BYE BYE “OPISTHOBRANCHIA”!
A REVIEW ON THE CONTRIBUTION OF MESOPSAMMIC SEA SLUGS TO EUTHYNEURAN SYSTEMATICS

SCHRÖDL M(1), JÖRGER KM(1), KLUSSMANN-KOLB A(2) & WILSON NG(3)

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ABSTRACT

During the last decades, textbook concepts of “Opisthobranchia” have been challenged by morphology-based and, more recently, molecular studies. It is no longer clear if any precise distinctions can be made between major opisthobranch and pulmonate clades. Worm-shaped, mesopsammic taxa such as Acochlidia, Platychelydidae, Philinoglossidae and Rhodopemorpha were especially problematic in any morphology-based system. Previous molecular phylogenetic studies contained a very limited sampling of minute and elusive meiofaunal slugs. Our recent multi-locus approaches of mitochondrial COI and 16S rRNA genes and nuclear 18S and 28S rRNA genes (“standard markers”) thus included representatives of most mesopsammic “opisthobranchs” within a comprehensive euthyneuran taxon set.

The present study combines our published and unpublished topologies, and indicates that monophyletic Rhodopemorpha cluster outside of Euthyneura among shelled basal heterobranchs, acteonids are the sister to rissoellids, and Nudipleura are the basal offshoot of Euthyneura. Furthermore, Pyramidellidae, Sacoglossa and Acochlidia cluster within paraphyletic Pulmonata, as sister to remaining “opisthobranchs”. Worm-like mesopsammic heterobranch taxa have clear independent origins and thus their similarities are the result of convergent evolution. Classificatory and evolutionary implications from our tree hypothesis are quite dramatic, as shown by some examples, and need to be explored in more detail in future studies.

We do not claim that these concatenated “standard marker” gene trees reflect the true phylogeny of all groups; exploring additional, suitable markers is required. We do claim, however, that improved taxon sampling and improved data quality (such as sequences, alignments) were beneficial towards

(1) Bavarian State Collection of Zoology. Münchhausenstr. 21, D-81247 Munich, Germany.
(2) Institute for Ecology, Evolution and Diversity, Goethe-University, Siesmayerstr. 70, 60054 Frankfurt am Main, Germany.
(3) The Australian Museum, 6 College Street, Sydney NSW, 2010 Australia.
Email: Michael.Schroedl@zsm.mwn.de, Katharina.Joerger@zsm.mwn.de, klußmann-kolb@bio.uni-frankfurt.de, Nerida.Wilson@austmus.gov.au
revealing relationships of higher euthyneuran taxa, and that phylogenetic hypotheses based on this data set are converging. The traditional taxon concept of Opisthobranchia is clearly artificial and thus obsolete. Novel phylogenetic hypotheses, as disturbing they may be at first glance, give us the opportunity and perhaps the obligation to refine our approaches and rethink older paradigms. Most importantly, we see no more way to explore morphology, systematics and evolution of “opisthobranchs” separately from “lower heterobranchs” and “pulmonates”.

INTRODUCTION

Milne Edwards (1848) split the gastropods into Prosobranchia, Pulmonata and Opisthobranchia. The latter two taxa are usually combined as Euthyneura. Both researchers and amateurs easily associate opisthobranchs as marine slugs or snails, with a more or less reduced or internalized shell, having an almost bilaterally symmetrical body and either a head shield or head tentacles, whereas pulmonates appear almost exclusively related to limnic and terrestrial habitats. Unconventional taxa such as interstitial worm-like forms, limnic opisthobranchs and marine pulmonates occur, but are obviously too exceptional to challenge the practical value of the traditional Opisthobranchia-Pulmonata concept. The often beautifully coloured and bizarrely shaped approx. 6000 opisthobranch species thus are treated as belonging to a clade in virtually all older field guides and zoological textbooks (e.g. Westheide & Rieger, 2007), current molluscan classifications (e.g. Bouchet & Rocroi, 2005), and reviews (e.g. Schmekel & Portmann, 1982, Schmekel, 1985, Rudman & Willan, 1998), including the most recent one by Wägele et al. (2008) that was published within a compendium on molluscan phylogeny and evolution (Ponder & Lindberg, 2008). Recent comprehensive field guides on Caribbean and Indo-Pacific opisthobranchs, however, left monophyly open (Valdés et al., 2006, Gosliner et al., 2008).

