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Monoplacophora (Tryblidia)–Some unanswered questions*

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Abstract: A review of the current state of knowledge on the Monoplacophora, a taxon crucial for assessing phylogeny of the Mollusca, is provided. A number of questions related to this taxon have been resolved; the seriality of some organ systems is now regarded as secondarily gained within mollusks and shared with polyplacophorans; the tergomyan-cyclomyan condition does not reflect a principal difference in organization. Other topics remain to be resolved. These concern the relationships amongst monoplacophorans and the placement of the Monoplacophora within the Mollusca. Furthermore we point out a number of issues to be investigated (*e.g.*, mechanism of excretion or development sequence of gills and muscles, gene expression) by fine structural, ontogenetic, or molecular analyses.

Key words: phylogeny, review, deep phylogeny, living fossil

Since the discovery of the first extant representatives in the 1950s, the Monoplacophora (Tryblidia is the more precise taxon name because it does not include many extinct conchiferan clades of uncertain phylogenetic affinities, see Haszprunar (2008)) have always played a crucial role in discussions on the evolution and phylogeny of the Mollusca. Currently, more than 30 extant species are known, reflecting a radiation starting in the Mesozoic (Kano *et al.* 2012), whereas the origin of the respective clade certainly lies deep in the Paleozoic and probably occurred already in the Lower Cambrian (*e.g.*, Yu 1979).

Recent reviews have focused on species composition in space and time (Haszprunar 2008, Schwabe 2008), history of discovery (Lindberg 2009) and phylogeny and evolution (Kano *et al.* 2012). Advanced morphological methodologies such as application of scanning electron microscopy (SEM) of hard and external parts (most of recent species descriptions) and transmission electron microscopy (TEM) of soft parts (Haszprunar and Schaefer 1997b), and the semi-thin sectioning technique combined with manual graphic (*e.g.*, Schaefer and Haszprunar 1997a, Haszprunar and Schaefer 1997a) or computer-aided 3D-visualization (Ruthensteiner *et al.* 2010) have substantially improved our knowledge of monoplacophoran anatomy. Furthermore, the first (though still scarce) molecular data are now available (Giribet *et al.* 2006, Wilson *et al.* 2010, Kano *et al.* 2012). Despite this progress, there are a

number of important topics remaining concerning this still enigmatic molluscan taxon; these are addressed below.

Resolved: autapomorphic seriality versus symplesiomorphic (annelid-like) segmentation

With the first description of monoplacophoran anatomy by Lemche (1957a, 1959a,b, Lemche and Wingstrand 1959a, b), the discussion of the interpretation of the serial repetitions of various organ systems, namely shell muscles, ctenidia, nephridia, gonads, and latero-ventral neural connectives was immediately addressed (*e.g.*, Yonge 1957, Beklemishev 1958, Felisiak 1959, Steinböck 1962) and two competing hypotheses emerged: 1) This serial repetition reflects a (somewhat modified) plesiomorphic state of Mollusca being a heritage from annelid-like, truly segmented ancestors; 2) The serial repetition is an autapomorphic feature of Monoplacophora reflecting a derived organization of this molluscan clade rather than a primitive trait. In light of the discovery of an apparent progenetic monoplacophoran taxon (genus *Micropilina* Warén 1989) and recent investigations on monoplacophoran anatomy, this question now appears largely resolved (Haszprunar and Schaefer 1997a, Ruthensteiner *et al.* 2010). It has been shown that the eight pairs of shell muscles are probably direct homologues to those of the Polyplacophora, where they are secondarily formed out of a multiple serial condition during ontogeny (Haszprunar and Wanninger 2000,

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Wanninger and Haszprunar 2002). The position of neural lateroventral connective does not fully coincide with the position of ctenidial bases and urinogenital openings. Most significantly, the ctenidia and all coelomatic structures (gonads, gononephroducts, nephridia) appear to be (*i.e.* based on progenetic conditions) serially formed from posterior to anterior, whereas annelid segments are formed in the opposite direction. Accordingly, the serial repetition of monoplacophorans is regarded partly as a symplesiomorphy with chitons (shell muscle bundles), and partly as an autapomorphy of Monoplacophora (Haszprunar and Schaefer 1997a, Haszprunar 2008, Ruthensteiner *et al.* 2010). Thus, Monoplacophora cannot be regarded as “living fossils” in the sense of an Urmollusk (Lindberg 2009, Kano *et al.* 2012).

