E): 15.7 mm long, 11.2 mm wide excluding the spines (Table 1).

DISCUSSION

The fossil record of polyplacophorans and the origin of multiplacophorans

Molecular divergence estimates (Vinther *et al.* 2012) of the polyplacophoran crown group (357 Ma (408–297)) (Fig. 4) accord well with the fossil record. The occurrence of several Carboniferous polyplacophorans with sutural laminae (Hoare *et al.* 1972, 1983; Hoare and Mapes 1985a, b; Hoare 2001) suggests that the crown divergence was around this time (*c.* 350 Ma according to Sigwart (2009)). A confident minimum for the divergence of the crown group would require the identification of forms that clearly lie on one of the branches within the crown group (i.e. Lepidopleurida or Chitonida). This proves to be difficult, because although most fossil Carboniferous polyplacophorans have been classified within the Lepidopleurida, their morphology is most likely plesiomorphic of the crown group. The Chitonida have evolved lateral insertion plates with slits. One Early Carboniferous fossil *Glyptochiton* (Smith 1971) exhibits prominent articular extensions along most shell margins and could be a chitonid stem form. If so, this would provide a minimum for the crown group in the Lower Carboniferous, consistent with the recent molecular clock analysis (Vinther *et al.* 2012). The Chitonida are estimated to have diverged in the Permian (*c.* 269 Ma) roughly coincident with the appearance of *Ochmazochiton* (Hoare and Smith 1984) which has slitted insertion areas on the lateral mar-

gins of the intermediate plates. *Ochmazochiton* is slightly older than the molecular divergence estimates (Vinther *et al.* 2012), a difference that may be due to estimation error. Chitonid characters, however, must have appeared somewhere on the chitonid stem lineage prior to the divergence of the crown group. Moreover, the three small adjacent slits on *Ochmazochiton* differ from the condition in the crown group with its single larger slit. This led Hoare and Smith (1984) to place them in the Lepidopleurina while noting that *Ochmazochiton* presumably marks the appearance of a character that later leads to the slitted insertion plates in Chitonida. Thus, *Ochmazochiton* could be accommodated on the chitonid stem lineage as posited herein. On this basis, the molecular clock is consistent with a divergence of the Chitonida after the Carboniferous and likely early in the Permian. Future fossil finds are needed to test this hypothesis.

The 95 per cent credibility interval for the polyplacophoran crown group divergence (408–297 Ma) does not extend to the Wenlock (428–423 Ma) which yielded the earliest multiplacophoran. Therefore, the molecular clock is not only consistent with the fossil record of polyplacophorans, but supports the exclusion of multiplacophorans from the crown group.

Convergent evolution of shell characters

Multiplacophorans and crown group polyplacophorans exhibit morphological similarities (see introduction), but close scrutiny of these fails to support homology. The pectinated insertion plates of Chitoniidae have a major slit, a diagnostic character of the higher ranked Chitonida that does not occur in multiplacophorans. Neither the position nor the shape of sutural laminae is identical in multiplacophorans and crown group polyplacophorans. The morphological similarities are therefore considered to be convergent, given the phylogenetic and temporal evidence presented here, presumably in response to their evolution for the same function. Sutural laminae and insertion plates attach the shell firmly to the underlying tissue. The faceted plates and distinct lateral and median intermediate shell areas reflect the tight juxtaposition of the adjacent plates and result in more effective armour. The Chitoniidae, with most characters in common with multiplacophorans, are mostly intertidal rocky shore dwellers. Lepidopleurids, which lack insertion plates, live in deeper water and mostly on the underside of hard substrates such as rocks and shells. We suggest that multiplacophorans evolved armour similar to that of Chitoniidae (within the crown group) because of their exploitation of similar habitats, that is, exposed hard substrates with higher predation pressure and surf, in contrast to the coeval stem group polyplacophorans which probably lived

in less exposed and/or deeper water environments. The temporal gap between crown group polyplacophorans and multiplacophorans, which the molecular clock (Fig. 4) demonstrates is real and not a taphonomic artefact, is consistent with the inferred convergent evolution of the plate morphology.

