

## **Recent Advances and Unanswered Questions in Deep Molluscan Phylogenetics**

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## Recent advances and unanswered questions in deep molluscan phylogenetics\*

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**Abstract.** Despite the diversity and importance of Mollusca, evolutionary relationships among the eight major lineages have been a longstanding unanswered question in Malacology. Early molecular studies of deep molluscan phylogeny, largely based on nuclear ribosomal gene data, as well as morphological cladistic analyses largely failed to provide robust hypotheses of relationships among major lineages. However, three recent molecular phylogenetic studies employing different markers and more data have significantly advanced understanding of molluscan phylogeny by providing well-supported topologies and generally congruent results. Here, evolutionary relationships among the major lineages of Mollusca and implications of recent findings for understanding molluscan evolution are reviewed. Most notably, all three of the recent studies reviewed herein recovered a monophyletic Aculifera, a clade including Aplacophora (Neomeniomorpha + Chaetodermomorpha; worm-like molluscs) and Polyplacophora (chitons). This finding argues against the previously widely-held notion of an aplacophoran-like ancestor of Mollusca. Also, these studies counter the widely held view that Gastropoda and Cephalopoda are sister taxa - a result with important implications for the field of neurobiology where representatives of both taxa are used as models. Surprisingly, the one study that sampled the limpet-like Monoplacophora recovered it sister to Cephalopoda. Placement of Scaphopoda remains ambiguous as two studies place it sister to a Bivalvia–Gastropoda clade (Pleistomollusca) with strong support but another places Scaphopoda sister to Gastropoda with strong support. Ongoing work in several labs employing new sequencing technologies and analytical methods as well as morphological and developmental studies will undoubtedly continue to improve understanding of deep molluscan phylogeny and evolution.

**Key words:** phylogenomics, Aculifera, Aplacophora, Pleistomollusca

With estimates of up to 200,000 extant species (Ponder and Lindberg 2008), the phylum Mollusca is second in number of species only to Arthropoda. Moreover, with species as different as meiofaunal worms and giant squid, Mollusca is also one of the most morphologically variable metazoan phyla. Many molluscs are economically, ecologically, or biomedically important. Despite their diversity and importance, the extreme disparity in morphology among the major lineages (i.e., “classes”) has prompted numerous conflicting phylogenetic hypotheses (Haszprunar *et al.* 2008, Ponder and Lindberg 2008). Thus, the relationships among the major lineages of Mollusca are a great unanswered question, the answer to which is important for comparative studies in malacology as well as numerous other diverse fields. For example, because molluscs are well represented in the early animal fossil record, understanding molluscan evolutionary history has significant implications for understanding early animal evolution and the identity of several Cambrian fossil taxa hypothesized to be stem-group molluscs including *Odontogriphus omalus* Conway Morris 1976 and *Kimberella quadrata* Glaessner and Wade, 1966 (Caron *et al.* 2006, Fedonkin *et al.* 2007, Ivantsov 2009, 2010). Also, several molluscs are important models for the study of learning and memory (Moroz 2009).

To date, analyses of morphology (*e.g.*, Salvini-Plawen and Steiner 1996, Haszprunar 2000) and molecular datasets dominated by nuclear ribosomal genes (*e.g.*, Passamanek *et al.* 2004, Giribet *et al.* 2006, Wilson *et al.* 2010) have been unable to robustly resolve deep molluscan phylogeny. However, three recent studies employing a molecular phylogenetic approach with new data from nuclear protein-coding genes have greatly advanced understanding of molluscan phylogeny (Kocot *et al.* 2011, Smith *et al.* 2011, Vinther *et al.* 2011). Here, I review hypotheses of molluscan phylogeny proposed to date and summarize the current understanding of deep molluscan phylogeny in light of recent results. Remaining unanswered questions and future directions that should help answer them are discussed.

### DEEP MOLLUSCAN PHYLOGENY

#### Morphological and previous molecular hypotheses

Most traditional hypotheses of molluscan phylogeny are based on adult morphological characters (Haszprunar *et al.* 2008). The worm-like aplacophorans, Chaetodermomorpha

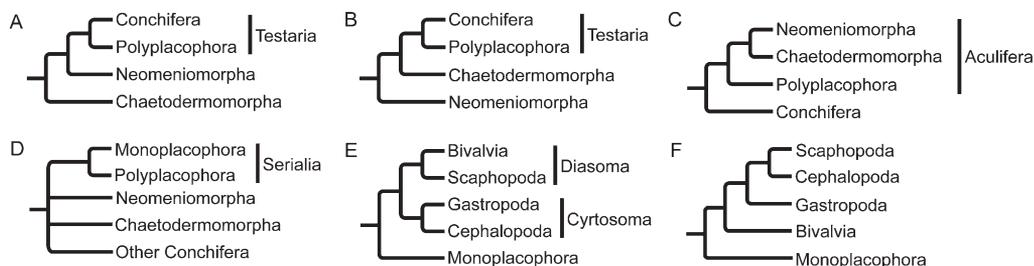
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(= Caudofoveata) and Neomeniomorpha (= Solenogastres), have traditionally been considered plesiomorphic and “basal” because of their relatively simple morphology and/or possession of aragonitic sclerites rather than one or more shells (Salvini-Plawen 1980, 1981, 1985, 1990, 2003, Salvini-Plawen and Steiner 1996, Haszprunar 2000). Whether these two groups constitute a monophyletic taxon, Aplacophora (Scheltema 1993, 1996, Ivanov 1996, Waller 1998), or a paraphyletic grade (e.g., Salvini-Plawen 1985, Salvini-Plawen and Steiner 1996, Haszprunar 2000) has been widely debated (reviewed by Haszprunar *et al.* 2008, Todt *et al.* 2008). Morphology has been variously interpreted to suggest basal placement for chaetoderms (Adenopoda hypothesis; Salvini-Plawen 1985; Fig. 1A) as well as neomenioids (Hepagastralia hypothesis; Salvini-Plawen and Steiner 1996, Haszprunar 2000; Fig. 1B). Studies (Bartolomaeus 1993, Ax 1999, Haszprunar and Wanninger 2008, Wanninger *et al.* 2007, Wanninger 2009) examining the anatomy of the phylum Entoprocta (= Kamptozoa), a hypothesized molluscan sister taxon, strengthened support for the Hepagastralia hypothesis. Most notably, the neomenioid nervous system and preoral sensory organ are strikingly similar to those of larval entoprocts (Wanninger *et al.* 2007). In contrast to hypotheses placing aplacophorans basal, the Aculifera hypothesis (Scheltema 1993, 1996, Ivanov 1996; Fig. 1C) unites molluscs that possess sclerites by placing Polyplacophora as the sister taxon of Aplacophora. Aculifera is sometimes also called Amphineura although this latter term has also been confined to refer only to chitons by some workers (see Salvini-Plawen 1980 and Scheltema 1993 for discussion). Other workers place chitons sister to Conchifera (Monoplacophora [= Tryblidia], Gastropoda, Cephalopoda, Scaphopoda, and Bivalvia) under the Testaria hypothesis (Salvini-Plawen 1985, Salvini-Plawen and Steiner 1996, Haszprunar 2000) uniting molluscs with one or more shells. Molecular studies (Giribet *et al.* 2006, Wilson *et al.* 2010; see below) have suggested a close relationship

between Polyplacophora and Monoplacophora (Fig. 1D) uniting the extant shelled molluscs with serially repeated muscles and ctenidia (except *Nautilus*). Within Conchifera, the previously most widely held hypothesis places Monoplacophora basal to two clades: Cyrtosoma (= Visceroconcha; Gastropoda and Cephalopoda) and Diasoma (= Loboconcha; Bivalvia, Scaphopoda, and the extinct class Rostroconchia) (Runnegar and Pojeta 1974, Pojeta and Runnegar 1976, Salvini-Plawen 1985, Trueman and Brown 1985, Salvini-Plawen and Steiner 1996; Fig. 1E). Notably, Cyrtosoma was originally described to include Monoplacophora (Runnegar and Pojeta 1974) but the term has more recently been used by some (including Passamaneck *et al.* 2004, Kocot *et al.* 2011, Smith *et al.* 2011, and Fig. 1E of the present contribution) to describe a clade including only gastropods and cephalopods.

Because of conflicting hypotheses based on morphological data, molecular data are desirable as an independent source of data to address deep molluscan evolutionary relationships. Prior to the three most recent investigations of molluscan phylogeny, molecular studies have relied primarily on the nuclear small subunit (SSU or 18S) and large subunit (LSU or 28S) ribosomal genes (Winnepenninckx *et al.* 1996, Rosenberg *et al.* 1997, Passamaneck *et al.* 2004, Giribet *et al.* 2006, Meyer *et al.* 2010, Wilson *et al.* 2010). Briefly, the results of some of the most recent studies will be summarized. A maximum likelihood (ML) analysis of complete 18S and partial 28S sequences from 32 molluscs performed by Passamaneck *et al.* (2004) recovered all classes except for Bivalvia monophyletic, but support values at higher-level nodes were generally weak. Notably, analyses of 28S recovered Aplacophora monophyletic and strongly contradicted the previously widely accepted Diasoma hypothesis suggesting that scaphopods are more closely related to gastropods and/or cephalopods than bivalves (Fig. 1F). Giribet *et al.* (2006) analyzed a combined dataset with sequences from 18S, 28S,



**Figure 1.** Summary of leading hypotheses of molluscan phylogeny (modified from Kocot *et al.* 2011). **A**, Adenopoda hypothesis placing Chaetodermomorpha basal. **B**, Hepagastralia hypothesis placing Neomeniomorpha basal. **C**, Aculifera hypothesis placing Aplacophora sister to Polyplacophora. **D**, Serialia hypothesis allying Polyplacophora and Monoplacophora. **E**, Diasoma and Cyrtosoma hypotheses allying Bivalvia to Scaphopoda and Gastropoda to Cephalopoda, respectively. **F**, Unnamed hypothesis, allying Scaphopoda and Cephalopoda.