There has always been a certain disagreement with regards to which major subtaxa should be included into Opisthobranchia (Gosliner, 1981). Commonly accepted “core groups” are Cephalaspidea, Anaspidea, Thecosomata, Gymnosomata, Sacoglossa, Acochlidia, Tylodinoidea (=Umbraculida) and Nudipleura, the latter consisting of side-gilled Pleurobranchomorpha and Nudibranchia, which are the sea slugs in a strict sense. Some taxa with more or less well-developed helicoidal shells such as Acteonoidea (see Mikkelsen, 1996 vs. 2002) and Pyramidelloidea (e.g. Fretter & Graham, 1949) and the limpet-like Siphonarioidea have also occasionally been discussed as part of Opisthobranchia (see review by Wägele et al., 2008). While the worm-like Rhodopemorpha were either seen as turbellarians or transitional forms between worms and gastropods in early approaches, most modern authors treated them as euthyneurans or integral part of opisthobranchs (e.g. Haszprunar & Heß, 2005).

Establishing the Heterobranchia concept, Haszprunar (1985, 1988) reconstructed an apomorphy-based phylogeny implying a progressive evolution from simple “allogastropod” (=“lower heterobranch”) taxa such as Valvatoidea, Architectonicoidea and Pyramidelloidea towards Pentaganglionata (=Euthyneura). Haszprunar’s phylogeny showed Acteonoidea (Architectibranchia) as the sister to monophyletic Pulmonata (including pentaganglionate Rhodopemorpha), which was itself the sister to remaining opisthobranchs (including vermiform Smeagolidae), rendering “Opisthobranchia” paraphyletic. Haszprunar thus was the first to phylogenetically infer and discuss the artificial nature of Opisthobranchia rather than comparing similarities and modifying the inclusiveness of the concept. Using cladistic analyses on a morphological dataset, Salvini-Plawén & Steiner (1996) recovered monophyletic Euthyneura, and Pulmonata plus Thecosomata as sister to remaining Opisthobranchia including Rhodopemorpha (as Rhodopida) as sister to equally shell-less and small-sized Acochlidia and Gymnosomata. Dayrat & Tillier (2002) found Pyramidelloidea within euthyneuran taxa and summarized an unresolved euthyneuran topology with
monophyletic Pulmonata arising as one of many clades from an opisthobranch grade of organization. An even more comprehensive morphology-based parsimony analysis by Wägele & Klussmann-Kolb (2005) showed Pteropoda (Gymnosomata plus Thecosomata) as sister to Pulmonata plus remaining Opisthobranchia, but this is contradicted by a more focused molecular study (Klussmann-Kolb & Dinapoli, 2006). In the study by Wägele & Klussmann-Kolb (2005) the remaining Opisthobranchia included a clade of exclusively interstitial (and/or small sized) cephalaspidean subtaxa, Rhodopemorpha and Acochlidia as sister to Sacoclossa, rendering Cephalaspidea polyphyletic. In the light of the latest morphology-based cladistic analysis focussing on Acochlidia (Schrödl & Neusser, 2010), such results are in doubt. While resolving inner relationships of Acochlidia quite nicely, other mesopsammic euthyneurans included, regardless their supposed affiliation, had a tendency to cluster with Acochlidia; Schrödl & Neusser (2010) explained that by parallel concerted reductions of body-size and organs, but also by convergent evolution of vermiform bodies having a set of special organs as adaptations to a special habitat. Summarizing, 1) the Heterobranchia concept has always conflicted with a monophyletic Opisthobranchia, 2) no morphology-based analyses have recovered a monophyletic Opisthobranchia, 3) morphology-based analyses are mislead by problems of interpreting morphological similarities and a generally high degree of parallelism (Gosliner, 1981, 1991); in particular, convergences displayed by small-sized slugs that occur in many subgroups may outnumber characters showing true phylogenetic signal, and thus lead to unreliable or completely wrong topologies.

