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REVIEW

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Flashback and foreshadowing—a review of the taxon Opisthobranchia

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Abstract Opisthobranchia have experienced an unsettled taxonomic history. At the moment their taxonomy is in state of dramatic flux as recent phylogenetic studies have revealed traditional Opisthobranchia to be paraphyletic or even polyphyletic, allocating some traditional opisthobranch taxa to other groups of Heterobranchia, e.g. Pulmonata. Here we review the history of Opisthobranchia and their subgroups, explain their traditionally proposed relationships, and outline the most recent phylogenetic analyses based on various methods (morphology, single gene and multiple gene analyses, as well as genomic data). We also present a phylogenetic hypothesis on Heterobranchia that, according to the latest results, represents a consensus and is the most probable one available to date. The proposed phylogeny supports the Acteonoidea outside of monophyletic Euthyneura, the basal euthyneuran split into Nudipleura (Nudibranchia plus Pleurobranchoidea) and the recently established taxon Tectipleura. The latter divides into the Euopisthobranchia, containing most of the major traditional opisthobranch clades, and the Panpulmonata, with a mix of the former opisthobranch, putative allogastropod and pulmonate taxa. This "new euthyneuran tree" rejects the traditional taxa Opisthobranchia and Pulmonata, and, in particular, has profound implications for preconceived textbook scenarios of opisthobranch and pulmonate evolution, which must now be reconsidered. In the absence of systematic barriers, research communities—which have traditionally investigated marine and non-marine heterobranchs separately—need to interact and finally merge for the sake of science.

Keywords Gastropoda · Heterobranchia · Review · Opisthobranchia · Morphology · Molecular Phylogeny · Systematics · Taxonomy

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Introduction

Opisthobranch snails and slugs are some of the ecologically and morphologically most diverse groups within Gastropoda. They comprise some of the most enigmatic invertebrates with regards to ecological and physiological adaptations. Several key innovations, like functional kleptoplasty, i.e. incorporation of kleptocnides and defense by incorporation of secondary metabolites (kleptochemistry), have driven evolution within certain opisthobranch groups. Moreover, opisthobranch species afford important model organisms in various disciplines of life sciences, ranging from neurobiology [see the ground breaking work of Eric Kandel on *Aplysia* (e.g. Kandel 1979)], to ecotoxicology, to pharmaceutical research (e.g. Kijjoa and Sawangwong 2004). Therefore, a coherent taxonomy and understanding of the evolutionary relationships of this group are of paramount interest to many biologists.

Questions relating to the taxonomy, systematics and phylogeny of Opisthobranchia have been repeatedly challenged over the years. Morphology based studies have been hampered by the parallel evolution of numerous organ systems and structures (e.g. miniaturisation and wormlike body shape in meiofaunal lineages, splitting or fusion of ganglia and reproductive ducts, reduction of the shell and other organs), creating homoplasies in the datasets that have led to erosion of the phylogenetic signal (Ghiselin 1969; Gosliner and Ghiselin 1984; Gosliner 1985, 1991; Mikkelsen 1998a, b, 2002; Wägele and Klussmann-Kolb 2005; Schrödl and Neusser 2010). Heterochronic processes also obscured ontogenetic and phylogenetic transformations (Martynov et al. 2011). Molecular phylogenetic studies face conflicting phylogenetic signals with respect to the markers and methods used for inference (see below). This results in conflicting phylogenetic hypotheses and competing, or even contradictory, taxonomic classifications leading to an enormous spate of taxonomic names and concepts.

Haszprunar (1985a) addressed some of these problems in his important work in which he broadened our view on Euthyneura and redefined the Heterobranchia concept. More than 25 years later, we feel that it is about time to review the taxonomic literature of opisthobranch Gastropoda, to eludicate affiliation of heterobranch subgroups and to summarise plausible current systematic concepts that may serve as the basis for future studies on these enigmatic animals.

Historical review of the classification and transformation concepts of Opisthobranchia

Early nineteenth century

The first century of intensive studies into the morphology and taxonomy of opisthobranch Gastropoda focused on the unification, regrouping and naming of taxa resulting in partly very different and conflicting ideas of relationships and evolution of these marine snails and slugs. In his epochal “Le règne animal… Tome 2” (1817a), the well known naturalist Georges Cuvier distinguished three different phenotypes of Opisthobranchia based on the position of the gill and presence or absence of a protective shell, namely the Nudibranchia (a name introduced by Blainville in 1814, see Bouchet and Rocroi 2005), the Inferobranchia (phyllidiid nudibranchs) and the Tectibranchia. The latter group comprised mainly opisthobranch taxa with lateral gills and an external or internal shell. Blainville had already introduced the name Monopleurobranchiata Blainville, 1816 (see Bouchet and Rocroi 2005). Other names were subsequently proposed for this group, e.g. Steganobranchia von Ihering 1877 (see Bergh 1897). At that time, Pteropoda was regarded as a class level taxon with equal rank to Gastropoda and Cephalopoda. Cuvier (1817b) provided detailed studies of many opisthobranch genera still valid today. Many descriptions of families, such as *Doris, Tritonia, Phyllidia, Scyllaea, Aeolidia, Glaucus, Thethys, Pleurobranchus, Aplysia, Dolabella, Akera, Bulla, Philine, or Scaphander*, are based on these genera.

In 1848, Milne Edwards united sea slug and snail taxa under the name Opisthobranchia and proposed a three-taxon classification of Gastropoda: Prosobranchia, Opisthobranchia and Pulmonata. Gray (1840, see Haszprunar 1985a) had already united Opisthobranchia and Pulmonata under the name Heterobranchia. Von Ihering (1876) renamed the same group (Opisthobranchia plus Pulmonata) Ichnopoda and merged it with the Pteropoda into the Platymalakia, which he believed not to be closely related to his Cochlidae (= “Prosobranchia”). Mörch (1865) used hermaphroditism as a diagnostic character for this group (Opisthobranchia, Pulmonata and Pteropoda) and united the former taxa under the name Androgyna (Dayrat and Tillier 2002: 403).

Descriptions of opisthobranch species continuted to increase into the late nineteenth century, and new taxa on higher levels were proposed by several authors. Many of these taxa are still valid today in the same or a slightly modified sense (e.g. by using the ending -oidea or -idea to indicate a certain hierarchical order: e.g. Anthobranchia by Férussac, 1819 (see McDonald 2009), pleurobranchs by Férussac (1822), which are now arranged in Pleurobranchoidea (and within the Pleurobranchidae), Tylodinidae by Gray 1847, Cephalaspidea, Anaspidea and Notaspidea by Fischer 1883). In 1847, Gray performed a systematic arrangement of the known molluscan taxa, with a list of synonymies and types. Over the next few years, several famous malacologists, e.g. Risso, Delle Chiaje, G.O. Sars, Deshayes, Verany, Alder, Hancock, Bergh and Vayssière, published articles on various opisthobranch groups leading to a large increase in opisthobranch knowledge. For a good overview on the history of the first descriptions of Opisthobranchia and Nudibranchia, we refer the reader to Vayssière (1888, 1901).