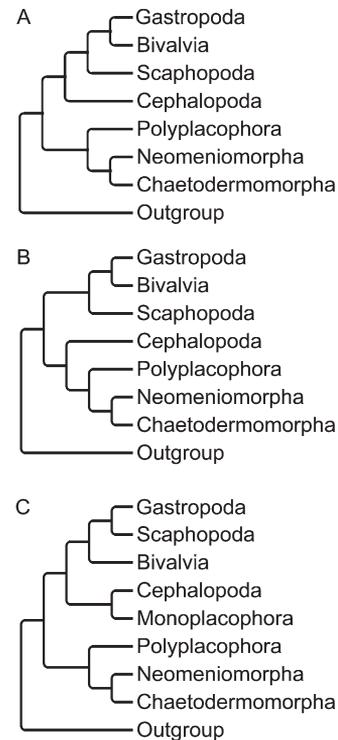
16S, cytochrome oxidase I (COI), and histone H3 from 101 molluscs using a dynamic homology approach with parsimony as the optimality criterion for direct optimization as well as a model-based approach using Bayesian inference (BI). As in Passamaneck *et al.* (2004), support values at higher-level nodes were generally weak. Also, neither Bivalvia nor Gastropoda were recovered monophyletic. Notably, a clade nesting

the monoplacophoran *Laevipilina antarctica* Warén and Hain, 1992 inside Polyplacophora, termed Serialia by the authors, was recovered and well-supported in both analyses. However, the single monoplacophoran 28S sequence analyzed was later shown to be a chimera of monoplacophoran and chiton 28S (Wilson *et al.* 2010). After adding authentic data from a second monoplacophoran species and removing the contaminated portion of the *Laevipilina antarctica* 28S sequence, ML and BI analyses of the same genes by Wilson *et al.* (2010) still found support for Serialia. However, Neomeniomorpha was placed in a clade with Annelida (including Sipuncula) rendering Mollusca paraphyletic. Wilson *et al.* (2010) noted that the available *Helicoradomenia* Scheltema and Kuzirian, 1991 (Neomeniomorpha, Simrothiellidae) 18S sequences appeared similar to available annelid 18S sequences but not unambiguously enough to support their exclusion. Subsequent work by Meyer *et al.* (2010) substantiated the notion that the available 18S sequences from *Helicoradomenia*, which, like at least some other simrothiellids (Todt, personal communication), is thought to feed on annelids (Todt and Salvini-Plawen 2005), and are chimeras with annelid 18S. Otherwise, Wilson *et al.* (2010) generally found weak support for other higher-level relationships as in previous studies.

Although nuclear ribosomal genes have been extremely informative to our understanding of deep metazoan phylogeny (*e.g.*, Halanych *et al.* 1995, Aguinaldo *et al.* 1997), several studies employing these markers have been unable to resolve deep molluscan phylogeny. Therefore, these studies suggested that the use of other molecular markers is necessary to resolve this question. Several studies have demonstrated that PCR-amplified fragments of conserved nuclear protein-coding genes can be very useful markers for higher-level metazoan phylogenetics (*e.g.*, Ruiz-Trillo *et al.* 2002, Anderson *et al.* 2004, Peterson *et al.* 2004, Helmkampf *et al.* 2008, Paps *et al.* 2009, Sperling *et al.* 2009, Regier *et al.* 2010). Moreover, several recent studies have addressed deep animal phylogeny using large amounts of nuclear protein-coding gene data derived from genomes and transcriptome data instead of using PCR to amplify targeted gene fragments (*e.g.*, Philippe *et al.* 2005, Matus *et al.* 2006, Bourlat *et al.* 2006, Dunn *et al.* 2008, Hejnol *et al.* 2009, Meusemann *et al.* 2010, Pick *et al.* 2010, Andrew 2011, Struck *et al.* 2011). These so-called phylogenomic studies, which employ dozens to hundreds of genes, have shown great promise in improving our understanding of animal phylogeny.

### Recent advances in deep molluscan phylogenetics

In 2011, three studies (results summarized in Fig. 2) addressed deep molluscan evolutionary relationships using sequence data from nuclear protein-coding genes: Kocot *et al.* (2011), Smith *et al.* (2011), and Vinther *et al.* (2011). Kocot *et al.* (2011) and Smith *et al.* (2011) employed a phylogenomic



**Figure 2.** Summary of relationships among major molluscan lineages recovered by **A**, Kocot *et al.* (2011), **B**, Vinther *et al.* (2011), **C**, Smith *et al.* (2011).

approach with data from fragments of many genes whereas Vinther *et al.* (2011) used PCR-amplified regions of seven genes in a target-gene approach. Although Kocot *et al.* and Smith *et al.* (2011) took a similar approach, it should be noted that these two studies used quite different methods to process transcriptome data, identify orthologous genes suitable for phylogenetic analysis, and curate final alignments prior to analysis. Therefore, these studies represent three largely independent assessments of molluscan phylogeny. In the following sections, results of these studies will be compared and contrasted and their implications for molluscan evolution will be discussed.

Taxon sampling was generally comparable across the three studies (Table 1). Of interest, the two phylogenomic studies have considerable overlap in taxon sampling as both studies built on available transcriptome and genome data, and employed similar taxa for which new data were collected. Both studies collected data from *Antalis* Adams and Adams, 1854, a gadilid scaphopod, *Solemya velum* Lamarck, 1818, a nuculid bivalve, *Octopus vulgaris* Cuvier, 1797, *Nautilus pompilius* Linnaeus 1758, and *Neomenia* Tullberg, 1875. Campbell and Lapointe (2009) suggested concatenation of closely related taxa to provide a more complete data matrix is superior

**Table 1.** Comparison of main data matrices analyzed by all three 2011 studies.

	Kocot <i>et al.</i>	Vinther <i>et al.</i>	Smith <i>et al.</i> small matrix	Smith <i>et al.</i> big matrix
No. genes	308	7	301	1,185
Alignment length (AAs)	84,614	2,026	50,930	216,402
No. taxa	49	51	46	46
No. molluscs	42	31 (30 genera)	35 (31 genera)	35 (31 genera)
Ave. gene occupancy	41%	85%	50%	40%
Matrix completeness	26%	81%	27%	21%
Placement of Scaphopoda	Sister to (Gastropoda + Bivalvia)	Sister to (Gastropoda + Bivalvia)	Sister to Gastropoda	Sister to Gastropoda

to using more taxa which are less well-sampled. As such, Kocot *et al.* (2011) combined data from closely related species (for example from two species of *Crassostrea* Sacco, 1897) into composite taxa in order to reduce the amount of missing data in the final alignments. All three studies sampled at least one representative of each major lineage of Mollusca except for Monoplacophora, which was sampled only by Smith *et al.* (2011).

Outgroup taxa sampled by Vinther *et al.* (2011) included two nemerteans, five annelids, four brachiopods, and nine ecdysozoans. Smith *et al.* (2011) tested two different sets of outgroups. The first, larger set included one ecdysozoan (*Drosophila*), three flatworms, three annelids, two brachiopods, and two nemerteans. The second, reduced set excluded the flatworms and *Drosophila*. Kocot *et al.* (2011) experimented with several different sets of outgroups. The largest set included one cnidarian, two entoprocts, one cycliophoran, two nemerteans, one brachiopod, and seven annelids. The cnidarian (*Nematostella*) was included in order to verify that the neomenioid data did not contain cnidarian (prey) contamination as has been shown to be a problem in studies of neomenioid ribosomal genes (Okusu and Giribet 2003, Meyer *et al.* 2010). Additional outgroup sets were also analyzed: excluding the distant outgroup *Nematostella*, excluding all outgroups except Annelida (which was placed sister to Mollusca with strong support in ML analyses), excluding all outgroups except Entoprocta + Cycliophora (which were placed sister to Mollusca with weak support in BI analyses), and excluding all outgroups except Entoprocta (because the cycliophoran *Symbion* was a long-branch taxon).

Gene sampling was more variable across the three studies and each of the phylogenomic studies analyzed more than one data matrix. Vinther *et al.* (2011) sequenced seven nuclear “housekeeping” genes and only included taxa sampled for at least five of these genes. Although this data matrix is the smallest of the three, it is commendably the most complete of the three (Table 1). Studies have suggested that substantial amounts of missing data in phylogenomic studies do not result in systematic biases as long as sufficient data are available

to place each taxon (Wiens 2003, Philippe *et al.* 2004, Wiens and Moen 2008). However, Roure *et al.* (2012) recently showed that large amounts of missing data may exacerbate systematic errors by reducing the number of species effectively available for the detection of multiple substitutions. More studies are needed to rigorously address this issue. Kocot *et al.* (2011) sampled a subset of 308 genes from the 1,032 genes in the HaMStR model organisms dataset (Ebersberger *et al.* 2009). These genes were selected on the basis of several criteria designed to exclude paralogous groups and groups sampled for fewer than ten molluscs. Specifically, each alignment was manually evaluated and ML trees were made for each gene to screen for paralogs. Several additional datasets were assembled by Kocot *et al.* (2011) including a 243-gene subset of the 308-gene matrix assembled using an additional filter to screen out potential paralogs. Additionally, matrices of the top 200 and 100 best-sampled genes and matrices of just ribosomal and just non-ribosomal proteins were also analyzed to examine the effects of missing data. Smith *et al.* (2011) assessed sequence orthology in a manner similar to that of Hejnol *et al.* (2009) by comparing all sequences from all taxa using all-versus-all BLASTP and clustering similar sequences using a Markov algorithm employed by the program MCL (<http://micans.org/mcl/>). ML trees were generated for clusters with at least four taxa and only sequences corresponding to terminal nodes in subtrees with no more than one sequence per taxon were retained.