Molecular markers, in contrast, offer an extremely large number of characters (via nucleotide sequences)
and many genes such as rRNA genes may not be directly influenced by habitat-specific ecological selective pressures. Early molecular approaches on opisthobranch phylogeny counted with single genes (partial 16S rDNA, Tholleson, 1999a,b, Wägele et al., 2003; 18S rDNA, Wollscheid & Wägele 1999; partial 28S rDNA, Dayrat et al., 2001), for relatively small sets of taxa. Whenever pulmonates were included in such analyses, opisthobranchs were not recovered as monophyletic unless the taxon definitions were extraordinarily modified. The same happened to the mitochondrial genome-based data sets of Grande et al. (2004a,b, 2008) and Medina et al. (2011). Vonnemann et al. (2005) were the first to combine the more conservatively evolving nuclear 18S and 28S rRNA gene fragments sequenced from a larger and more representative euthyneuran taxon set (including 3 different acochlidian species), recovering monophyletic Opisthobranchia as sister to potentially paraphyletic Pulmonata, but only in Maximum Parsimony analysis of the combined data set. Successively extending the taxon sampling to further pulmonate subgroups and especially to lower heterobranchs, using a combined set of mitochondrial CO1, 16S rRNA gene fragments, and nuclear 18S rRNA (complete) plus 28S rRNA genes (D1-3), and applying Maximum Likelihood algorithms became the standard for further analyses. None of the studies increasing in sophistication (e.g. Klussmann-Kolb et al., 2008, Dinapoli & Klussmann-Kolb, 2010) recovered a monophyletic Opisthobranchia, usually due to acochlidian, but also sacoglossan and pyramidelloidean taxa clustering among pulmonates.

Since we failed to trace the origin of Acochlidia in morphology-based frameworks (Schrödl & Neusser, 2010), we carefully designed molecular studies including representatives of all the hard-to-find groups with interstitial slugs and all but one acochlidian families, plus all taxa that were mentioned to be potentially related to some of them (Jörger et al., 2010, Wilson et al., 2010). Special attention was paid to alignments and to the potential effect of ambiguous alignment portions, which were masked and more or less rigorously removed by the programs Aliscore and Gblocks (see Jörger et al., 2010 for details). The topology showing best likelihood resulting from Jörger et al. (2010) rejected all traditional hypotheses on the origin of Acochlidia, but indicate a pulmonate relationship of Acochlidia. In particular, tree hypotheses were considered as robust and reliable enough to propose a reclassification of Euthyneura, abandoning the taxon name and concept of Opisthobranchia.

The present paper combines results of Jörger et al. (2010), Dinapoli & Klussmann-Kolb (2010), Dinapoli et al. (2011) and some preliminary data on the origin of Rhodopemorpha (see Wilson et al., 2010), and reviews and discusses the status of Opisthobranchia in the light of improving data sets and analytical methods. Finally, it gives some examples how new phylogenetic hypotheses affect old paradigms on opisthobranch evolution, and recommends facing the consequences of changing concepts.