Late nineteenth century

Around the late nineteenth century, some of the most innovative studies discussing relationships of opisthobranch groups were published by von Ihering (1876, 1877). He based his ideas about molluscan systematics on anatomical information taken from Lacaze-Duthiers (1870, after Dayrat and Tillier 2002) and his own examinations of nervous systems. Von Ihering united Opisthobranchia (including the Rhodopidae, a taxon he described in 1876) and Pulmonata within his new taxon Ichnopoda, which comprised many heterobranchs. He considered the Pteropoda to be the ancestors of the Cephalopoda and therefore excluded them from the Ichnopoda. Within Ichnopoda, two taxa of the same hierarchical rank were opposed to the various groups later united under Opisthobranchia: Branchiopneusta (new name), comprising the Basommatophora, and Nephropneusta (new name for Stylommatophora already introduced by Schmidt in 1855. Von Ihering (1876) considered the Pulmonata “diphyletique” with two different origins within the Opisthobranchia. On the contrary, Pelseneer (1894) (Fig. 1a) proposed their unique origin from *Acteon* de Montfort (1810). According to Pelseneer, the same genus gave rise to the Opisthobranchia. Basal pulmonates were the Auriculidae (now known as Ellobiidae), which gave rise to the Stylommatophora, and Amphibolidae—the latter being the ancestor of *Chilina* and hence the Basommatophora in the sense of Pelseneer (now united under Hygrophila). Pelseneer’s hypothesis on opisthobranch relationships, which he based on many organ systems, was especially confirmed by studies on the nervous system by Guiart (1899) (Fig. 1b). However, Guiart

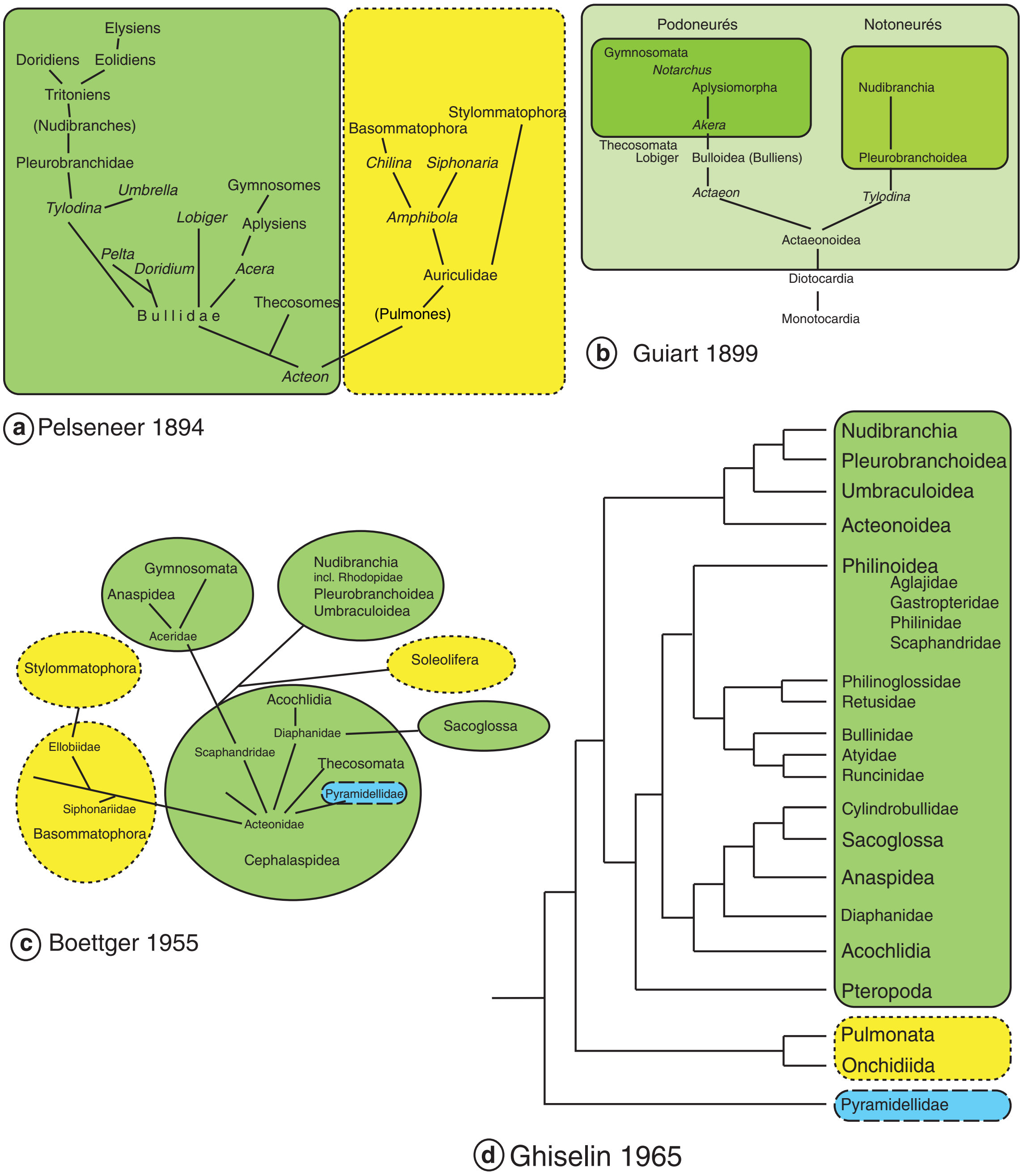

Fig. 1 Transformation series and evolutionary thinking in the time before phylogenetic analyses based on Hennigian principles: **a** Pelseneer 1894 (redrawn from original). **b** Guiart 1899 (redrawn from original). **c** Boettger 1955 (redrawn and summarised from original). **d** Ghiselin 1965 (redrawn as a phylogram and names altered according to up-to-date systematics). *Green* Traditional opisthobranch groups, *blue* (and with dashes) traditional lower heterobranchs, *yellow* (and with dots) traditional pulmonate groups

considered *Tylodina*, Pleurobranchoidea and Nudibranchia as having derived directly from Actenoidea and not from Bullidae. In contrast to, e.g. von Ihering (1876, see below), Pelseneer (1891, 1894, Fig. 1a) still considered Sacoglossa ("Elysiens") as members of the nudibranchs (in the sense of Cuvier). Guiart (1899) recognised the close relationship of Nudibranchia and Pleurobranchoidea: the former have evolved from the latter (now considered as sister taxa and united under Nudipleura by Wägele and Willan 2000). Guiart also considered the Aplysiomorpha, as derived from *Akera* (now both united under Anaspidea), and Gymnosomata as close relatives of the former.

Within the Opisthobranchia, von Ihering distinguished four orders, which were described in more detail in 1876 (von Ihering 1876): Protocochlides (name introduced by Ihering in 1876) with Rhodopidae, Tethyidae and Melibidae; Phanerobranchia (name introduced by von Ihering 1876) with all groups, which Cuvier had already united under the name Nudibranchia; Sacoglossa (name introduced by von Ihering 1876), with modern sacoglossan taxa included, except for *Ascobulla* and *Cylindrobulla*; Steganobranchia (name introduced by von Ihering 1876), which comprise taxa usually united as Tectibranchia Cuvier, 1817b (= Pleurobranchiata Gray, 1840) (e.g. Cephalaspidea, Acteonoidea and Anaspidea). None of the introduced names lasted, except for the Sacoglossa. However, the name Phanerobranchia was re-introduced by Bergh (1880) (as an adjective) for a subgroup of the nudibranch group Doridoidea with non-retractile gills (= Dorididae eleutherobranchiata see Bergh 1897), and this name has subsequently been used for this doridoidean group. Fischer (1883, see Valdés 2002a), who followed the suggestion of Bergh (1879) to separate dorids with retractable gills ("Dorididae cryptobranchiatae"), finally introduced the name Cryptobranchia for the latter group.

In 1880, von Ihering proposed the primitive nature of the Nudibranchia and argued their close relationship to turbellarian species. Only a year later, Spengel (1881) united the Opisthobranchia and Pulmonata under the new name Euthyneura, opposing them to the Prosobranchia. This concept endured for more than 100 years until Haszprunar (1985a) (Fig. 2a) showed that several former prosobranch groups, the Architectonicoidea and Pyramidelloidea, are related closely to the Euthyneura (see below). Pelseneer (1892) gave a short review on euthyneuran relationships and recognized only Tectibranchia (with all shelled groups indicated in his earlier works) and Nudibranchia within the Opisthobranchia. In 1894, he described and re-organised the known tectibranch groups, and indicated characters that united or separated different families (see the more detailed review of Mikkelsen 2002). Graff (1882) excluded *Rhopode* from the Turbellaria and included this enigmatic group within the Nudibranchia, whereas Bergh (1882:553) still considered it as a "modificirte Turbellarie".