#### *Aculifera*

Virtually all analyses of all three studies recovered the worm-like Neomeniomorpha (Solenogastres) and Chaetodermomorpha (Caudofoveata) in a monophyletic clade, Aplacophora, sister to Polyplacophora (chitons) with strong support. This clade, Aculifera, was originally hypothesized on the basis of shared characters of the nervous system, sclerites, and epidermal papillae (see Scheltema 1993 and references therein). This hypothesis is also supported by ciliary ultrastructure (Lundin and Schander 1999, 2001a,b, Nielsen *et al.* 2007, Lundin and Schander 2008, Lundin *et al.* 2009).

Additionally, the presence of dorsal, serially secreted calcareous structures may be a synapomorphy for Aculifera (Pruvot 1890, Sutton 2001, Sutton *et al.* 2001, 2004, Scheltema and Ivanov 2002, Henry *et al.* 2004, Nielsen *et al.* 2007; but see Okusu 2002, Todt and Wanninger 2010). Chitons have eight (rarely seven in presumably malformed individuals) dorsal shells or valves as adults. Aplacophorans lack shells and adult specimens of all species studied to date lack any sort of serial organization of the sclerites (Scheltema and Ivanov 2002). However, larvae of the chaetoderm *Chaetoderma* Lovén, 1844 (Chaetodermomorpha, Chaetodermatidae) exhibit seven serially arranged rows of glandular spiculoblasts (Nielsen *et al.* 2007). Additionally, sclerites of some (Pruvot 1890, Scheltema and Ivanov 2002) but not all (Thiele 1897, Baba 1938, Thompson 1960, Okusu 2002, Todt and Wanninger 2010) neomenioids exhibit some degree of serial arrangement during development. The postlarva of an unidentified species of neomenioid (probably belonging to the order Sterrofustia) described by Scheltema and Ivanov (2002) exhibited six dorsal groups of upright sclerites separated by seven areas of naked cuticle. Also, an earlier-stage larva of *Nematomenia banyulensis* Pruvot, 1890 (Neomeniomorpha, Dondersiidae) exhibited seven discrete rows of single, flat-lying sclerites arranged in a similar fashion except there did not appear to be any bare regions between rows. Additional studies of aplacophoran development and phylogeny are needed to address this issue further.

A molecular clock analysis by Vinther *et al.* (2011) indicates that Mollusca appeared in the early Cambrian and that crown-group aculiferans originated sometime in the Late Cambrian to the Early Ordovician. Specifically, an analysis using the CIR relaxed molecular clock model and their recovered topology (placing Cephalopoda sister to Aculifera; see below) estimated the most likely time of origin for crown aculiferans (extant chitons and aplacophorans) to be 488 million years ago (mya; right around the Cambrian-Ordovician interface). However, the oldest-known chitons occur in Upper Cambrian rocks and thus are older than the estimated age of the crown-group aculiferans. The oldest known chiton, *Chelodes whitehousei* Runnegar *et al.* 1979, is known from Upper Cambrian rocks of the Ninmaroo Formation (Datsonian) of Queensland, Australia and numerous other Upper Cambrian chitons are known from North America with an especially diverse fauna described from the Upper Cambrian Eminence Dolomite of east-central Missouri (see Pojeta *et al.* 2010 and references therein). Crown-group (extant) chitons were estimated to have originated 357 mya (Devonian) and Chitonida was estimated to have originated 272 mya (Permian) by Vinther *et al.* (2011). Notably, these estimates are not significantly affected when Cephalopoda was excluded. In light of the recovered topology, estimated divergence times, and the fossil record of chitons, Vinther *et al.* (2011) rather convincingly

argued that aplacophorans are derived from a chiton-like ancestor. Under this scenario, Upper Cambrian chitons such as *Chelodes* Davidson and King, 1874 may be interpreted as representing the plesiomorphic state of Aculifera. Also, three Paleozoic taxa, *Acaenoplax hayae* Sutton *et al.*, 2001, *Phthipodochiton* (formerly '*Helminthochiton*') *thraivensis* Sutton and Sigwart, 2012, and *Kulindroplax perissokomos* Sutton *et al.*, 2012 possess morphological features intermediate between chitons and extant aplacophorans and are interpreted to represent stem-group aplacophorans under this scenario (Sutton *et al.* 2001, Sutton *et al.* 2004, Sigwart and Sutton 2007, Sutton and Sigwart 2012). A recent cladistic morphological analysis including these and other fossil taxa as well as representatives of the extant aculiferan lineages also supports a chiton-like ancestor for extant aplacophorans (Sutton *et al.* 2012). Scheltema (1993) viewed aplacophorans as pedomorphic, retaining juvenile characters of chitons as adults. Some of the most convincing pieces of evidence in support of this hypothesis are the aplacophoran distichous radula and fusion of the gonads to the pericardium; character states that reflect the early ontogeny of chitons. Additionally, neomenioids have an anterior pedal gland, a structure found in chitons only as larvae (Scheltema 1993, Scheltema *et al.* 2003).

Aculiferan monophyly has important implications for studies of early molluscan evolution. Previously, a leading hypothesis of molluscan phylogeny (Haszprunar 2000, Haszprunar *et al.* 2008) placed neomenioid aplacophorans basal-most thus rendering "Aplacophora" as a basal, paraphyletic grade. Under this scenario, the last common ancestor of Mollusca would be predicted to be a neomenioid aplacophoran-like animal: a small, worm-like, carnivore with a distichous radula, a foot without intrinsic musculature, a simple midgut, and a dorsal mantle that secreted aragonitic sclerites but not shells (Haszprunar *et al.* 2008). In light of strong support for Aculifera, many neomenioid characters are most likely synapomorphies (*e.g.*, non-muscular foot, simple midgut, primarily distichous radula without subradular membrane). However, because the relationships within Aplacophora are poorly understood (reviewed by Todt *et al.* 2008), the phylogenetic framework needed to understand the evolutionary polarity of certain aplacophoran morphological characters – and therefore those of Aculifera and even Mollusca as a whole – has been lacking.

Ancestral state reconstruction based on the topology of Kocot *et al.* (2011) suggests that a ventral muscular foot, dorsal cuticularized mantle, mantle cavity containing ctenidia, and regionalized gut are plesiomorphic for Mollusca. However, for some characters, results of the ancestral state reconstruction analyses by Kocot *et al.* (2011) were ambiguous or in contrast with other studies. For example, ancestral state reconstruction suggested that the plesiomorphic condition of

the molluscan radula is broad and rasping with multiple teeth per row (polystichous) attached to a flexible radular membrane supported by muscular and cartilage-like bolsters as in chitons and most conchiferans (see Scheltema *et al.* 2003 and references therein). In contrast, two putative stem-group molluscs, *Odontogriphus* Caron *et al.*, 2006 and *Wiwaxia* Conway Morris 1985 have been interpreted to have had a narrow, distichous radula like that found in most aplacophorans (Caron *et al.* 2006, Scheltema *et al.* 2003) suggesting that a distichous radula is plesiomorphic for Mollusca. Under this scenario, the results of Kocot *et al.* (2011) would suggest that chitons and conchiferans appear to have independently evolved broad, rasping radulae while most aplacophorans have retained the plesiomorphic state. However, recently Smith (2012) examined the feeding apparatuses of over 300 specimens of *Odontogriphus* and *Wiwaxia* using backscatter electron microscopy and presented a dramatically different reconstruction of the radulae of these taxa. Smith found that *Odontogriphus* and *Wiwaxia* have two or three rows of teeth each with a single medial tooth flanked on either side by multiple, separate shoehorn-shaped teeth. Thus, *Odontogriphus* and *Wiwaxia* possessed a polystichous radula more like that of chitons and conchiferans than that of most aplacophorans.

The plesiomorphic state of the molluscan scleritome (shells and sclerites) also remains ambiguous. Kocot *et al.* (2011) and Smith *et al.* (2011) placed Aculifera sister to Conchifera. However, Vinther *et al.* (2011) recovered Aculifera sister to Cephalopoda thus rendering Conchifera paraphyletic. Although this topology is at odds with most traditional morphological hypotheses, it has been recovered in other studies with limited taxon sampling for Mollusca (Dunn *et al.* 2008, Lieb and Todt 2008, Meyer *et al.* 2011). If Conchifera is indeed paraphyletic with cephalopods sharing a more recent common ancestor with aculiferans than other conchiferans, this suggests that the shelled, conchiferan condition is plesiomorphic for Mollusca. However, Vinther *et al.* (2011) noted that the recovery of conchiferan paraphyly may be the result of an incorrectly placed root for Mollusca and therefore performed several tests to determine if this was the case. Interestingly, the observed placement of cephalopods was robust to both sequential exclusion of long-branched, unstable, and compositionally heterogeneous taxa and phylogenetic signal-dissection via slow-fast analysis. Despite this, because both Smith *et al.* (2011) and Kocot *et al.* (2011) recovered a monophyletic Conchifera, which is supported by several apparent synapomorphies (see below), the available data appear to favor conchiferan monophyly. Unfortunately, an aculiferan-conchiferan dichotomy makes it difficult to infer the plesiomorphic state of the molluscan scleritome. Although aculiferan sclerites, chiton valves, and conchiferan shells are all extracellular calcareous secretions of the mantle, structural and developmental differences suggest that these structures

are not strictly homologous (Haas 1981, Scheltema 1993, Furuhashi *et al.* 2009). Haas (1981) argued that secretion of aplacophoran and chiton sclerites, despite some differences in the mantle epithelium, takes place in nearly the same way. Aplacophoran sclerites studied to date are secreted by one basal cell whereas chiton sclerites may be secreted by one basal cell (microspines) or a proliferation of cells derived from the basal cell (megaspines). This suggests homology of aplacophoran and chiton sclerites. On the other hand, the lack of a true periostracum, periostracal groove, and a differentiated shell-secreting epithelium (shell gland) in chitons clearly distinguishes their shell structure and formation from that of the conchiferans. Therefore, it is puzzling that Haas (1981) argued in favor of the Testaria hypothesis and stated: "It is out of the question that the aplacophoran classes Solenogastres and Caudofoveata are phylogenetically closely related to the [poly]placophorans. Considering hardpart formation, such a relationship is not possible." Comparative studies examining the formation of sclerites and shell plates in aculiferans are desperately needed to improve understanding of the homology of these structures.

