



# Phylogeny and evolution of corambid nudibranchs (Mollusca: Gastropoda)

ALEXANDER MARTYNOV<sup>1</sup> and MICHAEL SCHRÖDL<sup>2\*</sup>

<sup>1</sup>Zoological Museum, Moscow State University, Bolshaya Nikitskaya str. 6, 125009, Moscow, Russia

<sup>2</sup>Zoologische Staatssammlung München, Münchhausenstr. 21, D-81247 München, Germany

Received 17 September 2010; accepted for publication 27 October 2010

Organismic diversity, as well as distributional and ecological patterns, can be fully understood in an evolutionary framework only. Reliable phylogenetic trees are required to ‘read history’, but are not yet available for most marine invertebrate groups. Molecular systematics offers an enormous potential, but still fails for ‘all-species approaches’ on groups with species that are rare or occur in remote areas only, simply because there is no easily collectable material available for sequence analyses. Exploring morphologically aberrant corambid nudibranch gastropods as a case study, we assess whether or not morphology-based phylogenetic analyses can fill this gap and produce a tree that allows a detailed view on evolutionary history. Morphology-based parsimony analysis of corambids and potential relatives resulted in a well-resolved and remarkably robust topology. As an offshoot of kelp-associated onchidoridid ancestors, and obviously driven by the heterochronic shortening of life cycles and morphological juvenilization in an ephemeral habitat, the ancestor of corambids originated in cool northern Pacific coastal waters. A basal clade (the genus *Loy*) diverged there, adapting to live on soft bottoms under successive reversals of paedomorphic traits. The more speciose *Corambe* lineage radiated preying upon short-lived encrusting bryozoa in a high-energy kelp environment. Selection favoured transformation of the mantle into a cuticle-covered shield, and successive paedomorphic translocations of dorid anal gills to the protected ventral side of the body, where compensatory, multiple gills evolved. *Corambe* species probably first colonized tropical American seas, and then radiated in worldwide temperate waters: this is explained by the excellent long-distance dispersal abilities afforded by rafting on kelp, with the subsequent divergence of colonizers in allopatry. The competitive coexistence of *Corambe pacifica* MacFarland & O’Donoghue, 1929 and *Corambe steinbergae* (Lance, 1962) off California is the result of independent colonization events. The closing of the Isthmus of Panama separated the latter species from a flock that have radiated within warm Atlantic waters since then. Our case study shows that morphological structures, if investigated in depth, bear the potential for an efficient phylogenetic analysis of groups that are still elusive to molecular analyses. Tracing character evolution and integrating a wide range of geographic, biological, and ecological background information allowed us to reconstruct an evolutionary scenario for corambids that is detailed and plausible, and can be tested by future molecular approaches.

© 2011 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2011, 163, 585–604.

doi: 10.1111/j.1096-3642.2011.00720.x

**ADDITIONAL KEYWORDS:** Doridoidea – habitat switches – heterochrony – histology – morphology – long-distance dispersal – Nudibranchia – paedomorphosis – radiation.

## INTRODUCTION

Our understanding of the present-day diversity, morphology, and ecology of organisms crucially depends

on our ability to reconstruct their origin and natural relationships. Advancing structural analytical, molecular, and statistical methods enabled new insights into phylogeny. For example, the traditional picture of animal phyla and classes, and their relationships, has been radically challenged (e.g. Aguinaldo *et al.*, 1997; Giribet *et al.*, 2006). However, tree

\*Corresponding author.

E-mail: michael.schroedl@zsm.mwn.de

calculations are always probabilistic, and fully and sensibly reflect the always restricted and usually selected data used. With the rise of molecular systematics, the number of competing, contradictory phylogenetic hypotheses in literature has increased rapidly, whereas their overall quality (in terms of robustness, congruence, and plausibility), at least regarding older diversifications and nonvertebrate marine groups, has been criticised (e.g. Wägele & Mayer, 2007; Wägele *et al.*, 2009). A promising way out of what creationists misrepresent as the 'crisis of evolution' is broadly investigating the phylogeny and evolution of many, usually very diverse and ancient, taxa by adding 'more data, more genes', and ultimately comparing genomic data sets (Dunn *et al.*, 2008).