The late nineteenth century was also the time at which discussion on the phylogenetic relationships for subordinated opisthobranch groups started. Fischer (1883) characterised three major groups within the Tectibranchia (Cephalaspidea, Anaspidea and Notaspidea), with the Cephalaspidea and Anaspidea being closely related, and the Notaspidea having a closer affinity to the Nudibranchia (see Bergh 1897). This was also assessed by Guiart (1899, 1900, 1901, Fig. 1b). Vayssière (1885) included the Peltidae (now known as Runcinidae), Pleurobranchoidea and Tylodinoidea in Fischer's Notaspidea.

Early twentieth century in the post-Darwinian era

It was not before 1890, after an extraordinarily extensive study on opisthobranch species and genera spanning over nearly 35 years, that Bergh presented his first evolutionary scenario on the Nudibranchia, which he divided into two major groups: the "Nudibranchiata cladohepatica" and "Nudibranchiata holohepatica" (Bergh 1890, 1891). The latter group is now called Anthobranchia—a name already introduced by Férussac (in 1819 see Valdés 2002b, or in 1822) (see above). It was only in 1984 that Willan and Morton introduced the name Cladobranchia for the cladohepatic nudibranchs in the sense of Bergh. Bergh indicated the origin of the Cladobranchia ("cladohepatische Nudibranchier") together with the Pulmonata in the tectibranch group. Sacoglossa were considered as a transitional state towards the Cladobranchia. The first group to have evolved from sacoglossans ("Phyllobranchidae, Ascoglossa") was the Aeolidoidea ("Aeolidiadae"), which in itself gave rise to three different groups: the Arminidae ("Pleurophyllidiadae" that then gave rise to "Pleuroluridae"), the "Tethymelibidae" and all other dendronotoidean families. Bergh considered the holohepatic form of the digestive gland as derived, and therefore also the Doridoidea (holohepatic nudibranchs), but he did not indicate the placement of this latter group in his tree. He addressed this question in 1906, when he published a transformational line from *Tritonia*, *Tritonidoxa* and *Doridoxa* to *Bathydoris* and from this group to the "Nudibranchiata holohepaticata" (sensu Doridoidea). His assumptions were based mainly on the digestive system, but considered also information from several other organ systems. In earlier years he had already mentioned unlikely relationships postulated by his colleagues, e.g., in 1888, he had noted that the taxon Inferobranchiata Cuvier 1817a, in which the Phyllidiidae (now considered members of the nudibranch taxon Anthobranchia) and the Arminidae ("Pleurophyllidiidae", now considered members of the Cladobranchia) were united, was artificial.

Pelseneer (1894) included the Pteropoda, which had been considered a separate molluscan group, within the Opisthobranchia (Fig. 1a). For a detailed review of the history of the systematic placement of pteropods, we refer to Lalli and Gilmer (1989). Pelseneer split the pteropods by rendering the Thecosomata (a name introduced by de Blainville in 1824) the most basal offshoot within the Opisthobranchia and the members of the Gymnosomata (a name also introduced by Blainville in 1824) as derived aplysiids. The latter proposition was confirmed in subsequent studies (e.g.Tesch 1904; Meisenheimer 1905; van der Spoel 1967, 1976). Another very interesting aspect in the light of recent analyses was his derivation of the Anaspidea from a Bullidae-like ancestor. According to his studies, Nudibranchia (used in the old sense and still including members of the Sacoglossa) have evolved from pleurobranchoidean forms and these in turn from *Tylodina*. Sacoglossa ("Elysiens") have evolved from the aeolidoidean group. The Nudibranchia and "Elysiens" split into three groups: the most basal taxon was

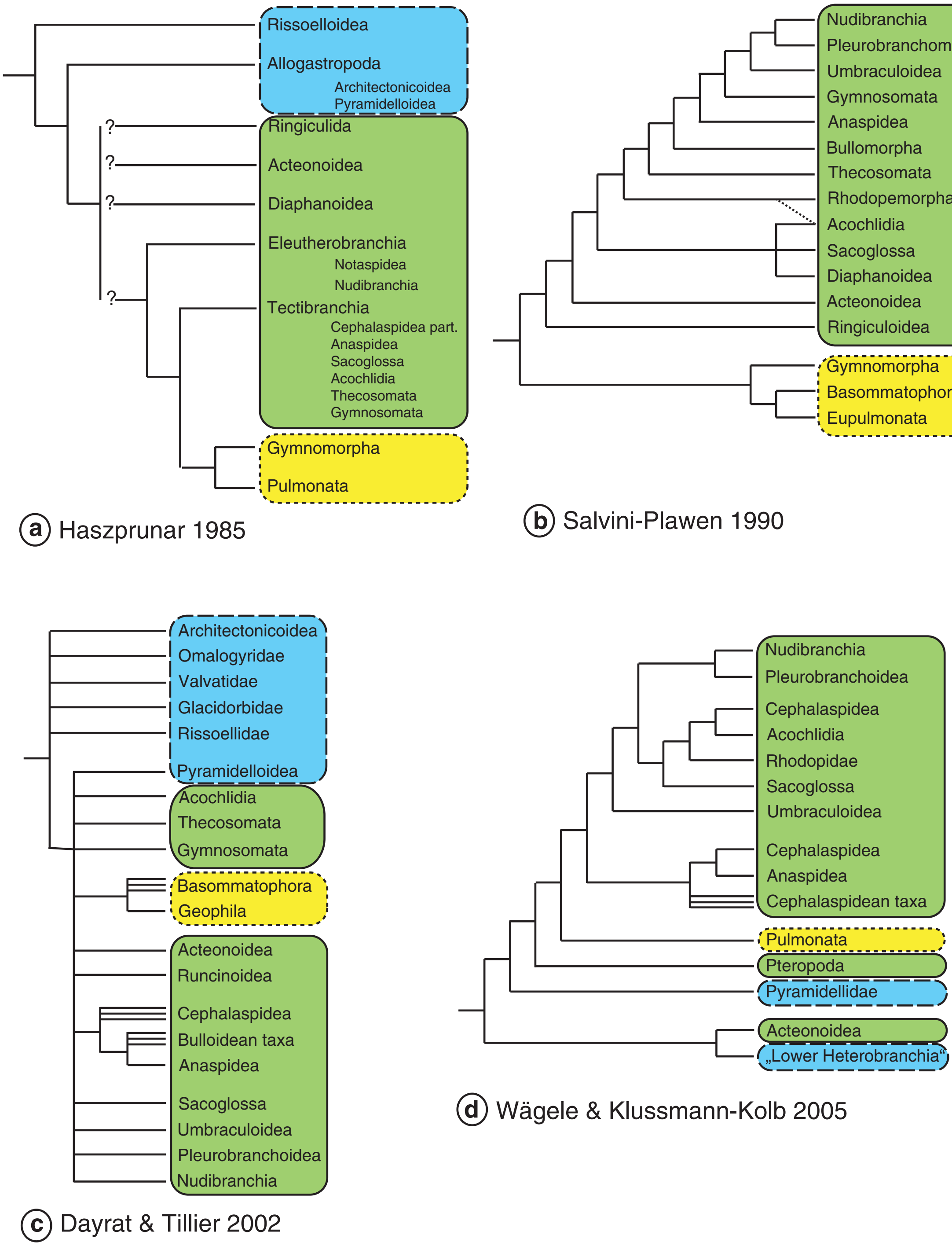

Fig. 2 First phylogenetic analyses based on morphological data (taxa partly combined, and higher taxa names used): **a** Haszprunar 1985a (redrawn as a phylogram and subgroups listed according to text). **b** Salvini-Plawen 1990 (redrawn and names altered according to up-to-date systematics). **c** Dayrat and Tillier 2002 (redrawn). **d** Wägele and Klussmann-Kolb 2005 (redrawn). *Green* Traditional opisthobranch groups, *blue* (and with dashes) traditional lower heterobranchs, *yellow* (and with dots) traditional pulmonate groups

represented by *Tritonia*. From this genus the Doridoidea originated, with *Phyllidia* being the most highly evolved genus. The second group showed the evolution of the sacoglossans *Elysia* and *Limapontia* with aeolid genera as transitional forms. A third group comprised the aberrant dendronotoidean genera *Tethys*, *Melibe*, *Scyllaea* and *Phyllirhoe*. It was Odhner (1922) who finally dropped the hypothesis of *Tritonia* being a transitional form to all nudibranchs and recognized that it had its own evolutionary history.