Developmentally speaking, chiton shells are secreted by cells that arise from postrochal (2d) cells (Heath 1899, Henry *et al.* 2004). The situation is similar in conchiferans (Lillie 1895, Conklin 1897) although other micromere lineages (2a, 2b, 2c, and sometimes 3c) also contribute in forming the conchiferan shell gland (Damen and Dictus 1994, Render 1997). Interestingly, chiton sclerite-secreting cells arise from postrochal (2a, 2c, 3c, and 3d) as well as pretrochal cells (1a and 1d) suggesting that chiton sclerites are not strictly homologous to chiton or conchiferan shells although the genetic mechanisms involved in their production and patterning on the body may be (Scheltema and Ivanov 2002). No cell lineage or developmental gene expression studies have been conducted in aplacophorans to date.

#### *Placement of Cephalopoda and Monoplacophora*

Cephalopods have long been thought to be closely related to gastropods on the basis of several morphological characters, most of which are related to the nervous system. Specifically, both cephalopods and gastropods possess a well-developed, free head with cephalic eyes and a visceral loop inwards of the dorsoventral musculature. Also, both groups have a morphologically posterior, terminal mantle cavity and a similar antagonistic, three-dimensional muscle-on-muscle system (Salvini-Plawen 1985, Trueman and Brown 1985, Runnegar 1996, Salvini-Plawen and Steiner 1996, Haszprunar *et al.* 2008). Surprisingly, none of the recent studies of molluscan phylogeny found any support for a close relationship between gastropods and cephalopods but instead placed gastropods in a clade with bivalves and/or scaphopods. Therefore, features uniquely shared by gastropods and cephalopods

must be reinterpreted as symplesiomorphies or convergences. Notably, the relatively complex brains of gastropods and cephalopods have been suggested to have evolved independently (Moroz 2009, 2012).

As discussed above, Vinther *et al.* recovered Cephalopoda sister to Aculifera but Kocot *et al.* and Smith *et al.* both recovered a monophyletic Conchifera in most analyses. Kocot *et al.* (2011), who did not sample Monoplacophora, placed Cephalopoda sister to a clade including Gastropoda, Bivalvia, and Scaphopoda. Conchiferan relationships recovered by Smith *et al.* (2011) were similar, but one key finding by Smith *et al.* (2011) was placement of Cephalopoda and Monoplacophora as sister taxa with strong support in most analyses. The topology of Smith *et al.* (2011) is in contrast to previous molecular studies suggesting that Monoplacophora and Polyplacophora form a clade, Serialia (Giribet *et al.* 2006, Wilson *et al.* 2010). Examination of site likelihoods by Smith *et al.* (2011) revealed that many more sites in their dataset are consistent with the recovered topology than Serialia. Recovery of conchiferan monophyly is perhaps no surprise to morphologists who have long viewed the uni- and bivalved molluscs as a natural group. As noted above, several morphological synapomorphies support Conchifera including shell(s) secreted by a shell gland, jaws, statocysts, the subrectal commisure, and cerebrally-innervated tentacles (reviewed by Salvini-Plawen 1980, Haszprunar 2000).

Perhaps more surprising to at least some morphologists is the recovery of a close relationship of cephalopods and tryblid monoplacophorans. Although the slow-moving, benthic, deep-sea monoplacophorans are at least in general appearance dramatically different from the highly active cephalopods, the fossil record (Yochelson *et al.* 1973, Chen and Teichert 1983, Webers and Yochelson 1989, Kröger and Mutvei 2005; reviewed by Kröger *et al.* 2011) and morphological characters shared by monoplacophorans and some cephalopods (Holland 1987, Runnegar 1996, Shigeno *et al.* 2010) appear to be at least consistent with the existence of a clade including monoplacophorans and cephalopods. However, it is generally accepted that the Paleozoic taxa ascribed to “Monoplacophora” do not represent a monophyletic taxon. The oldest *bona fide* cephalopod fossil is the middle Late Cambrian *Plectronoceras cambria* Walcott, 1905. *Plectronoceras cambria* was characterized by a dorsal, chambered shell and multiple paired serially arranged muscles, which left attachment scars reminiscent of those of tryblid and some other monoplacophorans. Thus, cephalopods have been suggested to be derived from chambered monoplacophoran-like taxa with either the tall, conical *Knighthoconus* Yochelson *et al.*, 1973 or the more slender *Tannuella* Rozanov *et al.*, 1969 being the most likely known candidates. However, the relationship of these fossil taxa to extant (tryblid) monoplacophorans is unclear (reviewed by Kröger *et al.* 2011).

Notably, Salvini-Plawen (1980) drew Monoplacophora and Cephalopoda (“Siphonopoda”) as sister taxa in his “Diagram of the phylogenetic radiation of the Mollusca” (Fig. 5) although other figures and the text of his paper generally argued for a closer relationship of Monoplacophora and Gastropoda among the extant molluscan taxa.

#### *Relationships among Gastropoda, Bivalvia, and Scaphopoda*

All three studies recovered a clade including Gastropoda, Bivalvia, and Scaphopoda. One potential synapomorphy for this grouping is a relatively thick, multilayered shell (Runnegar 1996, Smith *et al.* 2011) although scaphopods commonly only have two shell layers (Reynolds and Okusu 1999). Interestingly, the relationships among Gastropoda, Bivalvia, and Scaphopoda are not consistent across studies. Most analyses by Kocot *et al.* (2011) and Vinther *et al.* (2011) placed gastropods and bivalves as sister taxa with strong support whereas Smith *et al.* (2011) recovered gastropods and scaphopods as sister taxa. In all three studies, the position of Scaphopoda tends to be one of the most poorly-supported nodes suggesting that difficulties in reliably placing this group are likely responsible for the uncertainty in this region of the tree. Indeed, the two scaphopods sampled by Kocot *et al.* (2011) exhibit the two lowest leaf stability scores of any sampled taxa by far. Briefly, leaf stability scores are a measure of the consistency of a taxon’s position relative to other taxa among bootstrap pseudoreplicates. Taxa with low leaf stability “bounce around” among bootstrap replicates and thus tend to cause overall low support for that region of the tree (Dunn *et al.* 2008). Additionally, Scaphopoda was one of or the most poorly-sampled major molluscan lineage in all three studies. Additional data from scaphopods may help improve resolution in this region of the tree.

The widely held Diasoma or Loboconcha hypothesis, which allies Scaphopoda and Bivalvia (along with the fossil taxon Rostroconcha), was not recovered by any of the three most recent molecular studies. A close relationship between these two taxa was first suggested on the basis of similarities of the weakly-developed head, pedal morphology and formation of mantle and shell. Subsequent paleontological studies led to the suggestion that Rostroconchia, a fossil group of laterally-compressed, bivalve-like molluscs, represents the stem group of Bivalvia and Scaphopoda (Runnegar and Pojeta 1974, Pojeta and Runnegar 1976, Pojeta 1985). This hypothesis has been widely cited (see Steiner and Dreyer 2003 and references therein), however, discrepancies in the development of rostroconch and scaphopod body axes (Steiner 1992) and in the protoconch formation of scaphopods and bivalves have been noted (Wanninger and Haszprunar 2001). Therefore, at least some characters shared by scaphopods and bivalves interpreted as synapomorphies for Diasoma may instead represent convergent adaptations to a burrowing

lifestyle. Alternatively, Scaphopoda has been suggested to be closely related to Gastropoda on the basis of similarities of their head tentacles, prominent dorsoventral body axes, and the occurrence of shell slits (e.g., Plate 1892) but workers espousing this viewpoint usually also placed these taxa close to cephalopods (see Steiner and Dreyer 2003 and references therein), which does not appear to be the case.

A Gastropoda-Bivalvia relationship has received little consideration in the literature. However, it has been recovered in previous studies with limited taxon sampling for Mollusca (Dunn *et al.* 2008, Meyer *et al.* 2011). Similarities in gastropod and bivalve veliger larvae have long been recognized – both have unique larval retractor muscles and a velum muscle ring, characters absent from all other conchiferans (although monoplacophoran larvae have not been studied and cephalopods have highly modified larvae; Waininger and Haszprunar 2002). Another potential synapomorphy is loss of the anterior ciliary rootlet in locomotory cilia (Lundin *et al.* 2009). Kocot *et al.* (2011) noted that gastropods and bivalves are by far the most successful molluscs in terms of number of species and conservatively estimated that most (> 95%) molluscs fall within this clade. Because of a lack of a clear morphological synapomorphy that unambiguously distinguishes gastropods and bivalves from all other molluscs and is amenable to a scientific name, they proposed the name Pleistomollusca (*pleistos* from Greek for “most”) for this hypothesis to include the last common ancestor of Gastropoda and Bivalvia and all descendents.

#### *Relationships within major lineages*

In addition to utility for deep phylogenetics (e.g., the relationships among major molluscan lineages), nuclear protein-coding genes appear to have great potential to help to resolve unanswered questions about relationships within major molluscan lineages (e.g., Kocot and Halanych 2009, Aktipis and Giribet 2010). None of the three most recent studies sampled enough aplacophorans, chitons, or scaphopods to discuss relationships within these groups. Likewise, taxon sampling for Cephalopoda was limited in all three studies although the traditional placement of *Nautilus* sister to Coleoidea with Octopodiformes/Vampyropoda sister to Decapodiformes/Decabrachia was recovered by all.