An interesting observation is that most multiplacophorans appear to be preserved in calcium carbonate, whereas fossil polyplacophorans typically are preserved as moulds or as silicified material. The shell of extant polyplacophorans is aragonite, which is unstable in early diagenesis; calcite is more stable and often preserved in fossils, suggesting that multiplacophoran plates may have been calcitic rather than aragonitic. The preservation of molluscs in the Devonian Silica Formation of Ohio, from which *Protobalanus spinicoronatus* was collected, lends support to this hypothesis. Fossil bivalves and gastropods that presumably were originally aragonitic are preserved as moulds, whereas calcitic snails like *Platyceras* associated with the crinoid *Arthroacantha* preserve shell material as calcite, as does *Protobalanus*.

Multiplacophoran origins

The earliest undisputed relatives of polyplacophorans are the Late Cambrian mattheviids (e.g. *Matthevia* and *Chelodes*) (Runnegar *et al.* 1979; Vendrasco and Runnegar 2004; Pojeta *et al.* 2010), which are either stem polyplacophorans (Pojeta *et al.* 2010) or stem aculiferans (Vinther *et al.* 2012) with a single column of 7–8 shell plates. The older assemblage of *Ocruranus* and *Eohalobia* has valves that resemble those of polyplacophorans (Vendrasco *et al.* 2009), but they may be stem aculiferans considering their early appearance and close similarity to forms such as the sachitids (Vinther 2009), which exhibit a variable numbers of shell plates. Mattheviids bore highly arched conical plates that did not overlap, but projected dorsally with one or two lacunae (tunnels in Vendrasco and Runnegar 2004) in each plate. A single larger lacuna was present in the plates of mattheviids such as *Chelodes*, *Hemithecella* and *Eukteanochiton*. A lacuna also occurs in the articulated and eight-plated Late Ordovician paleoloricate *Echinochiton* (Pojeta *et al.* 2003; Pojeta and DuFoe 2008), which confirms the chiton-like nature of these previously debated (Yochelson 1966) fossils. The reduction of lacunae in later forms (Vendrasco and Runnegar 2004) has been posited to coincide with the increase in overlap between plates as in, for example, *Septemchiton*. Forms referred to *Chelodes*, with prominent lacunae, occur in the Silurian of Gotland (Cherns 1998a, b, 2004) as do *Heloplax*, *Enetoplax* and *Arctoplax* (Cherns 1998a, 2004), which are related to the aplacophoran relative *Acaenoplax* (Sutton *et al.* 2001; Sutton *et al.* 2004; Sigwart and Sutton 2007). The subapical cavity in these forms, which has been

homologized with the more extensive lacunae of mattheviids, provides a putative morphological link to Ordovician and late Cambrian forms (Cherns 2004).

The ventral side of *Protobalanus spinicoronatus* exhibits subapical cavities on outer intermediate plates 2–5 (Fig. 2E, H), which suggests that multiplacophorans also stem from Ordovician paleoloricates. Thus multiplacophorans may have diverged from the polyplacophoran stem lineage in the Ordovician–Llandovery. The Silurian paleoloricate polyplacophorans have secondary thickening of the shell plates (Cherns 2004), a prerequisite for the evolution of the articulamentum and sutural laminae. Thus, these polyplacophorans may have arisen from a common progenitor to both multiplacophorans and the polyplacophoran crown group. Alternatively, neoloricates with sutural laminae may await discovery in the Silurian, in which case they could have given rise to multiplacophorans. However, among 26 records of multiplated mollusc species recorded in the Silurian (compared to 12 and 28, respectively, in late to middle Ordovician and Devonian; Cherns 2004) no neoloricates have been found.