A complementary approach is to focus efforts on the detailed exploration of model taxa. In an 'all known species approach', the basal phylogeny and evolutionary key features of acochlidian gastropods could be resolved based on a comprehensive morphological cladistic analysis (Schrödl & Neusser, 2010), as confirmed in a first molecular approach (Jörger *et al.*, 2010). The present study aims to resolve in detail the phylogeny of corambid sea slugs, another worldwide distributed opisthobranch group without adequate material available for molecular analyses, but combining manageable species diversity with high morphological variability. Corambid nudibranchs are known to ecologists as locally and seasonally abundant members of kelp-frond communities. The life cycles of the temperate north-eastern Pacific species *Corambe steinbergae* (Lance, 1962) (as *Doridella*) and *Corambe pacifica* MacFarland & O'Donoghue, 1929 were studied, and both species were shown to live in competitive coexistence (Yoshioka, 1986a, b). The underlying evolutionary history and phylogeography of such species, however, has never been adequately addressed. Since the description of *Corambe obscura* in the 1870s (Verrill, 1870; Bergh, 1871), corambids were always considered as being 'primitive', 'aberrant', and enigmatic (Schrödl & Wägele, 2001). This is because members combine an array of unusual features for dorid nudibranchs, such as having a flattened body that may show a posterior notch, a fleshy notum covered by a shedding cuticle, a ventral anus and multiple ventral gills, and pleural ganglia that are separate from the cerebral ganglia. Assumptions on the apparently primitive nature of mantle organ features led some authors to establish an own order Corambida at the basis of dorids (Baranets & Minichev, 1994). Because of the possession of special radula features and of a well-developed buccal pump, Corambidae were regarded as relatives of the phanerobranch dorids group Suctoria (Fischer, 1891; Millen & Nybakken, 1991). The discovery of the deep-water corambid species *Loy* and *Proloy* with dorsal or

subventral anus and gills between asymmetrical notal lobes (Martynov, 1994a) revealed corambids as highly modified suctorial phanerobranch dorids. These corambids resemble early postlarval stages of cryptobranch and phanerobranch dorids, such as *Cadlina laevis* (Linnaeus, 1767) and *Adalaria proxima* (Alder & Hancock, 1854) (Thompson, 1958, 1967). Martynov (1994b, 1995) thus proposed pedomorphosis as the driving evolutionary force for corambid organ transformation and successive juvenilization. A preliminary phylogenetic analysis of corambid genera by Valdés & Bouchet (1998) supported this hypothesis, revealing a basal position of the genus *Loy* in a broader sense (including *Psammodoris*, *Loy*, and *Proloy*), relative to other more aberrant corambid species. That analysis, however, suffered from misinterpreting *Echinocorambe brattegardii* Valdés & Bouchet, 1998 (now *Akiodorididae*) as a corambid (Millen & Martynov, 2005), from limited out-group and inner-corambid taxon sampling, and from inadequate character sampling (with just ten coded features, and some coding errors involved; Schrödl, 2003). The phylogeny of corambids is thus largely unresolved, as is their evolutionary history.

The present study gives a comprehensive phylogenetic analysis on all 11 corambid species considered valid herein, including a recently described species from Peru (Martynov *et al.*, 2011), and an additional three undescribed corambid species (Gosliner, 1987; Rudman, 1998; A. Martynov and M. Schrödl, unpubl. data), using a wide range of morphological, histological, and some biological characters. The resulting tree hypothesis is tested by bootstrap analysis, and its plausibility is assessed by its fit into biogeographic and evolutionary scenarios, which are developed by comparison with distributional, functional, ecological, and ontogenetic data (Thompson, 1967; Bickell & Chia, 1979; Bickell, Chia & Crawford, 1981; Martynov *et al.*, 2011). We show that corambids are an offshoot of *Adalaria jannae* Millen, 1987, like onchidoridid nudibranchs that originated in the northern Pacific. Driven by heterochronic changes of the ontogenetic programme and ecologically induced selection, one lineage adapted to life on sandy bottoms, whereas another clade further specialized for life on shallow water macroalgae. Excellent long-distance dispersal abilities favoured repeated colonization of remote areas and speciation in allopatry. Exemplarily we show that the evolutionary history of certain marine invertebrates can be read from a well-resolved and robust tree, even in the absence of molecular data, that the fit into geographical and ecological contexts can be assessed, and that driving forces and mechanisms leading to radiation and adaptation can be inferred conclusively.