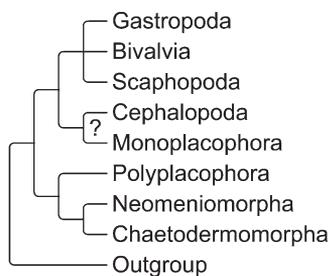
Within Bivalvia, most analyses by Kocot *et al.* (2011) and Smith *et al.* (2011) recovered Protobranchia monophyletic and sister to all other bivalves but Vinther *et al.* (2011) placed the single sampled protobranch *Nucula* Lamarck, 1799 sister to the arcoid *Anadara* Gray, 1847 with strong support. Smith *et al.* (2011) sampled all three lineages of protobranch bivalves and recovered Protobranchia monophyletic with Solemyoidea sister to a clade of Nuculoidea + Nuculanoida, inconsistent with the Opponobranchia hypothesis that places Nuculoidea sister to Solemyoidea (Giribet 2008). Kocot *et al.*

(2011) and Smith *et al.* (2011) both recovered Pteriomorpha monophyletic but relationships within the group were variable across analyses. Interestingly, Kocot *et al.* (2011) place the unionid mussel *Hyriopsis* Conrad, 1853 sister to Veneroidea + Anomalodesmata with strong support in all analyses but Smith *et al.* place *Hyriopsis* sister to Veneroidea + Pteriomorpha with strong support in all analyses.

Relationships among major clades within Gastropoda were also somewhat variable and inconsistent across studies. Vinther *et al.* and most analyses by Smith *et al.* (2011) placed the patellogastropod *Lottia* Gray, 1833 sister to Vetigastropoda consistent with the Archaeogastropoda hypothesis (Haszprunar 1988) but most analyses by Kocot *et al.* (2011) placed *Lottia* sister to all other gastropods consistent with the Patellogastropoda-Orthogastropoda hypothesis (Ponder and Lindberg 1997). Kocot *et al.* (2011) sampled only one vetigastropod, *Haliotis* Linnaeus, 1758, but they also sampled the neritimorph *Theodoxus* Montfort, 1810. Most analyses place *Haliotis* and *Theodoxus* as sister taxa or as part of a polytomy with Caenogastropoda + Euthyneura but support for any relationships among these taxa was generally weak. All analyses of all three studies recover Caenogastropoda and Euthyneura as sister taxa with strong support. Kocot *et al.* (2011) and Vinther *et al.* (2011) both sampled the littorinomorph caenogastropods *Littorina* Férussac, 1822, *Strombus* Linnaeus 1758, and *Crepidula* Lamarck 1799 and agreed on the relationships among these taxa: *Littorina* was placed sister to a clade including *Strombus* and *Crepidula*. However, placement of Neogastropoda differed between these studies. Vinther *et al.* recovered Littorinomorpha monophyletic and sister to *Neptunea* Röding, 1798 + *Buccinum* Linnaeus, 1758 (both Neogastropoda, Buccinidae) with strong support while Kocot *et al.* (2011) recovered Littorinomorpha paraphyletic with *Ilyanassa* Stimpson, 1865 (Neogastropoda) sister to *Crepidula* with strong support in all analyses. Within Euthyneura, Kocot *et al.* (2011) had the broadest taxon sampling. Opisthobranchia was paraphyletic with respect to Pulmonata in agreement with recent studies showing that the “sea slugs” do not form a natural group (Wägele *et al.* 2008, Schrödl *et al.* 2011). Notably Anaspidea was placed sister to Pulmonata by Kocot *et al.* This result was echoed by Vinther *et al.* who placed *Aplysia* Linnaeus, 1767 sister to *Biomphalaria* Preston, 1910 to the exclusion of *Coryphella* Gray 1850. The monophyly of Nudipleura (Nudibranchia + Pleurobranchioidea) was sensitive to analytical method: Bayesian inference tended to recover Nudipleura monophyletic whereas maximum likelihood tended to recover this clade paraphyletic with *Pleurobranchaea* Bergh, 1897 sister to Anaspidea + Pulmonata. As noted by Smith *et al.* (2011), with as many as 100,000 living gastropod species, the sampling of gastropods in all three studies does not even begin to cover the diversity of this speciose and successful group.

## CONCLUSIONS AND FUTURE DIRECTIONS

The three most recent studies addressing deep molluscan phylogeny have demonstrated that molecular data in the form of nuclear protein coding gene sequences are useful for improving understanding of evolutionary relationships both among and within the major lineages of Mollusca. A consensus tree depicting the current understanding of deep molluscan phylogeny as inferred by these studies is presented in Fig. 3. Aplacophora is a monophyletic clade sister to Polyplacophora. Together Aplacophora and Polyplacophora constitute a clade called Aculifera, a group estimated to be around 488 million years old (Ordovician). In light of these results, the worm-like aplacophorans have been suggested to be derived from a chiton-like ancestor (Vinther *et al.* 2011), a hypothesis that is at least consistent with the fossil record. Comparative studies examining the developmental timing of features suggested to be pedomorphic in aplacophorans relative to the adult condition of chitons will undoubtedly help provide insight into this issue. In this vein, virtually all aspects of the biology of Aplacophora warrant further study (See paper by Todt in this issue). Although aplacophorans are both common and relatively diverse, in the last twenty years, only around ten workers have performed descriptive work on the group. Approximately 400 species are named but many more are known and await formal description (Glaubrecht *et al.* 2005, Todt unpublished data). Also, the aplacophoran fauna of many regions (*e.g.*, Australia) has received virtually no attention and behavioral and physiological studies on the group are practically non-existent. Currently the phylogeny of both aplacophoran clades is poorly understood although work is underway (Mikkelsen *et al.* unpublished data, Kocot *et al.* unpublished data). Understanding the evolutionary relationships within Aplacophora is important because a well-resolved phylogeny of this group would greatly inform studies



**Figure 3.** Consensus tree of hypothesized evolutionary relationships among major molluscan lineages based on Kocot *et al.* (2011), Vinther *et al.* (2011), and Smith *et al.* (2011). Cephalopoda is placed according to the results of Kocot *et al.* and Smith *et al.* The Cephalopoda + Monoplacophora node is labeled with a question mark because this surprising result has been recovered by only one study.

addressing the evolution of several key molluscan characters for which the plesiomorphic state of Aplacophora is unknown. Comparative studies of representatives of Aplacophora and putative relatives of Mollusca (*e.g.*, Entoprocta) will likely prove equally interesting as aplacophorans (especially neomenioids) possess some morphological features strikingly similar to those of larval entoprocts.

Within Conchifera, Cephalopoda and Gastropoda are not sister taxa as previously thought. This finding will undoubtedly have important implications for workers in the field of Neurobiology who have long used gastropods and cephalopods as models for studies of learning and memory. The presence of relatively complex nervous systems in both gastropods and cephalopods suggests that either this condition evolved independently in both lineages or has been secondarily simplified in the headless bivalves and, to a lesser extent, in scaphopods and monoplacophorans. As few studies have examined the nervous system of Scaphopoda (but see Wanninger and Haszprunar 2003), work on this group could prove interesting and important for understanding the evolution of the conchiferan nervous system. Instead of being closely related to Gastropoda, Cephalopoda appears to be the sister taxon of Monoplacophora (Tryblidia) although more sequence data from *Laevipilina antarctica* plus additional species would help strengthen confidence in this result. Like the aplacophorans, more studies of virtually all aspects of the biology of the difficult-to-collect monoplacophorans would be of great interest to those interested in understanding deep molluscan phylogeny and evolution.

Scaphopoda has proven to be a difficult group to place. Considering that transcriptome data are available from only a handful of representatives of this group, it is likely that additional data from scaphopods as well as basal gastropods and bivalves will help improve resolution among these three taxa. However, another potential source of difficulty in placing Scaphopoda may stem from a partial genome duplication. The results of PCRs with primers for nuclear protein-coding genes performed on cDNA indicate duplications and divergence of at least three genes known to be single-copy in most other metazoan genomes (Vinther, pers. comm.). A partial genome duplication, which results in two copies of a gene with subsequent independent evolutionary histories, can complicate phylogenetic inference (*e.g.*, Dehal and Boore 2005, Sanderson and McMahon 2007). The genome of the annelid *Helobdella robusta* appears to have undergone a partial genome duplication in which many, but not all, nuclear protein-coding genes have been duplicated (Cho *et al.* 2010, Veenstra 2011). In single-gene phylogenies including these sequences, one or both copies (inparalogs) often appear as long branches and/or do not cluster with sequences from other annelids, possibly suggesting subfunctionalization and an increased evolutionary rate in one or both copies.

However, the branch lengths for Scaphopoda in the recent studies are not exceptionally long. Also, the completely sequenced genomes of the gastropods *Lottia gigantea* Sowerby, 1834 and *Aplysia californica* Cooper, 1863 do not exhibit evidence of such a substantial partial genome duplication.

As DNA sequencing technologies continue to decrease in cost while simultaneously improving in both read length and data quality, molluscs and other related lophotrochozoans will hopefully begin to catch up with ecdysozoans (e.g., *Drosophila melanogaster* and *Caenorhabditis elegans*) in the field of genomics. Genome-level data for molluscs will undoubtedly help improve our understanding of molluscan evolutionary relationships while allowing for detection of phenomena such as partial genome duplications which can mislead phylogenetic analyses. Moreover, comparative genomic studies armed with a well-resolved phylogeny of Mollusca will provide insight into the genetics and molecular mechanisms involved in all aspects of molluscan biology. Currently, genome projects are underway for several conchiferan molluscs and hopefully Aculifera, the other major clade of Mollusca, will soon begin to receive genome-scale attention as well.

Phylogenomics has substantially advanced our understanding of the relationships among the major lineages of Mollusca and will likely continue to do so. However, an independent source of molecular characters useful for formulating and testing phylogenetic hypotheses is desirable (Rokas and Holland 2000). Rare genomic changes, such as indels, retroposon integrations, signature sequences, gene order differences, gene duplications, and codon code differences are one such source of molecular characters. Likewise, non-coding ultraconserved genomic elements (UCEs) provide another source of genomic data useful for phylogeny reconstruction (Faircloth *et al.* 2012). Studies of rare genomic changes and UCEs will likely be important in continuing to resolve and validate our current understanding of molluscan phylogeny in the future.