**Challenging the Opisthobranchia concept**

Combining the results on the origin of Acochlidia by Jörger et al. (2010) with a preliminary analysis on the origin of Rhodopemorpha by Wilson et al. (2010) by hand shows a consensus topology (Fig. 1) that radically differs from traditional heterobranch classifications. Monophyletic Rhodopemorpha cluster among basal, shelled lower heterobranchs with high support; thus, based on molecular data, Rhodopemorpha are preliminary not related to any of the euthyneuran taxa or even to dorid nudibranchs as was suspected based on morphological data before. The Opisthobranchia are polyphyletic: Acteonoidea plus Rissoelloidea is the sister to Euthyneura, with Nudipleura as first euthyneuran offshoot. Pulmonates in a traditional sense are paraphyletic, including the “opisthobranch” clades Sacoglossa and Acochlidia, and the potential lower heterobranchs Glacidorbis and Pyramidellidae, and thus were called Panpulmonata by Jörger et al. (2010). The remaining opisthobranchs form a clade called Euopisthobranchia by Jörger et
al. (2010). Several, but not all of these nodes (Fig 1; see Jörger et al., 2010) are robustly supported and the topologies slightly vary according to different analyses and parameters. Nevertheless, Opisthobranchia are not recovered monophyletic under any circumstances. In particular, worm-like sluggish opisthobranch taxa undoubtedly have independent origins and thus structural, functional and biological similarities evolved convergently due to selective pressure in an extreme habitat (Jörger et al., 2010, Schrödl & Neusser, 2010, Wilson et al., 2010). Bootstrap support and posterior probability values are high for most of the morphologically well-defined opisthobranch and pulmonate subclades usually treated as superfamilies or (sub)orders (collapsed to terminal taxa in Fig 1). Excluding the historically enigmatic Rhodopemorpha and Acteonoidea conceptually still results in paraphyletic Opisthobranchia at best, with Nudipleura as sister to all other euthyneurans, and both Sacoglossa and Acochlia clustering among pulmonate taxa. Constraining the analyses of Jörger et al. (2010) towards monophyletic Opisthobranchia was highly significantly rejected based on their data. Excluding Acochlia or Sacoglossa or both from an Opisthobranchia concept still does not render them monophyletic. Standard molecular markers clearly reject the monophyly of Opisthobranchia under any historic or reasonable taxon definition, and the topology (Fig. 1) differs from any morphology-based classifications, apomorphy-based reconstructions and, in particular, cladistic analyses that, thus, all were misled.

New trees, new truths?

By showing the non-monophyly of Euthyneura, Opisthobranchia and Pulmonata in a traditional sense, our standard marker based tree hypothesis (Fig. 1) is consistent to most previous molecular analyses available, regardless of using single genes, combinations of nuclear and mitochondrial genes or mitochondrial genomic data. More problematic than showing the deficiency of traditional classifications, however, is to present a convincing alternative: data sets, methods used and resulting topologies may greatly differ depending on the data used and there is no way of a direct numerical evaluation of how reliably these trees reflect evolutionary history.

However, there is some evidence that the design and performance of molecular studies on heterobranchs evolved over time, and thus there is hope that some of the latest topologies are superior to previous ones. Early single gene analyses (e.g. Thollesson, 1999a,b) were limited by still poor taxon and character sampling, simplistic alignment tools and parsimony as a single optimization criterion. Studies using mitochondrial genes (Grande et al. 2004a,b) or mitochondrial genomes (Grande et al., 2002, 2008, Medina et al., 2011) also were based on inadequate and unrepresentative heterobranch taxon sampling, the signal to noise ratio of markers remains untested, and topologies still differ. Supplementing the landmark studies on combined 18S and 28S rRNA genes by Vonnemann et al. (2005) by further taxa and using the whole set of what we now call “standard” genes of Klussmann-Kolb et al. (2008) and Dinapoli & Klussmann-Kolb (2010), our current approaches (Jörger et al., 2010, Wilson et al., 2010) use a multi-locus set of a truly representative taxon sampling i.e. several lineages of lower heterobranchs, all previously recognized or suspected euthyneuran clades, and all the enigmatic interstitial target taxa in question are included, plus assumed relatives of Rhodopemorpha such as dorid nudibranchs and several runcinids. In addition, the few European acochlidian taxa used in previous analyses (e.g. Vonnemann et al. 2005, Dinapoli & Klussmann-Kolb, 2010) were shown to be highly derived ones; especially Hedylopsis spiculifera, but also the microhedylacean species Pontohedyle milaschewitschii and Microhedyle glandulifera showed long branches due to aberrantly evolved loci in comparison to other, more slowly evolving acochlidian species from other parts of the worlds oceans (Jörger et al., 2010). Selecting a sufficient number of basal and slow-evolving taxa from old groups is clearly beneficial for minimizing branch
lengths and the effects of signal erosion (e.g. Wägele & Mayer, 2007). On the data quality side, state of the art procedures have been applied to minimize errors and noise, i.e. sequences were checked by BLAST searches and hypervariable regions of the alignments removed by masking programs, and only the most recent studies (e.g. Dinapoli & Klussmann-Kolb, 2010, Holznagel et al., 2010, Jörger et al., 2010, Dayrat et al., 2011, Dinapoli et al., 2011,) used both ML and Bayesian analyses, which is beneficial to reveal and control for effects of different evolutionary rates among lineages (e.g. Paps et al., 2009). While Holznagel et al. (2010) limited their study on partial 28S of an incomplete panpulmonate sampling, i.e. lacking Sacoglossa and Acochlidia, the more representative and comprehensive standard gene studies by Dinapoli & Klussmann-Kolb (2010) and Jörger et al. (2010) seem to converge towards a topology that is largely congruent to Fig. 1. We thus assume that this topology will be fairly robust to taxon addition. In particular, adding several more species of Pyramidellidae to the standard gene set, Dinapoli et al. (2011) already confirmed the Pyramidellidae as part of a common clade with Glacidorbis and Amphiboloidea. Göbbeler & Klussmann-Kolb (2010) showed that the node of Rissoelloidea and Acteonoidea is robust to adding representatives of all acteonidean families.