Resolved: Tergomya and Cyclomya are not principally different

The idea of a substantial tergomyan-cyclomyan distinctness (apex outside or inside of the scars of the shell muscles) and thus the far-reaching separation of Tryblidia among other monoplacophoran taxa in the fossil record has been argued for decades (*e.g.*, Horný 1991, Peel 1991, Parkhaev 2002a, b) and is still present in the paleontological literature (*e.g.*, Ebbestad 2008). However, it has been shown recently (Haszprunar 2008) that the principal differences serving as basis for the tergomya-cyclomya hypothesis are not valid if the positions of the insertion areas of the mantle retractors are additionally considered; the latter always encircle the apex. Indeed, the sole difference is the position of the apex inwards or outwards of the shell aperture. However, this represents a minor difference, which also varies within patellogastropod taxa.

Unresolved: the phylogenetic position of Monoplacophora within the Mollusca

During the last decades the Monoplacophora were generally regarded as an early branch of the Conchifera. This hypothesis has been seriously challenged by molecular data, which suggest a sister-group relationship of Polyplacophora and Monoplacophora. Both form the so-called “Serialia” (Giribet *et al.* 2006, Wilson *et al.* 2010, Kano *et al.* 2012). However, recent molecular studies on deep molluscan phylogeny substantially contradict each other (*e.g.*, Smith *et al.* 2011 vs. Kocot *et al.* 2011) and the entire molluscan tree currently is even less stable than ever before (Haszprunar and Wanninger 2012) (Fig. 1).

While there is no doubt that Polyplacophora and Monoplacophora share many structural details (*e.g.*, shell muscles, radular apparatus; cf. Wingstrand 1985), a sister-group relationship of both taxa appears unlikely because of other morphological conditions: The “Serialia” concept would either imply a plesiomorphic state of shell plates and accordingly the independent acquisition of the shell in Monoplacophora

or the modification of a plesiomorphic conchiferan shell into the polyplacophoran shell plates during evolution.

Unresolved: the ingroup relationships and classification of Monoplacophora

About 10 supraspecific taxa have been proposed to group the 30 extant monoplacophoran species (recently reviewed by Haszprunar 2008, Kano *et al.* 2012), mainly based on shell size and structure, radular details, and soft part morphology (as available). However, serious doubts regarding this classification were expressed in some studies (Urgorri *et al.* 2005, Ruthensteiner *et al.* 2010, Kano *et al.* 2012). In particular the genus *Micropilina* and the associated family Micropilinidae (and Neopilinidae for all other extant monoplacophorans) are questioned, since *Micropilina* species are all characterized by progenesis, which may have occurred independently. Unfortunately anatomical data are available for only six species, and molecular data exist for only two of them, *Laevipilina hyalina* McLean, 1979 (cf. Giribet *et al.* 2006) and *Veleropilina seisuimaruae* Kano, Kimura, Kimura and Warén, 2012 (cf. Kano *et al.* 2012). Most recently Kano *et al.* (2012) proposed a two clade phylogeny (*Micropilina* plus *Veleropilina* Starobogatov and Moskalev, 1987 vs. remaining monoplacophorans) with a calculated splitting event in the Late Cretaceous. This hypothesis is based on few characters, of which the presence/absence of the prismatic shell layer seems most convincing. This character is also available for fossil taxa if shell material is preserved. If both conditions are present before the Late Cretaceous, the hypothesis would require modification. However, testing this by fossils currently is impossible, because the fossil record of monoplacophorans in post-Devonian layers is extremely poor (Kano *et al.* 2012). Nevertheless, it remains likely that the ingroup relationships of extant Monoplacophora will continue to be subject to modification as more morphological and molecular data are added.