For now, ongoing work in several labs employing next-generation sequencing as well as more traditional morphological and developmental studies will undoubtedly continue to improve understanding of molluscan evolution while simultaneously raising new questions about this fascinating group of animals.

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#### LITERATURE CITED

- Aguinaldo, A. M., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff, and J. A. Lake. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* **387**: 489–493.
- Aktipis, S. W. and G. Giribet. 2010. A phylogeny of Vetigastropoda and other "archaeogastropods": Re-organizing old gastropod clades. *Invertebrate Biology* **129**: 220–240. doi: 10.1111/j.1744-7410.2010.00198.x.
- Anderson, F. E., A. J. Córdoba, and M. Thollessen. 2004. Bilaterian phylogeny based on analyses of a region of the sodium–potassium ATPase Beta-subunit gene. *Journal of Molecular Evolution* **58**: 252–268.
- Andrew, D. R. 2011. A new view of insect–crustacean relationships II. Inferences from expressed sequence tags and comparisons with neural cladistics. *Arthropod Structure & Development* **40**: 289–302. doi: 10.1016/j.asd.2011.02.001.
- Baba, K. 1938. The later development of a solenogastre, *Epimania verrucosa* (Nierstraz). *Journal of the Department of Agriculture of Fukuoka University* **6**: 21–40.
- Bourlat, S. J., T. Juliusdottir, C. J. Lowe, R. Freeman, J. Aronowicz, M. Kirschner, E. S. Lander, M. Thorndyke, H. Nakano, A. B. Kohn, A. Heyland, L. L. Moroz, R. R. Copley, and M. J. Telford. 2006. Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida. *Nature* **444**: 85–88. doi: 10.1038/nature05241.
- Campbell, V. and F.-J. Lapointe. 2009. The use and validity of composite taxa in phylogenetic analysis. *Systematic Biology* **58**: 560–572. doi: 10.1093/sysbio/syp056.
- Caron, J. B., A. Scheltema, C. Schander, and D. Rudkin. 2006. A soft-bodied mollusc with radula from the Middle Cambrian Burgess Shale. *Nature* **442**: 159–163.
- Chen, J. and C. Teichert. 1983. Cambrian Cephalopoda of China. *Paleontographica A* **181**: 1–102.
- Cho, S.-J., Y. Vallès, V. C. Giani, E. C. Seaver, and D. A. Weisblat. 2010. Evolutionary dynamics of the wnt gene family: A lophotrochozoan perspective. *Molecular Biology and Evolution* **27**: 1645–1658. doi: 10.1093/molbev/msq052.
- Conklin, E. G. 1897. The embryology of *Crepidula*. *Journal of Morphology* **13**: 1–226.
- Damen, P. and W. J. A. G. Dictus. 1994. Cell lineage of the prototroch of *Patella vulgata* (Gastropoda, Mollusca). *Developmental Biology* **162**: 364–383. doi: 10.1006/dbio.1994.1094.
- Dehal, P. and J. L. Boore. 2005. Two rounds of whole genome duplication in the ancestral vertebrate. *PLoS Biology* **3**: e314. doi: 10.1371/journal.pbio.0030314.

- Donovan, S. K., M. D. Sutton, and J. D. Sigwart. 2010. Crinoids for lunch? An unexpected biotic interaction from the Upper Ordovician of Scotland. *Geology* **38**: 935.
- Dunn, C. W., A. Hejnol, D. Q. Matus, K. Pang, W. E. Browne, S. A. Smith, E. Seaver, G. W. Rouse, M. Obst, G. D. Edgecombe, Martin V. Sørensen, S. H. D. Haddock, A. Schmidt-Rhaesa, A. Okusu, R. M. Kristensen, W. C. Wheeler, M. Q. Martindale, and G. Giribet. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* **452**: 745–749.
- Ebersberger, I., S. Strauss, and A. Von Haeseler. 2009. HaMStR: Profile hidden Markov model based search for orthologs in ESTs. *BMC Evolutionary Biology* **9**: 157. doi: 10.1186/1471-2148-9-157.
- Faircloth, B. C., J. E. McCormack, N. G. Crawford, M. G. Harvey, R. T. Brumfield, and T. C. Glenn. 2012. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology*. doi: 10.1093/sysbio/sys004.
- Fedonkin, M. A., A. Simonetta, and A. Y. Ivantsov. 2007. New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): Palaeoecological and evolutionary implications. *Geological Society, London, Special Publications* **286**: 157–179. doi: 10.1144/SP286.12.
- Furuhashi, T., C. Schwarzinger, I. Miksik, M. Smrz, and A. Beran. 2009. Molluscan shell evolution with review of shell calcification hypothesis. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* **154**: 351–371.
- Giribet, G. 2008. Bivalvia. In: W. F. Ponder and D. R. Lindberg, eds., *Phylogeny and Evolution of the Mollusca*. University of California Press, Berkeley and Los Angeles, California. Pp. 105–141.
- Giribet, G., A. Okusu, A. R. Lindgren, S. W. Huff, M. Schrödl, and M. K. Nishiguchi. 2006. Evidence for a clade composed of molluscs with serially repeated structures: Monoplacophorans are related to chitons. *Proceedings of the National Academy of Sciences* **103**: 7723–7728.
- Glaubrecht, M., L. Maitas, and L. v. Salvini-Plawen. 2005. Aplacophoran Mollusca in the Natural History Museum Berlin. An annotated catalogue of Thiele's type specimens, with a brief review of "Aplacophora" classification. *Zoosystematics and Evolution* **81**: 145–166. doi: 10.1002/mmnz.200510009.
- Haas, W. 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia* **21**: 403–418.
- Halanych, K. M., J. D. Bacheller, A. M. Aguinaldo, S. M. Liva, D. M. Hillis, and J. A. Lake. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science* **267**: 1641–1641.
- Haszprunar, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura (Mollusca). *Journal of Molluscan Studies* **54**: 367–441.
- Haszprunar, G. 2000. Is the Aplacophora monophyletic? A cladistic point of view. *American Malacological Bulletin* **15**: 115–130.
- Haszprunar, G., C. Schander, and K. M. Halanych. 2008. Relationships of higher molluscan taxa. In: W. F. Ponder and D. R. Lindberg eds., *Phylogeny and Evolution of the Mollusca*. University of California Press, Berkeley and Los Angeles, California. Pp. 19–32.
- Haszprunar, G. and A. Wanninger. 2008. On the fine structure of the creeping larva of *Loxosomella murmanica*: Additional evidence for a clade of Kamptozoa (Entoprocta) and Mollusca. *Acta Zoologica* **89**: 137–148. doi: 10.1111/j.1463-6395.2007.00301.x.
- Heath, H. 1899. Development of *Ischnochiton*. *Zoologische Jahrbuecher Abteilung fuer Anatomie und Ontogenie der Tiere* **12**: 567–656. [In German]
- Hejnol, A., M. Obst, A. Stamatakis, M. Ott, G. W. Rouse, G. D. Edgecombe, P. Martinez, J. Bagunà, X. Bailly, U. Jondelius, M. Wiens, W. E. G. Müller, E. Seaver, W. C. Wheeler, M. Q. Martindale, G. Giribet, and Casey W. Dunn. 2009. Assessing the root of bilaterian animals with scalable phylogenomic methods. *Proceedings of the Royal Society B: Biological Sciences* **276**: 4261–4270.
- Helmkamp, M., I. Bruchhaus, and B. Hausdorf. 2008. Multigene analysis of lophophorate and chaetognath phylogenetic relationships. *Molecular Phylogenetics and Evolution* **46**: 206–214. doi: 10.1016/j.ympev.2007.09.004.
- Henry, J. Q., A. Okusu, and M. Q. Martindale. 2004. The cell lineage of the polyplacophoran, *Chaetopleura apiculata*: Variation in the spiralian program and implications for molluscan evolution. *Developmental Biology* **272**: 145–160.
- Holland, C. H. 1987. The nautiloid cephalopods: A strange success. *Journal of the Geological Society* **144**: 1–15. doi: 10.1144/gsjgs.144.1.0001.
- Ivanov, D. L. 1996. Origin of Aculifera and problems of monophyly of higher taxa in molluscs. In: J. D. Taylor, ed., *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford. Pp. 59–65.
- Ivantsov, A. Y. 2009. New reconstruction of *Kimberella*, problematic Vendian metazoan. *Paleontological Journal* **43**: 601–611. doi: 10.1134/S003103010906001X.
- Ivantsov, A. Y. 2010. Paleontological evidence for the supposed precambrian occurrence of mollusks. *Paleontological Journal* **44**: 1552–1559. doi: 10.1134/S0031030110120105.
- Kocot, K. M., J. T. Cannon, C. Todt, M. R. Citarella, A. B. Kohn, A. Meyer, S. R. Santos, C. Schander, L. L. Moroz, B. Lieb, and K. M. Halanych. 2011. Phylogenomics reveals deep molluscan relationships. *Nature* **477**: 452–456. doi: 10.1038/nature10382.
- Kocot, K. M. and K. M. Halanych. 2009. Investigation of molluscan phylogeny using nuclear protein-coding genes. *The Malacologist* **53**: 18–20.
- Kröger, B. and H. Mutvei. 2005. Nautiloids with multiple paired muscle scars from Lower–middle Ordovician of Baltoscandia. *Palaentology* **48**: 781–791. doi: 10.1111/j.1475-4983.2005.00478.x.
- Kröger, B., J. Vinther, and D. Fuchs. 2011. Cephalopod origin and evolution: A congruent picture emerging from fossils, development and molecules. *BioEssays* **33**: 602–613. doi: 10.1002/bies.201100001.
- Lieb, B. and C. Todt. 2008. Hemocyanin in mollusks—A molecular survey and new data on hemocyanin genes in Solenogastres and Caudofoveata. *Molecular Phylogenetics and Evolution* **49**: 382–385.
- Lillie, F. R. 1895. The development of the Unionidae. *Journal of Morphology* **10**: 1–100.