Despite all these efforts to optimize taxon sampling, data quality, and alignment procedures, neighbornet analyses by Dinapoli & Klussmann-Kolb (2010) and Jörger et al. (2010) show a still high level of conflict in the data, with split support for some groups only. Since none of the well-supported nodes in the tree is contradicted by the split analyses, we do not interpret this as general evidence against our tree but as a warning that the power of our standard marker set for resolving heterobranch evolution has its limitations. The topology shown herein (Fig. 1) needs to be tested and refined by a truly independent set of molecular markers showing a high signal to noise ratio and minimizing the risk of alignment artefacts, i.e. conservative, protein coding nuclear genes.

Violating morphology?

Our phylogenetic consensus hypothesis (Fig. 1) is based on a large and representative taxon sampling, and on alignments of several thousands of nucleotides; its major weakness is due to just 4 - and always the same - “standard genes” involved. However, most of the traditionally accepted heterobranch taxa on order or family level such as Nudipleura, Acochlidia, Sacoglossa, Eupulmonata and Ellobioidea were recovered as robustly supported lineages. These molecular results are congruent with morphology-based ideas, and thus are likely to represent the evolutionary history. This also implies that both morphology-based inference and standard genes are informative at least at these levels. What remains problematic are the interrelationships between such major clades that have just poorly supported and sometimes incongruent trees based on standard markers. There is no doubt that much of the conflict with previous morphology-based hypotheses (e.g. Wägele & Klussmann-Kolb, 2005 as the most comprehensive one) is due to misconceptions that based on misinterpretations of homology and on extreme levels of homoplasy in the latter, as already suspected by Gosliner (1981) and Gosliner & Ghiselin (1984). The best examples refer to mesopsammic, convergently evolved worm-like taxa (Fig. 1) all showing a similar set of reductions and innovations (e.g. Jörger et al., 2010, Schrödl & Neusser, 2010), that are obviously adaptive to their special habitat. Moreover, at present, we are not able to present any conspicuous apomorphies for the recently established clades, except for Euopisthobranchia having evolved an oesophageal/gizzard cuticle (Jörger et al., 2010). Morphology thus has to be re-examined carefully and a priori homology assumptions might have to be changed according to a posteriori relationships unravelled. On the other hand, even some of the most intriguing relationships proposed by recent molecular analyses (Dinapoli & Klussmann-Kolb, 2010; 2011; Jörger et al., 2010) may fit within a morphological framework. Glacidorbis clusters within pulmonates,
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BY Ponder (1986), rather than being related with lower heterobranchs as proposed by Haszprunar (1985, 1988). The Pyramidellidae sensu stricto, i.e. all those Pyramidelloidea having a buccal stylet rather than a complex jaw apparatus as in Murchisonellidae) is an integral part of Euthyneura even when comparing mitochondrial genomes (Grande et al., 2008). This placement is supported by central nervous features such as the possession of giant nerve cells and a rhinophoral ganglion (see Huber, 1993). Siphonarian intertidal (or even fully marine) limpets were suggested to be opisthobranchs (Haller, 1892) or most basal pulmonates based on i.e. as sister of Amphiboidea, as suggested by their morphology (Hyman, 1967), which fits with Ponder (1986), rather than being related with their position as early panpulmonate descendants of an opisthobranch grade. As discussed by Jörger et al. (2010), morphological features usually suggested to be synapomorphic for pulmonates are either plesiomorphic, poorly explored, or of limited significance. Even more straightforward, accepting the proposed homology of the pulmonate procerebrum and opisthobranch rhinophoral ganglia (Haszprunar, 1988) that has received increasing evidence from results of several microanatomical studies (e.g. Huber, 1993, Neusser et al. 2007), there is not a single putative synapomorphy left for Opisthobranchia (Jörger et al., 2010).