In his handbook on molluscan taxa, Thiele (1931) united Cephalaspidea and Anaspidea under the Pleurocoela [= Tectibranchia (partim)], and the Notaspidea and Nudibranchia under the Acoela (= Eleutherobranchia, a new name introduced by Haszprunar in 1985a). The Pteropoda and Sacoglossa had equal ranks to the Pleurocoela and Acoela. The Nudibranchia did now comprise the Doridacea Thiele, 1931(= Holohepatica, = Doridoidea, now Anthobranchia), Aeolidacea Thiele, 1931 (= Cladohepatica, now Cladobranchia) and the Rhodopidae. Following descriptions of Bergh (1895), Thiele (1931) still grouped the Hedylidae within the "Aeolidacea". Odhner (in 1936 and more thoroughly described in 1938) considered the family Hedylidae as a separate taxon from the Nudibranchia and arranged this group under the name Hedylacea separately but within the Acoela. Later, Odhner (1939) considered the two taxa Acoela and Pleurocoela as superfluous. He gave the Hedylacea (then named by him Acochlidiacea, and later modified to Acochlidia by Wawra 1987) an equal rank to the Cephalaspidea, Anaspidea, Sacoglossa and others, taking into account their distinctiveness to the Nudibranchia and Notaspidea.

It was Odhner (1934, 1936, 1939) who revised the Nudibranchia by emphasising again the exclusion of the Sacoglossa. He omitted the old taxa names Holohepatica and Cladohepatica, redefined the taxon name Aeolidacea of Thiele (1931) and raised the three major nudibranch subgroups to equal ranks: Doridacea (= Doridoidoidea), Dendronotacea (= Dendronotoidea) and Aeolidacea (= Aeolidoidea). Additionally, he formed a new group, the Arminacea (= Arminoidea) (Odhner 1934). He also favored the hypothesis that the Nudibranchia had originated within the Notaspidea.

Comprehensive anatomical analyses of Opisthobranchia in the light of euthyneuran relationships were presented again in the mid-1950s of the last century. Boettger (1955, Fig. 1c) proposed an evolutionary scenario based mainly on the nervous system. He distinguished six major groups within Euthyneura: (1) Cephalaspidea; (2) Anaspidea; (3) Sacoglossa; (4) Nudibranchia sensu Acoela (with Nudibranchia—as understood today—and Notaspidea); (5) Eupulmonata (with Basommatophora and Stylommatophora as understood today); (6) Soleolifera. The most basal taxon presented were the Acteonidae, which gave rise to all mentioned euthyneuran groups. Some major results of Boettger's studies were the paraphyly of the pulmonates, because the Soleolifera represented a separate evolutionary line originating from the stemline of the Notaspidea and Nudibranchia. He included the Pyramidellidae, Acochlidiacea and Thecosomata into the Cephalaspidea and also grouped the Gymnosomata within the Anaspidea. He assumed that the four nudibranch groups outlined by Odhner (1934) (Doridoidea, Dendronotoidea, Arminoidea and Aeolidoidea) evolved from a *Tylodina*-like group and not from pleurobranchs. Furthermore, Boettger (1955) considered the Rhodopidae to be a family of the Doridoidea based on the presence of spicules in both groups. This opinion was also adopted by Odhner (1968).

Second half of the twentieth century: evolutionary thinking

Although Hennig published his first concepts on analysing phylogenetic relationships to understand evolution on the basis of shared and derived characters in 1950 in German and 1966 in English (Hennig 1955, 1966), his methods were not applied in opisthobranch studies until the late 1980s (see below). Malacologists still rather tried to *explain* evolution and deduced phylogenetic relationships while describing morphological transformation processes and subsequently superimposing a tree on these assumptions.

Ghiselin (1965) (Fig. 1d) presented a comprehensive evolutionary scenario of the Opisthobranchia, in which he concentrated not only on the patterns of morphological characters, but also on a transformation series of morphological structures within the genital system. His results certainly laid the major groundwork for many forthcoming studies on Opisthobranchia, those of the present authors included. In contrast to Boettger (1955), Ghiselin (1965) excluded the Pyramidellidae, the Onchidiida (= todays Systellommatophora Pilsbry, 1948) and the Pulmonata from the Opisthobranchia. The Opisthobranchia were divided into two major groups. The first group comprised the Umbraculoidea (= Tylodinoidea), Pleurobranchoidea and Nudibranchia, the latter with Acteonoidea as sister taxon. The second group comprised the following taxa: Sacoglossa (with Cylindrobullida) and Anaspidea as sister taxa, both originating from a diaphanid-like form. Together, they were the sister group to the Acochlidia and these again the sistergroup of all other Cephalaspidea. From that stemline, the monophyletic Pteropoda originated.

Salvini-Plawen (1970) drew attention to the Rhodopidae, which in his opinion should have been transferred from the Doridoidea (Nudibranchia) to the Gymnomorpha [new name introduced by Salvini-Plawen, 1970, (= Systellommatophora)]. According to Salvini-Plawen, Gymnomorpha and Anaspidea had a common ancestor within Cephalaspidea, together with a second clade comprising Sacoglossa, Notaspidea and Nudibranchia. Pulmonata arose separately.

In 1970, Tardy published his hypothesis on nudibranch evolution based on his observations on metamorphosis. One new aspect in this study was the inclusion of the former anthobranch *Doridoxa* in the Cladobranchia, as the most basal taxon; this view was supported by comparative anatomy later and the taxon name Dexiarchia was introduced (Schrödl et al. 2001). Furthermore, Tardy excluded Rhodopidae (in concordance with Salvini-Plawen 1970) from the Doridoidea without any assumption about its closest relatives.

In the same year, Minichev (1970) published ideas on the evolution of the Nudibranchia. He considered this group polyphyletic, the Doridoidea originating from cephalaspideans and the other groups (Nudibranchia sensu Minichev, now understood as Cladobranchia) from the pleurobranchs. His hypotheses were based mainly on the circulatory system and respiratory organs. Even more unexpected were the evolutionary scenarios on euthyneurans presented by Minichev and Starobogatov (1978). In their short note, these latter authors proposed an independent origin of four different clades from diotocardian prosobranch ancestors, i.e. a prosobranch with a pair of auricles. These four clades comprised the following groups: (1) Siphonariidae; (2) Pulmonata; (3) Opisthobranchia (s.str.) with Cephalaspidea, Anaspidea, Sacoglossa and Nudibranchia; (4) Dextrabranchia comprising Thecosomata, Acochlidia, Notaspidea (more recently no longer united, but considered as separate taxa Pleurobranchoidea and Tylodinoidea, see Schmekel 1985; Wägele and Willan 2000), and Systellommatophora. This classification was based on a single organ system (characters of the reproductive tract) and provided minimum justification and discussion relative to competing classifications (Martynov 2011). Baranetz and Minichev (1994, 1995) suggested an evolutionary shift of the anus and gills from an ancestral frontal to a lateral right side position in Doridoxidae, to a ventral and terminal position in Corambidae and Phyllidiidae, and finally to the dorsal side in other Doridoidea. These authors renewed an earlier proposal of basal orders “Corambida” and “Phyllidiida” (see Minichev and Starobogatov 1979), separate from other Doridoidea plus Bathydoridoidea (the latter two groups now united under the name Anthobranchia). Only recently, cladistic approaches have suggested that phyllidiids are members of doridoidean porostomes (Valdés 2002a), and corambids are derived rather than basal doridoidean nudibranchs (Martynov et al. 2011; Martynov and Schrödl 2011).