Larsson *et al.* (2009) described a multiplated organism from the Early Cambrian of North Greenland, *Trachyplax arctica*, and suggested affinities with multiplacophorans. Although the skeleton of *Trachyplax* includes both symmetric and asymmetric plates that resemble those of multiplacophorans, the delicately preserved plate surfaces show no indication of aesthete canals, a clear synapomorphy of polyplacophorans and multiplacophorans, nor a secondary shell layer, sutural lamina or insertion plates. Some *Trachyplax* shell plates resemble tommotiids (stem brachiopods) (Li and Xiao 2004; Skovsted *et al.* 2009), and others resemble the plates of the putative sachitids *Oikozetetes* and *Ocruranus* (Paterson *et al.* 2009; Vendrasco *et al.* 2009). The reconstruction of *Trachyplax* (Larsson *et al.* 2009, fig. 7) does not reflect an organization similar to multiplacophorans with seven transverse shell rows, or a configuration that is homologous to crown aculiferans. *Trachyplax* may be a member of the early aculiferan stem lineage of multiplated molluscs with a configuration different from primitive aculiferans with eight plates such as the halkieriids (Conway Morris and Peel 1995; Vinther and Nielsen 2005; Vinther 2009) and *Orthrozanclus* (Conway Morris and Caron 2007). Alternatively, *Trachyplax* may represent a tommotiid (Skovsted *et al.* 2009) or be a chimaeric taxon.

Homology and serial homology of aculiferan mineralized elements

Multiplacophorans appear to have evolved from presumably eight-plated polyplacophorans and subdivided their intermediate shell fields laterally. The acanthochitoninid *Schizoplax brandtii* evolved a similar configuration inde-

pendently with divided intermediate fields and a single anterior and posterior terminal plate. In some modern polyplacophorans, the intermediate fields are isolated into a left and right region during initial shell deposition in the postmetamorphic juvenile, while the anteriormost shell field is a single median region (Bartolomaeus 1989). Thus, the terminal plates may be independent entities that are always expressed as a single shell, while the intermediate shell fields are serial homologues that have the potential to divide laterally into separate shell fields as apparently happened at least twice. Cambrian stem group aculiferans, like *Halkieria*, have a single anterior and posterior shell plate (Conway Morris and Peel 1995) which may be deep homologues of the anterior and posterior plates of crown and stem group polyplacophorans (Fig. 5), including multiplacophorans.

It seems that the possession of seven plates or transverse shell fields evolved secondarily in *Acaenoplax* and multiplacophorans from a primitive eight-plated condition. All articulated stem polyplacophorans and putative stem aplacophorans from the Ordovician are eight-plated (Rolfe 1981; Pojeta *et al.* 2003; Pojeta and DuFoe 2008; Donovan *et al.* 2010). It therefore appears that one of the intermediate plates is lost or gained while the terminal plates stay fixed. Similarly, occasional teratomorphic living polyplacophorans with seven shell plates usually retain the terminal plates (JV, pers. obs.). The eighth plate is laid down after the intermediate plates during development and was thought to have been absent in early forms (Hyman 1967). However, it appears that the primitive condition for crown Aculifera is the possession of eight transverse shell plates and that the later ontogenetic anlagen of the eighth plate is unrelated to the secondary development of seven shell fields in some stem groups. It seems that the latest common ancestor of aplacophorans had seven shell plates considering fossil forms such as *Acaenoplax* and the embryological expression in modern aplacophorans of a dorsal sevenfold iteration (Scheltema and Ivanov 2002; Nielsen *et al.* 2007).

Aesthetes. Aesthete canals are present in multiplacophoran shell plates as in those of modern and fossil polyplacophorans, but also in the large spines of the multiplacophoran girdle where they are unknown in any modern group. The sachtitids from the early and middle Cambrian, including *Halkieria*, also have a canal system in the girdle sclerites, which has been homologized to the aesthete system (Vinther 2009), but they lack a canal system in the shell plates. Thus, multiplacophorans represent an intermediate level between the Cambrian stem group aculiferans with aesthetes in their sclerites, and the modern condition with aesthetes in the shell plates only (Vinther 2009). Nothing is known about the mantle sclerites of Early Palaeozoic paleoloricates, but there appear to be