Figure 2:
Evolution of “opisthobranchs”. Taxa with interstitial members are framed in red; mesopsammic habitat is basal in Acochlidia and possibly Rhodopemorpha only; meiofaunal subclades, all more or less vermiform and showing an array of further adaptations, thus evolved many times independently among Heterobranchia. Taxa with at least one secure pentagangliionate stage known in at least a single species (see Dayrat & Tillier, 2000) are marked red; the only regularly pentagangliionate higher taxa may be Rhodopemorpha (juveniles only of Rhodope, adults of Helminthope) and Acteonoidea (adult). Stem lineages of taxa showing monaulic reproductive systems are colored black, those having androdiaulic (including triaulic) conditions are green; clades with mixed states are broken black/green, and clades with just exceptional and/or non-basal androdiaulic taxa are dotted black/green. Note that it is parsimonious to assume that monauly evolved in the common, tectipleuran ancestor of Euopisthobranchia and Panpulmonata. If so, true androdiaulic (gonoducts split into oviduct and vas deferens proximal to the female gland mass) re-evolved in the stem lineages of Sacoglossa, Glacidorboidea and within several other panpulmonate subclades. Also note that a variety of structurally differing monaulic and diaulic conditions occur and that different authors use different terms; e.g. the special androdiaulic condition occurring in some acochlidians is called monaulic by Valdés et al. (2010). In the light of novel phylogenetic hypotheses, the characters and evolution of heterobranchs need to be re-examined in much greater depth.
Summing up, it is the absence of contradiction, rather than unambiguous support, which makes the novel euthyneuran phylogenetic hypothesis presented by Jörger et al. (2010) and herein alluring. Still, the monophyly of Pulmonata and Opisthobranchia are clearly rejected by current knowledge (Fig. 1) and this fact cannot be longer ignored.

Consequences

Accepting the core topology presented here (Fig. 1), or just parts of it, has dramatic consequences for opisthobranch (and pulmonate) research.

First, neither “Opisthobranchia” nor “Pulmonata” can be retained as monophyletic taxa and thus have to be abandoned from our thinking and the literature. A reclassification has been proposed by Jörger et al. (2010) recently, modifying old names according to new concepts, i.e. Nudipleura as sister to a clade composed of Euopisthobranchia plus Panpulmonata; the latter, well-supported clade (Fig. 1) is named Tectipleura herein. In particular, polyphyletic “Opisthobranchia” do not even form a grade that can be characterized by any conspicuous set of plesiomorphies. Traditional “Opisthobranchia” thus are nothing else than an artificial assemblage of usually marine slugs or snails with limpet-like, bivalved or bubble shells showing tendencies of reduction or internalization, having a more or less detorted and externally bilateral symmetrical body with usually at least one pair of head tentacles or a head shield, including many exceptions. Rather than having a phylogenetic or evolutionary or even merely descriptive value, the “Opisthobranchia” concept is of historical and –to many of us– emotional value “only”.