Classification and phylogenetic concepts of Opisthobranchia since the 1980s

Morphology-based phylogenetic approaches

A real impulse to phylogenetic studies in Opisthobranchia was observable from the 1980s onwards, when Hennigian phylogenetic and later cladistic methods became available. A milestone was the formal establishment of the Heterobranchia concept by Haszprunar (1985a, Fig. 2a), uniting the clades Allogastropoda (now a grade “lower heterobranchs”) and Pentaganglionata (Euthyneura, still including Architectibranchia, such as Acteonoidea, Diaphanoidea and Ringiculoidea). Rissoelloidea (with Rissoellidae and Omalogyridae) was first considered to be the sister taxon to Heterobranchia (Fig. 2a) (Haszprunar 1985a), but was later included in the latter (Haszprunar 1988). Ectobranchia (name preferable over Valvatoidea Gray, 1840, see Haszprunar et al. 2011) were also added to Heterobranchia as their earliest offshoot; this is still regarded as valid (Haszprunar et al. 2011; Brenzinger et al. 2013a).

Since then a rash of phylogenetic analyses based on morphological data has appeared. Some studies have dealt with opisthobranch phylogeny in general (Gosliner 1981; Schmekel 1985; Salvini-Plawen 1990, 1991; Salvini-Plawen and Steiner 1996; Dayrat and Tillier 2002; Mikkelsen 2002; Wägele and Klussmann-Kolb 2005) (Fig. 2b–d); however, without recovering completely congruent and convincing topologies. In their morpho-anatomical cladistic analysis of Heterobranchia, Dayrat and Tillier (2002) emphasised that relationships of euthyneuran groups are mainly unresolved and that the low resolution reflects the high variability of euthyneuran anatomical characters (Fig. 2c). New ultrastructural data such as on osphradia and sperm were informative additional characters for resolving the phylogeny of several gastropod subgroups (Haszprunar 1985b, c; Healy 1991, 2005). Nevertheless, structural characteristics are quite homogeneous within several euthyneuran subgroups on the one hand, whereas other organs had not yet been explored comparatively across taxa (Dayrat and Tillier 2002).

Exploring and using morpho-anatomical characters, other authors investigated phylogenetic relationships within major subgroups (Edlinger 1980; Willan 1987; Jensen 1996; Mikkelsen 1996; Cervera et al. 2000; Medina and Walsh 2000; Wägele and Willan 2000; Schrödl et al. 2001; Klussmann-Kolb 2004; Wägele and Klussmann-Kolb 2005; Martynov and Schrödl 2008; Schrödl and Neusser 2010) or even at family and genus level (e.g. Gosliner 1980, 1989, 1995, 1996; Haszprunar 1985c; Gosliner and Kuzirian 1990; Gosliner and Willan 1991; Millen and Nybakken 1991; Gosliner and Johnson 1994, 1999; Kolb and Wägele 1998; Valdés and Bouchet 1998; Fahey and Gosliner 1999; Garavoy et al. 1999; Garovoy et al. 2001; Valdés and Gosliner 1999, 2001; Fahey and Gosliner 2000; Dorgan et al. 2002; Valdés 2002a, b; Bertsch et al. 2009; Martynov and Schrödl 2011; Corse et al. 2013; and many others). Based on some of these studies, new taxa were erected, e.g. the Nudipleura (Wägele and Willan 2000), which comprised monophyletic Nudibranchia and monophyletic Pleurobranchoidea as sister groups. Re-analyses of the latter dataset with modified taxon and character coverage indicated the sensitivity of morphology-based nudipleuran topologies (Martynov and Schrödl 2008; Martin et al. 2009, 2010); the same applies to much more extensive euthyneuran analyses, e.g. by Wägele and Klussmann-Kolb (2005) (Fig. 2d).

Using the taxon Acochlidia as a case study, Schrödl and Neusser (2010) hit further problems besides the legendary rampant level of homoplasy that limits the power of cladistic analyses based on morphology in euthyneurans and subgroups: the quantity of codable characters with sufficient information available was much lower than expected. Even more striking than the amount of missing data and unclear nature of earlier homology assignments was the inadequate quality of primary descriptions. Descriptions, especially of small sized species, were unreliable when based on dissections. However, even data obtained from paraffin-based histology (see Neusser and Schrödl 2007; Neusser et al. 2009a) turned out to be faulty enough to severely mislead cladistic analyses of acochlidians. Semithin histological techniques (e.g. Schrödl and Wägele 2001; Wägele and Cervera 2001; Göbbeler and Klussmann-Kolb 2010b), ideally combined with full, software-aided 3D microanatomical reconstructions (e.g. Neusser et al. 2006), paved the way for comparative studies across euthyneurans (e.g., Rückert et al. 2008; Neusser et al. 2009b, 2011a, b; Golding 2010; Wägele et al. 2010; Brenzinger et al. 2011a, b; Eder et al. 2011; Haszprunar et al. 2011; Kohnert et al. 2013). For example, Brenzinger et al. (2013a) could show that the close affinities of Rhodopemorpha with "lower heterobranchs" related to Murchisonellidae, and morphological features similar to Doridoidea, are due to convergences. The phylogenetic signal of previously neglected or misunderstood complex organ systems still needs to be unraveled.

The thankless task of presenting a classification of Opisthobranchia

Classification is desired in science and text books (e.g. *Mollusca: the southern synthesis*, edited by Beesley et al. 1998) but often turns out to be a difficult task when phylogenetic analyses are contradictory, the denotation of names has changed several times, and a plethora of names for the same taxon is available. In 2005, Valdés and Bouchet (in Bouchet and Rocroi) published a compendium on the nomenclature of Gastropoda—their results and conclusions based mainly on morphological data. They considered Opisthobranchia and Pulmonata as informal groups. The aforementioned major taxa of Opisthobranchia were classified as follows, partly introducing new names or re-introducing less used names (for clarity we have added more commonly used names in brackets)

Informal Group Opisthobranchia

- Clade Cephalaspidea
- Clade Thecosomata
- Clade Gymnosomata
- Clade Aplysiomorpha (Anaspidea)
- "Group" Acochlidiacea (Acochlidia)
- Clade Sacoglossa
- "Group" Cylindrobullida (with only the genus *Cylindrobulla*, now assigned to Sacoglossa)
- Clade Umbraculida (Umbraculomorpha, Tylodinoidea)
- Clade Nudipleura
  - Clade Pleurobranchomorpha (Pleurobranchoidea)
  - Clade Nudibranchia
    - Clade Euctenidiacea (Anthobranchia)
      - Subclade Gnathodoridacea (Bathydoridoidea)
      - Subclade Doridacea
        - Doridoidea (Labiostomata; Cryptobranchia *partim*)
        - Phyllidioidea (Porostomata; Cryptobranchia *partim*)
        - Onchidoridoidea (Suctoria; Phanerobranchia *partim*)
        - Polyceroidea (non-Suctoria, Phanerobranchia *partim*)
    - Clade Nudibranchia Dexiarchia
      - Clade Pseudoeuctenidiacea (Doridoxoidea)
      - Clade Cladobranchia
        - Subclade Euarminida (comprising Arminidae and Doridomorphidae only)
        - Subclade Dendronotida (Dendronotoidea)
        - Subclade Aeolidida (Aeolidoidea)