- Lundin, K. and C. Schander. 1999. Ultrastructure of gill cilia and ciliary rootlets of *Chaetoderma nitidulum* Lovén 1844 (Mollusca, Chaetodermomorpha). *Acta Zoologica* **80**: 185–191.
- Lundin, K. and C. Schander. 2001a. Ciliary ultrastructure of proto-branches (Mollusca, Bivalvia). *Invertebrate Biology* **120**: 350–357.
- Lundin, K. and C. Schander. 2001b. Ciliary ultrastructure of neomeniomorphs (Mollusca, Neomeniomorpha = Solenogastres). *Invertebrate Biology* **120**: 342–349.
- Lundin, K. and C. Schander. 2008. Ciliary ultrastructure of polyplacophorans (Mollusca, Amphineura, Polyplacophora). *Journal of Submicroscopic Cytology and Pathology* **33**: 93–98.
- Lundin, K., C. Schander, and C. Todt. 2009. Ultrastructure of epidermal cilia and ciliary rootlets in Scaphopoda. *Journal of Molluscan Studies* **75**: 69–73.
- Matus, D. Q., R. R. Copley, C. W. Dunn, A. Hejnol, H. Eccleston, K. M. Halanych, M. Q. Martindale, and M. J. Telford. 2006. Broad taxon and gene sampling indicate that chaetognaths are protostomes. *Current Biology* **16**: R575–576. doi: 10.1016/j.cub.2006.07.017.
- Meusemann, K., B. M. von Reumont, S. Simon, F. Roeding, S. Strauss, P. Kück, I. Ebersberger, M. Walz, G. Pass, S. Breuers, V. Achter, A. von Haeseler, T. Burmester, H. Hadrys, J. W. Wägele, and B. Misof. 2010. A phylogenomic approach to resolve the arthropod tree of life. *Molecular Biology and Evolution* **27**: 2451–2464. doi: 10.1093/molbev/msq130.
- Meyer, A., C. Todt, N. Mikkelsen, and B. Lieb. 2010. Fast evolving 18S rRNA sequences from Solenogastres (Mollusca) resist standard PCR amplification and give new insights into mollusk substitution rate heterogeneity. *BMC Evolutionary Biology* **10**: 70. doi: 10.1186/1471-2148-10-70.
- Meyer, A., A. Witek, and B. Lieb. 2011. Selecting ribosomal protein genes for invertebrate phylogenetic inferences: How many genes to resolve the Mollusca? *Methods in Ecology and Evolution* **2**: 34–42.
- Moroz, L. L. 2009. On the independent origins of complex brains and neurons. *Brain, Behavior and Evolution* **74**: 177–190. doi: 10.1159/000258665.
- Moroz, L. L. 2012. Phylogenomics meets neuroscience: How many times might complex brains have evolved? *Acta Biologica Hungarica* **63**: 3–19.
- Nielsen, C., G. Haszprunar, B. Ruthensteiner, and A. Wanninger. 2007. Early development of the aplacophoran mollusc *Chaetoderma*. *Acta Zoologica* **88**: 231–247.
- Okusu, A. 2002. Embryogenesis and development of *Epimeria babai* (Mollusca Neomeniomorpha). *The Biological Bulletin* **203**: 87–103.
- Okusu, A. and G. Giribet. 2003. New 18S rRNA sequences from neomenioid aplacophorans and the possible origin of persistent exogenous contamination. *Journal of Molluscan Studies* **69**: 385–387. doi: 10.1093/mollus/69.4.385.
- Paps, J., J. Bagunà, and M. Riutort. 2009. Bilaterian phylogeny: A broad sampling of 13 nuclear genes provides a new Lophotrochozoa phylogeny and supports a paraphyletic basal Acoelomorpha. *Molecular Biology and Evolution* **26**: 2397–2406.
- Passamaneck, Y. J., C. Schander, and K. M. Halanych. 2004. Investigation of molluscan phylogeny using large-subunit and small-subunit nuclear rRNA sequences. *Molecular Phylogenetics and Evolution* **32**: 25–38.
- Peterson, K. J., J. B. Lyons, K. S. Nowak, C. M. Takacs, M. J. Wargo, and M. A. McPeck. 2004. Estimating metazoan divergence times with a molecular clock. *Proceedings of the National Academy of Sciences* **101**: 6536–6541. doi: 10.1073/pnas.0401670101.
- Philippe, H., N. Lartillot, and H. Brinkmann. 2005. Multigene analyses of bilaterian animals corroborate the monophyly of Ecdysozoa, Lophotrochozoa, and Protostomia. *Molecular Biology and Evolution* **22**: 1246–1253.
- Philippe, H., E. A. Snell, E. Bapteste, P. Lopez, P. W. H. Holland, and D. Casane. 2004. Phylogenomics of eukaryotes: Impact of missing data on large alignments. *Molecular Biology and Evolution* **21**: 1740–1752. doi: 10.1093/molbev/msh182.
- Pick, K. S., H. Philippe, F. Schreiber, D. Erpenbeck, D. J. Jackson, P. Wrede, M. Wiens, A. Alié, B. Morgenstern, M. Manuel, and G. Wörheide. 2010. Improved phylogenomic taxon sampling noticeably affects nonbilaterian relationships. *Molecular Biology and Evolution* **27**: 1983–1987.
- Plate, L. H. 1892. Über den Bau und die Verwandtschaftsbeziehungen der Solenoconchen. *Zoologische Jahrbücher der Anatomie* **5**: 301–386. [In German]
- Pojeta, J. 1985. Early evolutionary history of diasome mollusks. *University of Tennessee Studies in Geology* **13**: 102–121.
- Pojeta, J. and B. Runnegar. 1976. The paleontology of rostroconch mollusks and the early history of the phylum Mollusca. *U.S. Geological Survey Professional Paper* **986**: 1–88.
- Pojeta, J., M. J. Vendrasco, and G. Darrough. 2010. Upper Cambrian Chitons (Mollusca, Polyplacophora) from Missouri, USA. *Bulletins of American Paleontology* **379**: 1–82.
- Ponder, W. F. and D. R. Lindberg. 1997. Towards a phylogeny of gastropod molluscs: An analysis using morphological characters. *Zoological Journal of the Linnean Society* **119**: 83–265. doi: 10.1111/j.1096-3642.1997.tb00137.x.
- Ponder, W. and D. Lindberg. 2008. Molluscan evolution and phylogeny: An introduction. In: W. F. Ponder and D. R. Lindberg, eds., *Phylogeny and Evolution of the Mollusca*. University of California Press, Berkeley and Los Angeles, California. Pp. 1–17.
- Pruvot, G. 1890. Sur le développement d'un solenogastre. *Comptes Rendus de l'Académie des Sciences* **114**: 1211–1214. [In French]
- Regier, J. C., J. W. Shultz, A. Zwick, A. Hussey, B. Ball, R. Wetzer, J. W. Martin, and C. W. Cunningham. 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* **463**: 1079–1083.
- Render, J. 1997. Cell fate maps in the *Ilyanassa obsoleta* embryo beyond the third division. *Developmental Biology* **189**: 301–310. doi: 10.1006/dbio.1997.8654.
- Reynolds, P. D. and A. Okusu. 1999. Phylogenetic relationships among families of the Scaphopoda (Mollusca). *Zoological Journal of the Linnean Society* **126**: 131–154. doi: 10.1111/j.1096-3642.1999.tb00151.x.
- Rokas, A. and P. W. H. Holland. 2000. Rare genomic changes as a tool for phylogenetics. *Trends in Ecology and Evolution* **15**: 454–459. doi: 10.1016/S0169-5347(00)01967-4.
- Rosenberg, G., S. Tillier, A. Tillier, G. S. Kuncio, R. T. Hanlon, M. Masselot, and C. J. Williams. 1997. Ribosomal RNA phylogeny