Gaps of knowledge concerning fine structure (Fig. 2)

Only a single specimen of Monoplacophora, a male *Laevipilina antarctica* Warén and Hain, 1992, has been studied by means of TEM (Healy *et al.* 1995, Haszprunar and Schaefer 1997b, Schaefer and Haszprunar 1997a, b). However, preservation of this specimen was not optimal and several questions remained unresolved:

- * Structural details of sensory organs, namely the subradular organ and the statocysts, could only be sparsely assessed.

- * Fine structural details of oogenesis remain entirely unknown.

- * The mechanism of excretion remains unclear: although Haszprunar and Schaefer (1997b) claimed the finding of podocytes in the auricle, the site of ultrafiltration in the more anteriorly-placed nephridia is unclear, since they lack any

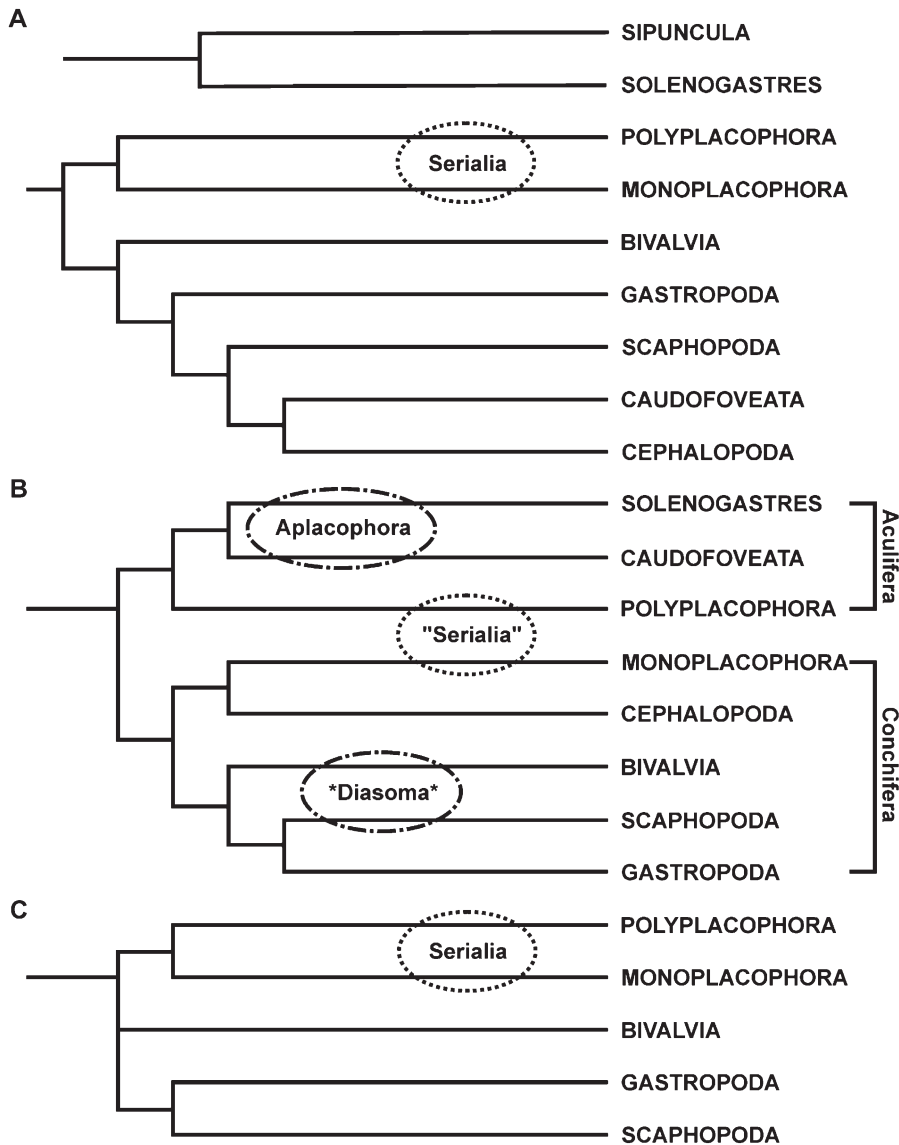


Figure 1. Recent molecular studies with extant Monoplacophora included in the analysis. Note that two studies (based on few genes) show the clade Serialia (Polyplacophora and Monoplacophora), whereas the phylogenomic study shows “Serialia” as diphyletic, but retains monophyletic Aculifera and Conchifera. **A**, Molecular tree based on eight genes (Wilson *et al.* 2010). **B**, Phylogenomic tree based on 216402 sites (11,185 gene regions) (Smith *et al.* 2011). **C**, Phylogenetic tree based on five genes (Kano *et al.* 2012).

connection with the pericardium. The same question arises for the nephridia of the progenetic *Micropilina* species. Generation of the ultrafiltrate in the pericardium plus heart is impossible, because this organ complex is entirely missing.

A major gap of knowledge: ontogeny (Fig. 2)

Presently, data concerning monoplacophoran ontogeny and reproduction are extremely scarce. Only the progenetic