## MATERIAL AND METHODS

## MORPHOLOGICAL TECHNIQUES

All out-group and in-group species were externally and anatomically reanalysed by dissection under a binocular microscope; exceptions included the well-known *Goniodoris castanea* Alder & Hancock, 1845 and two corambid species that have not been found again since their original description, i.e. *Corambe evelinae* Marcus, 1958 and *Corambe carambola* (Marcus, 1955). Body surfaces such as notum and gills, as well as hard parts (radula, spicules), were examined by scanning electron microscopy (SEM). Soft parts were critical-point dried, and samples were sputter coated (Polaron) and viewed in an LEO 1430 VP at 15 kV. Specimens were embedded in Spurr's low viscosity resin (Spurr, 1969), and serial histological semithin sections (1.5 µm) of *Acanthodoris falklandica* Eliot, 1907, all three *Loy* species, *Corambe lucea* Marcus, 1959, *Corambe pacifica*, and *Corambe obscura*, and *Corambe mancorensis* Martynov, Brenzinger, Hooker & Schrödl, 2011, from Peru, the anatomy of which was reconstructed three-dimensionally (Martynov *et al.*, in press) with AMIRA following standard procedures (e.g. Neusser & Schrödl, 2007; Neusser, Martynov & Schrödl, 2009), were prepared, stained with methylene-azure II (Richardson, Jarett & Finke, 1960), and analysed with a light microscope. The anatomy of the latter species was reconstructed three dimensionally (Martynov *et al.*, 2011) with AMIRA following standard procedures (e.g. Neusser & Schrödl, 2007; Neusser, Martynov & Schrödl, 2009).

## ANALYTICAL METHODS

All discernable structural and biological information on all nominal corambid (in-group) taxa was attributed to 73 coded characters. Character polarity was not assessed a priori. Out-group taxa were selected according to the results of previous taxonomic and cladistic studies. For a broader additional analysis, members of all onchidoridid genera, plus *Goniodoris castanea* Alder & Hancock, 1845 (Goniodorididae) and a cryptobranch dorid, were included. As a trial, three additional, probably undescribed, and only externally known corambid species were also considered. Analyses were performed with PAUP 4.0 beta 10 win (Swofford, 2001). Parameters of maximum parsimony analyses were: ACCTRAN, all characters unordered and unweighted; heuristic search options of stepwise addition = random, number of addition-sequence replicates = 100, and branch-swapping option = TBR. Trees were unrooted. Strict consensus trees and bootstrap 50% majority-rule trees (1000 replicates) were calculated.

## PHYLOGENETIC ANALYSIS

## TAXA

Previous taxonomic and comparative morphological approaches (Millen & Nybakken, 1991; Martynov, 1995; Schrödl & Wägele, 2001), as well as cladistic studies based on morphology (Millen & Martynov, 2005), indicated that corambids form a monophylum that is closely related to onchidoridid suctorial dorid nudibranchs, especially to the genus *Adalaria*. Thus, members of various onchidoridid genera (Martynov *et al.*, 2009) were selected as out-group taxa for the main analysis. Whenever phylogenetic hypotheses are available, basal members of out-group genera were selected, e.g. *Acanthodoris falklandica* is a basal offshoot of *Acanthodoris*, according to Fahey & Valdés (2005). As preanalyses indicated that corambids form a clade with *Adalaria jannae*, several more *Adalaria* species were added (Table 1). As the in-group, all valid corambid species, including some tropical Atlantic corambids with unclear synonymy (i.e. *Corambe burchi* and *Corambe carambola*) were considered. A new corambid from tropical northern Peru, with full anatomical data available (Martynov *et al.*, 2011), was also included in the main analysis. Three further, only externally known corambid species were considered for additional analysis (Table 1). In an additional analysis, the origin and monophyly of corambids was assessed, including the cryptobranch dorid *Cadlina* and further phanerobranch suctorial taxa such as *Goniodoris*, *Diaphorodoris*, and *Onchimira*. The abyssal *Echinocorambe brattgardii* Valdés & Bouchet, 1998 was originally regarded as a basal corambid offshoot; it is not considered herein, as Martynov (1999, 2000) recognized this species as being closely related to the akiodoridid genus *Doridunculus*, which was confirmed by the cladistic analysis of Millen & Martynov (2005).