- of selected major clades in the Mollusca. *Journal of Molluscan Studies* **63**: 301–309.
- Roure, B., Baurain, D., and Philippe, H. 2012. Impact of missing data on phylogenies inferred from empirical phylogenomic datasets. *Molecular Biology and Evolution*. doi: 10.1093/molbev/mss208.
- Ruiz-Trillo, I., J. Paps, M. Loukota, C. Ribera, U. Jondelius, J. Baganà, and M. Riutort. 2002. A phylogenetic analysis of myosin heavy chain type II sequences corroborates that Acoela and Nemertodermatida are basal bilaterians. *Proceedings of the National Academy of Sciences* **99**: 11246–11251. doi: 10.1073/pnas.172390199.
- Runnegar, B. 1996. Early evolution of the Mollusca. In: J. D. Taylor, ed., *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford. Pp. 77–87.
- Runnegar, B. and J. Pojeta Jr. 1974. Molluscan phylogeny: The paleontological viewpoint. *Science* **186**: 311–317.
- Salvini-Plawen, L. v. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* **19**: 249–278.
- Salvini-Plawen, L. v. 1981. On the origin and evolution of the Mollusca. *Atti dei Convegni Lincei* **49**: 235–293.
- Salvini-Plawen, L. v. 1985. Early evolution and the primitive groups. In: E. R. Trueman and M. R. Clarke eds., *The Mollusca vol. 10: Evolution*. Academic Press, Waltham, Massachusetts. Pp. 59–150.
- Salvini-Plawen, L. v. 1990. Origin, phylogeny and classification of the phylum Mollusca. *Iberus* **9**: 1–33.
- Salvini-Plawen, L. v. 2003. On the phylogenetic significance of the aplacophoran Mollusca. *Iberus* **21**: 67–97.
- Salvini-Plawen, L. v. and G. Steiner. 1996. Synapomorphies and plesiomorphies in higher classification of Mollusca. In: J. D. Taylor, ed., *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford. Pp. 29–51.
- Sanderson, M. J. and M. M. McMahon. 2007. Inferring angiosperm phylogeny from EST data with widespread gene duplication. *BMC Evolutionary Biology* **7**: S3. doi: 10.1186/1471-2148-7-S1-S3.
- Scheltema, A. H. 1993. Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *The Biological Bulletin* **184**: 57–78.
- Scheltema, A. H. 1996. Phylogenetic position of Sipuncula, Mollusca and the progenetic Aplacophora. In: J. D. Taylor, ed., *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford. Pp. 53–58.
- Scheltema, A. H., K. Kerth, and A. M. Kuzirian. 2003. Original molluscan radula: Comparisons among Aplacophora, Polyplacophora, Gastropoda, and the Cambrian fossil *Wiwaxia corrugata*. *Journal of Morphology* **257**: 219–245.
- Scheltema, A. H. and D. L. Ivanov. 2002. An aplacophoran postlarva with iterated dorsal groups of spicules and skeletal similarities to Paleozoic fossils. *Invertebrate Biology* **121**: 1–10.
- Schrödl, M., K. M. Jörger, A. Klussman-Kolb, and N. G. Wilson. 2011. Bye bye “Opisthobranchia”! A review on the contribution of mesopsammic sea slugs to euthyneuran systematics. *Thalassas* **27**: 101–112.
- Shigeno, S., S. Takenori, and S. von Boletzky. 2010. The origins of cephalopod body plans: A geometrical and developmental basis for the evolution of vertebrate-like organ systems. *Cephalopods—Present and Past* **1**: 23–34.
- Sigwart, J. D. and M. D. Sutton. 2007. Deep molluscan phylogeny: Synthesis of palaeontological and neontological data. *Proceedings of the Royal Society B: Biological Sciences* **274**: 2413–2419.
- Smith, S. A., N. G. Wilson, F. E. Goetz, C. Feehery, S. C. S. Andrade, G. W. Rouse, G. Giribet, and C. W. Dunn. 2011. Resolving the evolutionary relationships of molluscs with phylogenomic tools. *Nature* **480**: 364–367. doi: 10.1038/nature10526.
- Smith, M. S. 2012. Mouthparts of the Burgess Shale fossils *Odontogrifus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences* **274**: 4287–4295.
- Sperling, E. A., K. J. Peterson, and D. Pisani. 2009. Phylogenetic-signal dissection of nuclear housekeeping genes supports the paraphyly of sponges and the monophyly of Eumetazoa. *Molecular Biology and Evolution* **26**: 2261–2274. doi: 10.1093/molbev/msp148.
- Steiner, G. 1992. Phylogeny and classification of Scaphopoda. *Journal of Molluscan Studies* **58**: 385–400. doi: 10.1093/mollus/58.4.385.
- Steiner, G. and H. Dreyer. 2003. Molecular phylogeny of Scaphopoda (Mollusca) inferred from 18S rDNA sequences: Support for a Scaphopoda–Cephalopoda clade. *Zoologica Scripta* **32**: 343–356.
- Steiner, G. and L. Salvini-Plawen. 2001. Acaenoplax—Polychaete or mollusc? *Nature* **414**: 601–602. doi: 10.1038/414601a.
- Struck, T. H., C. Paul, N. Hill, S. Hartmann, C. Hoesel, M. Kube, B. Lieb, A. Meyer, R. Tiedemann, G. Purschke, and C. Bleidorn. 2011. Phylogenomic analyses unravel annelid evolution. *Nature* **471**: 95–98. doi: 10.1038/nature09864.
- Sutton, M. D. 2001. A three-dimensionally preserved fossil polychaete worm from the Silurian of Herefordshire, England. *Proceedings of the Royal Society B: Biological Sciences* **268**: 2355–2363. doi: 10.1098/rspb.2001.1788.
- Sutton, M. D., D. E. Briggs, D. J. Siveter, and D. J. Siveter. 2001. Invertebrate evolution (Communications arising): *Acaenoplax*—polychaete or mollusc? *Nature* **414**: 602.
- Sutton, M. D., D. E. Briggs, D. J. Siveter, and D. J. Siveter. 2004. Computer reconstruction and analysis of the vermiform mollusc *Acaenoplax hayae* from the Herefordshire Lagerstätte (Silurian, England), and implications for molluscan phylogeny. *Palaeontology* **47**: 293–318.
- Sutton, M. D. and J. Sigwart. 2012. A chiton without a foot. *Paleontology* **55**: 401–411.
- Sutton, M. D., D. E. G. Briggs, D. J. Siveter, D. J. Siveter, and J. D. Sigwart. 2012. A Silurian armoured aplacophoran and implications for molluscan phylogeny. *Nature* **490**: 94–97.
- Thiele, J. 1897. Zwei australische Solenogastres. *Zoologische Anzeiger* **20**: 398–400. [In German]
- Thompson, T. E. 1960. The development of *Neomenia carinata* Tullberg (Mollusca Aplacophora). *Proceedings of the Royal Society B: Biological Sciences* **153**: 263–278.
- Todt, C., A. Okusu, C. Schander, and E. Schwabe. 2008. Solenogastres, Caudofoveata, and Polyplacophora. In: W. F. Ponder and

- D. R. Lindberg, eds., *Phylogeny and Evolution of the Mollusca*. University of California Press, Berkeley and Los Angeles, California. Pp. 71–96.
- Todt, C. and L. Salvini-Plawen. 2005. The digestive tract of *Helicoradomenia* (Solenogastres, Mollusca), aplacophoran molluscs from the hydrothermal vents of the East Pacific Rise. *Invertebrate Biology* **124**: 230–253.
- Todt, C. and A. Wanninger. 2010. Of tests, trochs, shells, and spicules: Development of the basal mollusk *Wirenia argentea* (Solenogastres) and its bearing on the evolution of trochozoan larval key features. *Frontiers in Zoology* **7**: 6. doi: 10.1186/1742-9994-7-6
- Trueman, E. R. and A. C. Brown. 1985. The mechanism of shell elevation in *Haliotis* (Mollusca: Gastropoda) and a consideration of the evolution of the hydrostatic skeleton in Mollusca. *Journal of Zoology* **205**: 585–594. doi: 10.1111/j.1469-7998.1985.tb03546.x.
- Veenstra, J. A. 2011. Neuropeptide evolution: Neurohormones and neuropeptides predicted from the genomes of *Capitella teleta* and *Helobdella robusta*. *General and Comparative Endocrinology* **171**: 160–175. doi: 10.1016/j.ygcen.2011.01.005.
- Vinther, J., E. A. Sperling, D. E. G. Briggs, and K. J. Peterson. 2011. A molecular palaeobiological hypothesis for the origin of aplacophoran molluscs and their derivation from chiton-like ancestors. *Proceedings of the Royal Society B: Biological Sciences* **279**: 259–268. doi: 10.1098/rspb.2011.1773.
- Waller, T. R. 1998. Origin of the molluscan class Bivalvia and a phylogeny of major groups. In: P. A. Johnson and J. Haggart, eds., *The Bivalvia: Half a Billion Years of Evolution*. University of Calgary Press, Calgary, Canada. Pp. 1–47.
- Wägele, H., A. Klussmann-Kolb, V. Vonnemann, and M. Medina. 2008. Heterobranchia I. In: W. F. Ponder and D. R. Lindberg, eds., *Phylogeny and Evolution of the Mollusca*. University of California Press, Berkeley and Los Angeles, California. Pp. 385–408.
- Wanninger, A. 2009. Shaping the things to come: Ontogeny of lophotrochozoan neuromuscular systems and the tetra-neuralia Concept. *The Biological Bulletin* **216**: 293–306.
- Wanninger, A. and G. Haszprunar. 2001. The expression of an engrailed protein during embryonic shell formation of the tusk-shell, *Antalis entalis* (Mollusca, Scaphopoda). *Evolution and Development* **3**: 312–321.
- Wanninger, A. and G. Haszprunar. 2002. Muscle development in *Antalis entalis* (Mollusca, Scaphopoda) and its significance for scaphopod relationships. *Journal of Morphology* **254**: 53–64.
- Wanninger, A. and G. Haszprunar. 2003. The development of the serotonergic and FMRF-amidergic nervous system in *Antalis entalis* (Mollusca, Scaphopoda). *Zoomorphology* **122**: 77–85.
- Wanninger, A., J. Fuchs, and G. Haszprunar. 2007. Anatomy of the serotonergic nervous system of an entoproct creeping-type larva and its phylogenetic implications. *Invertebrate Biology* **126**: 268–278.
- Webers, G. F. and E. L. Yochelson. 1989. Late Cambrian molluscan faunas and the origin of the Cephalopoda. *Geological Society, London, Special Publications* **47**: 29–42. doi: 10.1144/GSL.SP.1989.047.01.04.
- Wiens, J. J. 2003. Incomplete taxa, incomplete characters, and phylogenetic accuracy: Is there a missing data problem? *Journal of Vertebrate Paleontology* **23**: 297–310. doi: 10.1671/0272-4634(2003)023[0297:ITICAP]2.0.CO;2.
- Wiens, J. J. and D. S. Moen. 2008. Missing data and the accuracy of Bayesian phylogenetics. *Journal of Systematics and Evolution* **46**: 307–314.
- Wilson, N. G., G. W. Rouse, and G. Giribet. 2010. Assessing the molluscan hypothesis Serialia (Monoplacophora+ Polyplacophora) using novel molecular data. *Molecular Phylogenetics and Evolution* **54**: 187–193.
- Winnepenninckx, B., T. Backeljau, and R. De Wachter. 1996. Investigation of molluscan phylogeny on the basis of 18S rRNA sequences. *Molecular Biology and Evolution* **13**: 1306–1317.
- Yochelson, E. L., R. H. Flower, and G. F. Webers. 1973. The bearing of the new Late Cambrian monoplacophoran genus *Knighticonus* upon the origin of the Cephalopoda. *Lethaia* **6**: 275–309. doi: 10.1111/j.1502-3931.1973.tb01199.x.

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