Micropilina species provide some indirect observations of postembryonal development, since they have brood protection in the mantle cavity (Haszprunar and Schaefer 1997a). From the live observations of Wilson *et al.* (2009), we know characteristics of freshly-laid eggs of a *Laevipilina* species. These allow deducing that development is indirect and lecithotrophic, with freely-moving larval stages involved. However, a substantial number of unresolved issues directly concern ontogeny:

* Is there a true shell gland involved in shell formation as in other conchiferans or is the shell formed differently? Is *engrailed* expressed as in Polyplacophora (serial expression pattern in addition to shell margins and spicules) or as in other Conchifera (shell margin only) (cf. Wray *et al.* 1995, Moshel *et al.* 1998, Jacobs *et al.* 2000, Nederbragt *et al.* 2001; Baratte *et al.* 2007, Iijima *et al.* 2008, Navet *et al.* 2010)?

* Does shell musculature formation resemble that of the Polyplacophora (cf. Wanninger and Haszprunar 2002)?

* Does an anterior pedal gland occur during development like in the Polyplacophora (see Hammarsten and Runström 1926)?

* Do the first ctenidium and gonad formed correspond to the most posterior adult ones as suggested by the progenetic species? Is there a common anlage for gonads and nephridia?

* How are the nephridia formed? Are they true outgrowths of the pericardium as in Polyplacophora (Salvini-Plawen and Bartolomaeus 1995, Baeumler *et al.* 2012) or do they originate independently like in bivalves (Altnöder and Haszprunar 2008)?

* Does the most anterior nephridium represent a paedomorphic larval protonephridium as suggested by its position (sector A), and by the conditions in Polyplacophora (Ruthensteiner *et al.* 2010, Baeumler *et al.* 2011)?

* How does formation of the intestine, which does not show a double-loop as usual in Mollusca, but is unique by its unidirectional looping, take place?