Several opisthobranch "clades" were revealed as non-monophyletic; e.g. "Polyceroidea" is a basket for enigmatic families (see Wägele and Willan 2000). Bouchet and Rocroi (2005) and their taxonomic group editors were of course aware of the conflicts of such a pragmatic classification; e.g. they presented several cladobranch families unassigned to higher taxa. Among doridoidean nudibranchs, the Cryptobranchia were long thought to be a clade nested among phanerobranchs [e.g. in seminal analyses by Valdés and Gosliner (2001) and Valdés (2002a)], while actually phanerobranch lineages may split off a cryptobranch stemline (see Martynov et al. 2009, 2011). The history of lineages that were assigned to and removed from the Cephalaspidea was reviewed by Brenzinger et al. (2013b), and basal sacoglossan systematics by Kohnert et al. (2013). The classification by Bouchet and Rocroi (2005) is still in use but, once established, it was challenged immediately by upcoming molecular systematic approaches.

Molecular approaches

Another major impetus was given in the 1990s by the development of molecular phylogenetic methodology. Starting with single marker analyses, traditional morphology-based hypotheses on relationships of major opisthobranch subgroups were already challenged (e.g. Thollesson 1999a, b; Wollscheid and Wägele 1999; Dayrat et al. 2001; Wollscheid-Lengeling et al. 2001) (Fig. 3a–d). Subsequently, multilocus analyses appeared utilizing a variety of nuclear and mitochondrial markers to unravel phylogenetic relationships within Opisthobranchia and subgroups (e.g. Wägele et al. 2003; Grande et al. 2004a, b; Vonnemann et al. 2005; Klussmann-Kolb and Dinapoli 2006; Händeler and Wägele 2007; Händeler et al. 2009; Malaquias et al. 2009; Göbbeler and Klussmann-Kolb 2010a, b, 2011; Maeda et al. 2010; Pola and Gosliner 2010; Moore and Gosliner 2011; Johnson and Gosliner 2012; Pola et al. 2012; Corse et al. 2013; Carmona et al. 2013, and many more) (Fig. 3a, b) or phylogenetic relationships of opisthobranch taxa within Euthyneura (Grande et al. 2004b; Klussmann-Kolb et al. 2008; Dinapoli and Klussmann-Kolb 2010; Jörger et al. 2010; Göbbeler and

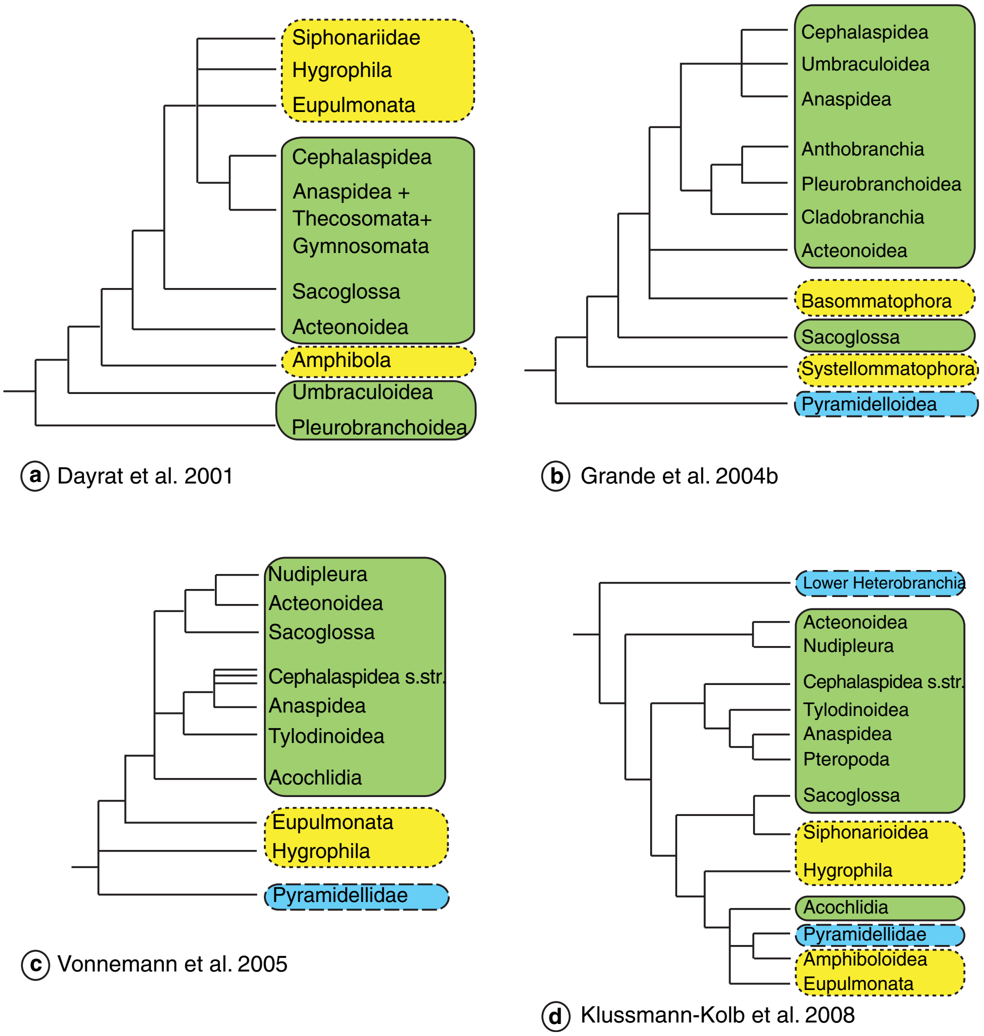

Fig. 3 First phylogenetic analyses based on molecular data (cladograms redrawn, taxa partly combined, and higher taxa names used): **a** Dayrat et al. 2001 (combined and higher taxa names used). **b** Grande et al. 2004b (combined and higher taxa names used). **c** Vonnemann et al. 2005 (combined and higher taxa names used). **d** Klussmann-Kolb et al. 2008 (combined and higher taxa names used). *Green* Traditional opisthobranch groups, *blue* (and with dashes) traditional lower heterobranchs, *yellow* (and with dots) traditional pulmonate groups

Klussmann-Kolb 2011; Dayrat et al. 2011; Schrödl et al. 2011a; Dinapoli et al. 2010) (Fig. 4a, c).

Klussmann-Kolb et al. (2008) (Fig. 3c) were the first to establish a mixed set of mitochondrial COI and 16S, and nuclear 18S and 28S markers on a broader sampling of opisthobranch, pulmonate and also several "lower heterobranch" taxa. They found the traditional Opisthobranchia to be paraphyletic, with Nudipleura clustering in a basal position. Dinapoli and Klussmann-Kolb (2010) and Jörger et al. (2010) added data with regards to taxon sampling, refined their analyses and got good support for a close relationship of the opisthobranch groups Acochlidia and Sacoglossa with pulmonate taxa.

Jörger et al. (2010) (Fig. 4a) thus proposed a new system of Euthyneura including the following clades: Nudipleura as the most basal offshoot, Euopisthobranchia (new name for the taxon that comprises Umbraculoidea = Tylodinoidea, Cephalaspidea, Runcinacea, Anaspidea and Pteropoda) and Panpulmonata (name also introduced by these authors). The latter include Siphonariidae, Sacoglossa (with *Cylindrobulla* nested within oxynaceans), Acochlidia (= Acochlidiacea, including Aitengidae Swennen and Buatip, 2009), Pyramidellidae (but not Murchisonellidae = Ebalidae), and all the former pulmonate groups including the aberrant Glacidorbidae and Amphibolidae. The sister clade of Nudipleura, composed of Euopisthobranchia and Panpulmonata, was given the name Tectipleura by Schrödl et al. (2011a). Acteonoidea are now considered to belong to the "lower Heterobranchia", based on results by Göbbeler and Klussmann-Kolb (2010a) and Dinapoli and Klussmann-Kolb (2010). "Lower heterobranchs" also include now Rhodopemorpha (Wilson et al. 2010; Brenzinger et al. 2013a).