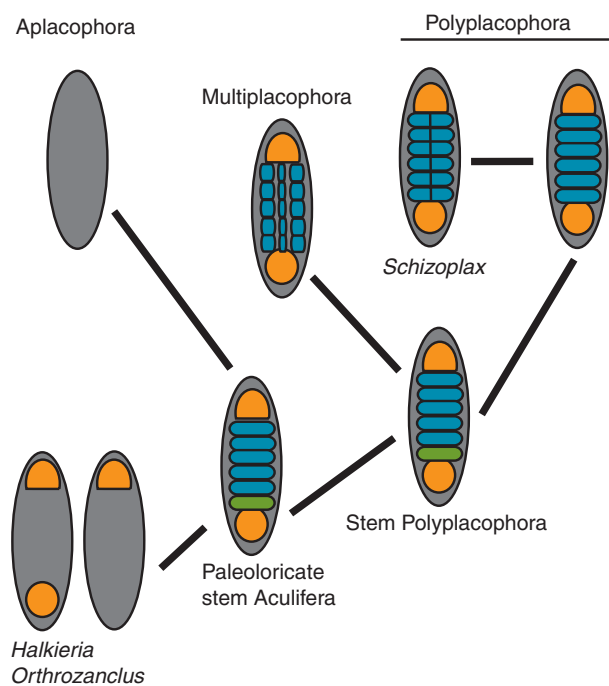


FIG. 5. Homology of shell plates in Aculifera. The anterior (up) and posterior (down) shell plates (orange) are conserved separate entities across the total group Aculifera, except in Aplacophora where shells are lost. The intermediate shell plates (blue) evolved prior to the divergence of crown group Aculifera. The intermediate shell plates have become laterally subdivided in the Multiplacophora and the extant *Schizoplax*. Early Palaeozoic aculiferans are known with seven dorsal shell fields as in *Acaenoplax* and Multiplacophora and others with eight shell fields (*Echinochiton*). The primitive condition of shell plate number seems to have been eight, but in stem forms of both polyplacophorans and aplacophorans, the number has been reduced to seven transverse shell regions (i.e. *Acaenoplax* and multiplacophorans). We show one intermediate shell field in these forms with a green colour to indicate this plasticity.

aesthete channels in the shell plates (Pojeta *et al.* 2010). *Echinochiton dufoei* Pojeta, Eernisse, Hoare and Henderson, 2003 has large hollow girdle spines similar to those of multiplacophorans (Hoare and Mapes 1995). Aesthetes may also have been present in the spines of this taxon, but the specimens are too coarsely preserved to show such features.

CONCLUSIONS

Multiplacophorans are stem group polyplacophorans with a skeleton of plates that were heavily interlocked and firmly embedded in their tissues. The appearance of crown group polyplacophorans in or after the early Carboniferous and stem members of the subgroup Chitonida in the early Permian is congruent with a molecular clock analysis

(Vinther *et al.* 2012) and supports the observation that multiplacophorans must be stem polyplacophorans that evolved some crown group characteristics (sutural laminae, ornamental division of the intermediate plates and pectinated insertion plates) convergently. Multiplacophorans evolved a unique 17-plated skeleton from an ancestor with 7–8 plates in a single column. We hypothesize that their more exposed life mode resulted in a more interlocked skeleton and structures to embed the shell plates firmly in the underlying tissues, which led to the convergent evolution of sutural laminae, distinctly divided dorsal shell areas, and pectinated insertion plates. The intermediate shell plates are serial homologues but appear to be patterned differently to the terminal shell plates. Total group polyplacophorans evolved laterally divided regions at least twice: in Multiplacophora and in *Schizoplax*. An intermediate transverse shell field was lost at least twice in the Aculifera: in multiplacophorans and the aplacophoran stem group.

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SUPPORTING INFORMATION

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

Appendix S1. A, *Hercolepas signata* NRM Ec 6108, from the Vattenfallet section, Gotland, Sweden. B, detail of sclerites with large radiating spines and smaller interfingering sclerites. C, *Protobalanus hamiltonensis* from the Hamilton Group, New York and D, Another specimen on the same slab AMNH 22866, Scale bars: A, 5 mm; B, 1 mm; C and D, 3 mm. (John S. Peel kindly provided the dimensions of *H. signata*)

Appendix S2. Movie file of *P. spinicoronatus* based on a microCT scan showing the specimen before and after segmentation and the sequential articulation of the specimen.

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