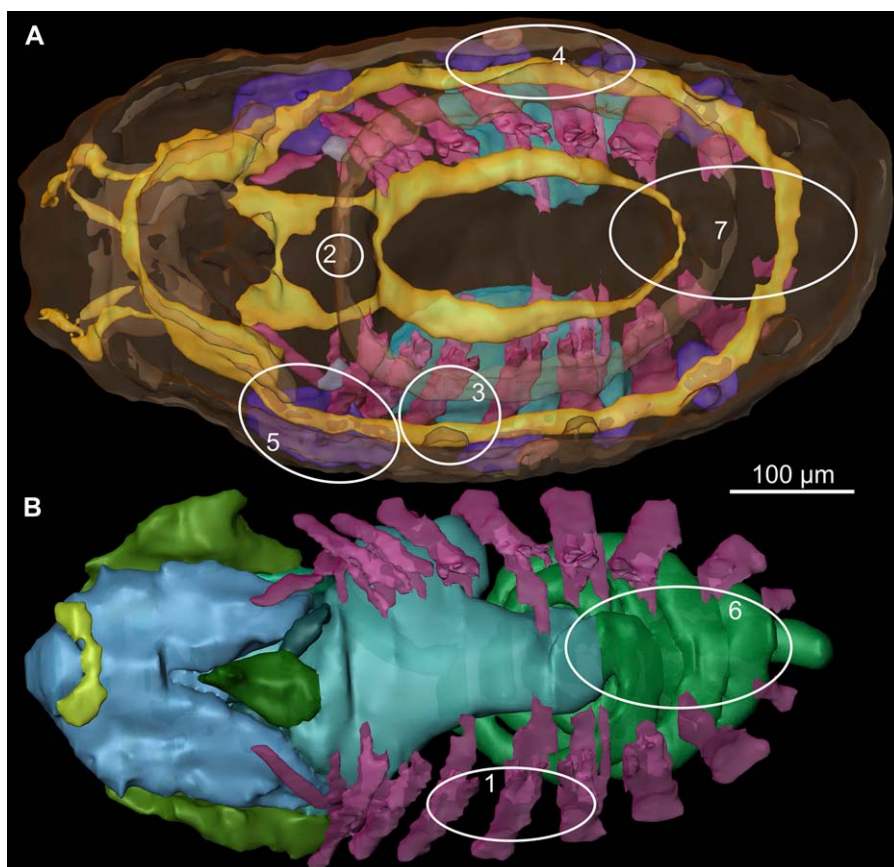


Figure 2. *Microplina minuta* Warén and Hain, 1992. Surface rendering from manual serial section segmentation (Ruthensteiner *et al.* 2010). Color coding present only in the electronic version. Ventral view. **A**, Nervous system (yellow), kidneys (purple), muscles (red), gonads (cyan) inside of transparent external surface (brown). **B**, Digestive system (green tones) and muscles (red). Encircled areas symbolize positions of unresolved questions on morphology of monoplacophorans. 1, development of muscle system; 2, occurrence of pedal gland during ontogeny, 3, sequence of appearance of gills and gonads; 4, origin of nephridia; 5, possible protonephridial nature of most anterior nephridium; 6, formation of the intestine; 7, differentiation of the nerve cords and condition of posterior pedal commissure.

* Are the longitudinal nerve cords and the latero-ventral neural connectives differentiated from posterior to anterior like in Polyplacophora (Friedrich *et al.* 2002, Voronezhskaya *et al.* 2002) or differently? Does the absence of posterior pedal commissures represent a secondary condition?

Considering all these questions, there is little doubt that ontogenetic studies of monoplacophoran species using state-of-the-art structural (e.g., detailed 3D organization) and molecular analysis (e.g. gene expressen) approaches are urgently needed for understanding various aspects of monoplacophoran morphology and evolution. Such study of any development stage ranging from early cleavage to late morphogenesis would be beneficial in this respect.

CONCLUSIONS

Despite their importance in understanding molluscan evolution and phylogeny, Monoplacophora remain poorly studied. Hopefully, recent collections at relatively low depth (less than 400 m), such as the one of *Laevipilina hyalina* off Southern California, U.S.A. (Wilson *et al.* 2009) can be reproduced to gain additional material that can be directly (freshly) processed as is required for most sophisticated techniques (e.g., TEM or molecular examination) and help to improve our knowledge of this still enigmatic group of the Mollusca.

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