These studies have been challenged recently by a mitogenomic study of Medina and co-workers in 2011 (Fig. 4b). These authors found Opisthobranchia (in a broader sense) again monophyletic, with Acteonoidea and Nudipleura being sister groups (the name Acteopleura was introduced by these authors). This sister group relationship had already been proposed by Ghiselin (1965) as well as by Grande et al. (2004b) and Vonnemann et al. (2005), but was rejected by studies

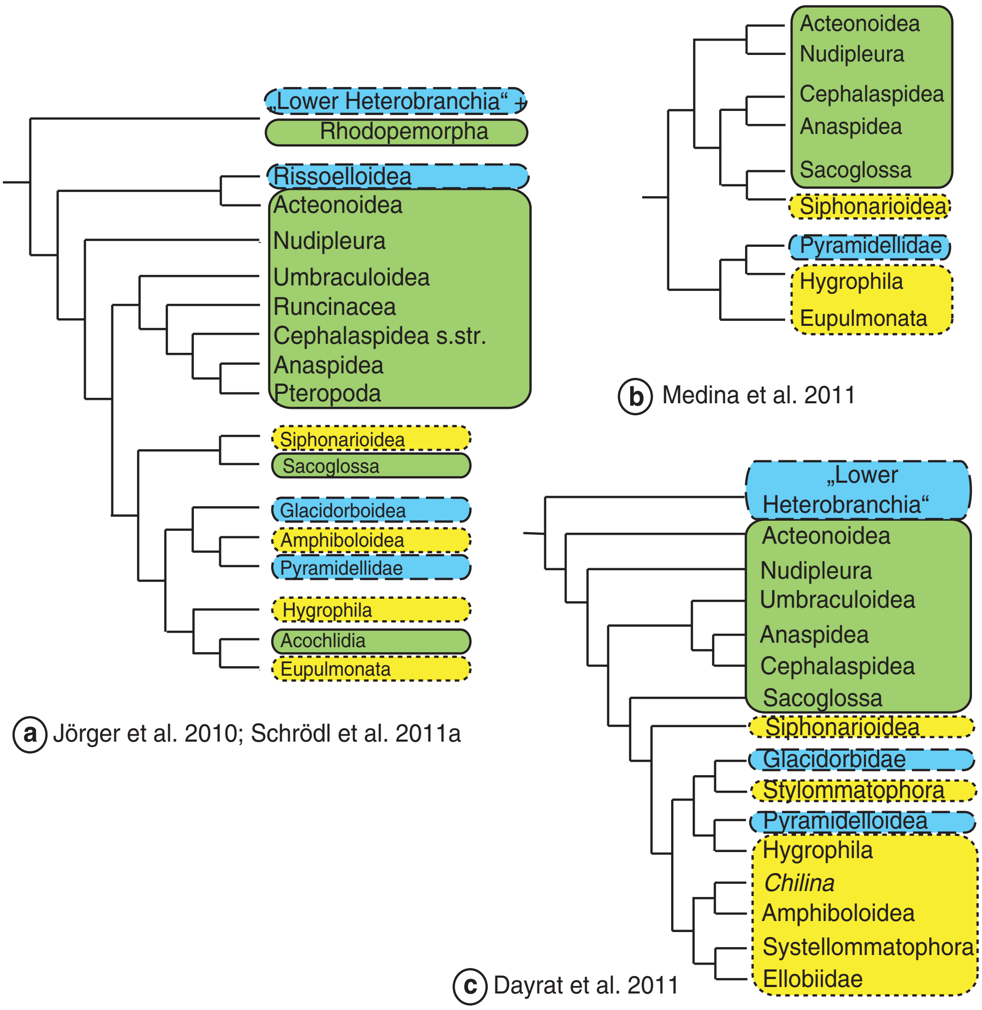

Fig. 4 Most recent phylogenetic analyses based on molecular data (cladograms redrawn, taxa partly combined, and higher taxa names used): **a** Jörger et al. 2010 (taxa summarised, rhodopemorphs added according to Schrödl et al. 2011a). **b** Medina et al. 2011 (mitochondrial genome data). **c** Dayrat et al. 2011. *Green* Traditional opisthobranch groups, *blue* (and with dashes) traditional lower heterobranchs, *yellow* (and with dots) traditional pulmonate groups

using a more comprehensive taxon sampling (see Schrödl et al. 2011b). Medina et al. (2011) recovered Cephalaspidea and Anaspidea as sister groups, naming this clade Placoesophaga due to the possession of a gizzard. This is a junior synonym of Thiele's (1931) Pleurocoela. Analyses including not only mitochondrial data but also nuclear loci (e.g. Malaquias et al. 2009; Dinapoli and Klussmann-Kolb 2010; Jörger et al. 2010) (Fig. 4a) clearly indicate a close relationship of Runcinacea and Pteropoda to the Pleurocoela (Placoesophaga) rendering the latter paraphyletic. If Medina and co-worker's Placoesophaga concept is extended to tectibranch taxa sharing an apomorphic oesophageal cuticle, it is synonymous to Euopisthobranchia (see Schrödl et al. 2011b). Medina et al. (2011) recovered Sacoglossa as sister taxon to Siphonarioidea comprising both the Siphoglossa (name introduced by these authors). A close association of Siphonarioidea and opisthobranch taxa had already been proposed by Haller (1892) based on morphology, but Jensen (2011) considered similar gill and mantle cavity organisation to be convergent. Schrödl et al. (2011b) commented that the clade of Sacoglossa and Siphonarioidea was recovered based on mitochondrial (Grande et al. 2004b) and combined mitochondrial and nuclear loci by Jörger et al. (2010), but without any support in the latter study, while Sacoglossa are unresolved or not direct sister to Siphonarioidea in other mixed multi-locus studies (Dinapoli and Klussmann-Kolb 2010; Dayrat et al. 2011) (Fig. 4c) and mitogenomic approaches (White et al. 2011).The use of mitochondrial markers, and especially of purely mitogenomic sequences, for resolving deep euthyneuran or gastropod nodes has been questioned (Schrödl et al. 2011a) and a specific critique of Medina et al.'s (2011) (Fig. 4b) systematic and evolutionary conclusions was presented by Schrödl et al. (2011b). Recent analyses of metazoan and all molluscan mitogenomes available in July 2011 show that Heterobranchia are on a very long branch that may suffer from artificial attraction of distant taxa (Stöger and Schrödl 2012). Since long-branched stylommatophoran pulmonates are recovered as the most basal heterobranchs, the authors assume that inner-heterobranch topology is not appropriately rooted. In fact, the topology by Medina et al. (2011) and, more generally, any traditional concepts of monophyletic Opisthobranchia and Pulmonata are contradicted by all phylogenomic and other approaches that include nuclear rather than mitochondrial genes. In contrast, topologies recovered by recent phylogenomic studies (Kocot et al. 2011, 2013; Smith et al. 2011) and a study based on housekeeping genes (Vinther et al. 2011) all are compatible with the backbone topology of the tree presented by Schrödl et al. (2011a).