Second, hypotheses on structures, functions or any other features, homology, character polarity, and evolution of opisthobranchs have to be reassessed in the light of new phylogenetic evidence. Some of the rampant parallelism assigned to Opisthobranchia is actually attributable to a taxon misconception, while even higher levels of homoplasy are indicated e.g. by the independent origins of meiofaunal groups showing an array of independently derived features (e.g. Jörger et al., 2010, Schrödl & Neusser, 2010). Intriguingly, basal Rhodopemorpha are one of the few taxa supposedly showing a pentaganglionate condition (in juveniles and/or adults), but, according to Figs. 1 and 2, are not part of the Pentaganglionata (=Euthyneura) sensu Haszprunar, a concept that has been criticized before (Dayrat & Tillier, 2000). Additionally, rhodopemorphs are euthyneurous slugs that are not part of Euthyneura (Fig. 2). The simple, monaulic condition of the reproductive system was taken for granted to be plesiomorphic for Opisthobranchia (e.g. Ghiselin, 1966, Gosliner, 1981, Valdés et al., 2010). Structurally more complex diaulic conditions with separate male and female gonoducts were thought to have evolved from such a “primitive” level of organization, either as a single event or in multiple convergence (Valdés et al., 2010), with the condition in pulmonates unclear (Wägele et al., 2008). Widening the taxonomic focus and mapping monaulic and diaulic conditions on our novel topology (Fig. 2) may question these paradigms at least. It appears that (andro)diauly evolved at least once already in the heterobranch stemline and was plesiomorphically retained in Nudipleura. Opisthobranch monaula thus evolved at least once from a diaulic condition, possibly already in the common ancestor of Euopisthobranchia and Panpulmonata; monaula may be a synapomorphy of Tectipleura. While basal clades of Euopisthobranchia are monaulic, a few androdiaulic taxa exist (“triaulic” Anidolyta, certain Ringicula spp; Valdés et al., 2010), indicating secondary androdiauly. Also, some secondary, more or less incomplete structural and functional subdivisions of gonoducts may occur in certain subtaxa, e.g. leading to a sometimes called “oodiaulic” system in Anaspidea (Gosliner, 1994) or some cephalaspidean genera (Rudman & Willan, 1998, Valdés et al., 2010). The situation within panpulmonates is very complex showing a mosaic of (primary or secondary) monaulic and diaulic conditions in many major subgroups (Fig. 2),
implying much homoplasy involved. Androdiauly in panpulmonates is structurally heterogeneous, e.g. the vas deferens may split off the hermaphroditic duct in a proximal (“true androdiauly”) or in more distal position (“special androdiauly”, e.g. of some Acochlidia), and may run freely in the body cavity or in association to the body wall (as a “sunken” or “closed” sperm groove) (e.g., see Hubendick, 1978; Golding et al., 2008; Schrödl & Neusser, 2010). Complex evolutionary scenarios proposed by Visser (1977, 1988) trusted on a direct descent of pulmonates from prosobranch ancestors that is, however, rejected by all modern phylogenetic results. The actual variation, homology and evolution of heterobranch genital systems clearly merit detailed comparative and integrative exploration. Even more fundamentally changing our view, rather than being a “crown group” the opisthobranchs including the diverse Nudipleura and Euopisthobranchia now may be considered as just moderately species rich and successful early offshoots of the panpulmonate stem line, leading to much higher ecological and species diversity therein (Fig. 1).

Third, and of practical importance, in future studies on traditional opisthobranch (or pulmonate) taxa it is no longer tenable to just define and use “Opisthobranchia” (or “Pulmonata”) as an ingroup, as a taxon concept, or just as a point of reference, without proving its monophyly by using an adequate heterobranch taxon sampling. In simple words, there is no more way to study opisthobranchs without considering lower heterobranchs and pulmonates, and vice versa. Instead, the traditionally isolated research communities on basal heterobranch, opisthobranch or pulmonate taxa have to recognize that barriers are perceived rather than of a systematic nature; the earlier we combine our knowledge and efforts the better it is for furthering our branch of science.

Fourth: Yes, we now advocate for renaming the International Opisthobranch workshops as Heterobranch workshops, to bring people together!

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REFERENCES


Phylogenetics and Evolution, 55: 60-76.


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BMC Evolutionary Biology, 10: 323.
BMC Evolutionary Biology, 8: 57.