Reviewing the "new euthyneuran tree" and its consequences

According to latest analyses of Heterobranchia (see review above), Schrödl et al. (2011a) noted that several nodes show high congruencies, whereas others are unresolved. They also stressed that the results of these analyses differ radically from those of traditional hypotheses. Most recently, Brenzinger et al. (2013a) highlighted the robust nodes in a simplified cladogram (combined from Jörger et al. 2010; Schrödl et al. 2011a, b; Dayrat et al. 2011) and summarised putative morphological apomorphies discussed, e.g., by Haszprunar (1985a), Dayrat and Tillier (2002), and Haszprunar et al. (2011). In Fig. 5 we modify the tree proposed by Brenzinger et al. (2013a) by collapsing the Ectobranchia (Valvatoidea) into a basal polytomy, considering that morphological evidence (see Hawe et al. 2013) conflicts with molecular evidence and sperm ultrastructure, as far as is known (see Brenzinger et al. 2013a for discussion). Reviewing current morphological knowledge (Fig. 5), Heterobranchia (1) are characterised by several apomorphic features, such as hyperstrophy of larval shell, pallial kidney, hypobranchial gland in anterior position, odontophoral cartilages lacking (or muscular), hermaphroditism, loss of parasperm, sperm spiral-shaped, coarse fibres, intra-axonemal dense granules. Euthyneura s.l. and Rissoelloidea/Acteonoidea (2) share giant neurons in macroscopic (larger) animals (Brenzinger et al. 2013a). Euthyneura s.l. (3) have rhinophores innervated by N3 (nervus rhinophoralis) (Staubach 2008; Klussmann-Kolb et al. 2013) and exhibit a euthyneurous nervous system (but with reversals in subgroups) (Brenzinger et al. 2013a). Rather than representing a derived branch within the Euthyneuran tree, Nudipleura are in a basal position, suggesting a set of partly plesiomorphic rather than entirely derived character conditions. Basal euthyneurans thus may have had nudipleuran-like androdiaulic reproductive systems (Schrödl et al. 2011a) and head tentacles. Tectipleura (4) are characterised by a monaulic genital system (Schrödl et al. 2011a). Euopisthobranchia (5), i.e. a considerably modified Tectibranchia in the sense of Cuvier (1817b), share a cuticularised oesophagus. Cephalaspidea, previously assumed to be among the most basal opisthobranchs with putatively plesiomorphic habitus, appear to be a derived taxon with derived features, such as head shields (Brenzinger et al. 2013b). Panpulmonata (6) have a procerebrum (or rhinophoral nerves) with double roots (Brenzinger et al. 2013a). Accepting former opisthobranch taxa such as Sacoglossa, Acochlidia as well as traditional basal heterobranch taxa such as Pyramidellidae, but also enigmatic taxa such as Glacidorbidae and Amphibolidae as part of a panpulmonate diversification (e.g. Dayrat et al. 2011; Fig. 4c), old views on the homology of organs have changed (see Jörger et al. 2010; Schrödl et al. 2011a). However, it is not only the evolution of organ systems that has to be re-evaluated. Evolutionary traits and strategies such as invasions of freshwater or terrestrial habitats (see Klussmann-Kolb et al. 2008) and exploitation of various food sources (Göbbeler and Klussmann-Kolb 2011; Neusser et al. 2011b) are also in need of re-investigation. Molecular chronograms indicate that euthyneuran diversification started in the Late Paleozoic (Jörger et al. 2010; Schrödl et al. 2011b), with species-rich extant clades such as marine Nudibranchia,

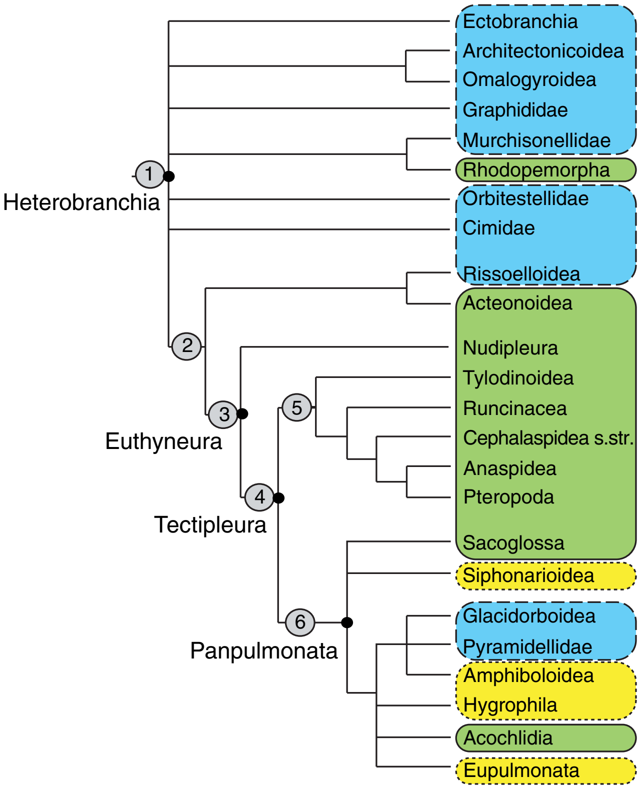

Fig. 5 Consensus tree and "new phylogenetic hypothesis" (combined from Dinapoli and Klussmann-Kolb 2010; Jörger et al. 2010; Schrödl et al. 2011a), with well-supported nodes (*dots*). Further putative heterobranch clades have not yet been included in molecular systematics and thus are not yet included in the tree. Ectobranchia is the preferred name for Valvatoidea (see text). Graphidae represents *Aclis* sp. sensu Dinapoli & Klussmann-Kolb (2010) (see Waren 2013). Numbers indicate putative apomorphies (partly adopted from Dayrat and Tillier 2002; Staubach 2008; Haszprunar et al. 2011; Klussmann-Kolb et al. 2013; Brenzinger et al. 2013a): *1* Hyperstrophy, pallial kidney, hypobranchial gland in anterior position, odontophoral cartilages lacking (or muscular), hermaphroditism, loss of parasperm, sperm spiral-shaped, coarse fibres, intra-axonemal dense granules. *2* Giant neurons in macroscopic (larger) animals. *3* Rhinophores innervated by N3 (nervus rhinophoralis), euthyneury, but with reversals in subgroups. *4* Monauly. *5* Cuticularised oesophagus. *6* Procerebrum with double root. *Green* Traditional opisthobranch groups, *blue* (and with dashes) traditional lower heterobranchs, *yellow* (and with dots) traditional pulmonate groups

Cephalaspidea, Pyramidellidae and highly diverse terrestrial stylommatophorans, all having independent Mesozoic origins.

Conclusion

There is thus increasing evidence that Spengel's old taxon Euthyneura will survive the molecular revolution in molluscan systematics, while the even older subtaxa Opisthobranchia and Pulmonata will not. These likely artificial concepts have never been strongly supported by morphological evidence (e.g. Haszprunar 1985a; Dayrat and Tillier 2002; unpublished data of the present authors), but were simple and attractive taxa reflecting the different researcher's preferences for fauna of either marine or terrestrial or limnic habitats. Paradigms on monophyletic Opisthobranchia and Pulmonata thus were both caused by and explain the lack of scientific correspondence between researchers focussing on marine or terrestrial / limnic taxa. Split by habitats, collection techniques, terminology, isolated data analyses and taxonomic tradition for two centuries, the euthyneuran research community should now at last merge. Furthermore, exploring the origin and natural history of opisthobranch sea slugs and snails needs to consider lower heterobranch and even "prosobranch" conditions. As in other invertebrate groups, opisthobranch research evolved as new materials and techniques became available, but was seriously misled in the past and still may be. At the beginning of the genomic era, we should open our minds to new methods of data acquisition and phylogenetic analyses. Opisthobranchia and Gastropoda in general are still underrepresented with regards to available genomic data, and concerted efforts should be made to try to fill this gap. Moreover, malacologists should be open to new challenges and further paradigm shifts to come.

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