## CHARACTERS

Characters have been selected according to the following mode: out-group specific characters are included to an extent that provides a reasonable out-group topology. For the in-group, all external and internal characters discernable, available, and relevant to corambids, plus some ecological characters, were compiled from literature and supplemented by the results of own examinations (see lists below). Character definitions are made with minimum a priori assumptions; the homology of gills has been evaluated in detail elsewhere (Martynov *et al.*, 2011). Only those characters showing too much ambiguity or lack of information within the in-group were excluded from analyses. The morphological information on out-groups is based on our own examinations,

**Table 1.** Species used for phylogenetic analysis

Species	Distribution	Data	Data source
<i>Cadlina laevis</i> (Linnaeus, 1767)	Amphiboreal species: North Atlantic and North Pacific	E, A	Rudman, 1984; Thompson & Brown, 1984; *
<i>Onchimira cavifera</i> Martynov <i>et al.</i> , 2009	North-western Pacific, Kamchatka	E, A	Martynov <i>et al.</i> , 2009; *
<i>Calycidoris guentheri</i> Abraham, 1876	Arctic and north-eastern Pacific	E, A	*
<i>Diaphorodoris lirulatocauda</i> Millen, 1985	North-eastern Pacific	E, A, H	Millen, 1985; *
<i>Acanthodoris falklandica</i> Eliot, 1907	Magellanic	E, A, H	Marcus, 1959; Schrödl, 2003; *
<i>Goniodoris castanea</i> Alder & Hancock, 1845	North Atlantic	E, A, H	Thompson & Brown, 1984; Wägele & Cervera, 2001; Martynov & Schrödl, 2008
<i>Onchidoris bilamellata</i> (Linnaeus, 1767)	Amphiboreal species: North Atlantic and North Pacific	E, A	Thompson & Brown, 1984; *
<i>Onchidoris muricata</i> (Müller, 1776)	Amphiboreal species: North Atlantic and North Pacific	E, A	Millen, 1985; Fahey & Valdés, 2005; Martynov <i>et al.</i> , 2009; *
<i>Adalaria proxima</i> (Alder & Hancock, 1854)	Amphiboreal species: North Atlantic and North Pacific	E, A	Thompson & Brown, 1984; Millen, 1985; Martynov, 2006; Martynov <i>et al.</i> , 2009
<i>Adalaria loveni</i> (Alder & Hancock, 1862)	North Atlantic	E, A	Bergh, 1880; Thompson & Brown, 1984; Millen, 1985; Millen, 1987
<i>Adalaria slavi</i> Martynov <i>et al.</i> , 2009	North-western Pacific, Kamchatka	E, A	Martynov <i>et al.</i> , 2009; *
<i>Adalaria jannae</i> Millen, 1987	Northern Pacific	E, A	Millen, 1987; Martynov <i>et al.</i> , 2009; *
<i>Loy meyeri</i> Martynov, 1994	North-western Pacific	E, A, H	Martynov, 1994a; *
<i>Loy millenae</i> Martynov, 1994	North-western Pacific	E, A, H	Martynov, 1994a; *
<i>Loy thompsoni</i> (Millen & Nybakken, 1991)	North-eastern Pacific	E, A, H	Millen & Nybakken, 1991; *
<i>Corambe obscura</i> (Verrill, 1870)	Amphiatlantic species	E, A, H	*
<i>Corambe burchi</i> (Marcus & Marcus, 1967)	Western Atlantic	E, A, H	Marcus & Marcus, 1967; *
<i>Corambe carambola</i> (Marcus, 1955)	Southern Atlantic	E, A	Marcus, 1955
<i>Corambe steinbergae</i> (Lance, 1962)	North-eastern Pacific	E, A, H	MacFarland, 1966; Lance, 1962; *
<i>Corambe testudinaria</i> Fischer, 1889	Eastern Atlantic	E, A	Fischer, 1891; García, Urgorri & López González, 1991; Edmunds, 2007
<i>Corambe lucea</i> Marcus, 1958	South-eastern Pacific	E, A, H	Marcus, 1959; Schrödl & Wägele, 2001; *
<i>Corambe pacifica</i> MacFarland & O'Donoghue, 1929	North-eastern Pacific	E, A, H	MacFarland & O'Donoghue, 1929; *
<i>Corambe mancorensis</i> Martynov <i>et al.</i> , 2009	Tropical northern Peru	E, A, H	*, Martynov <i>et al.</i> , 2011
<i>Corambe</i> sp.1	South Africa	E	Gosliner, 1987
<i>Corambe</i> sp.2	Australia	E	Rudman, 1998
<i>Corambe</i> sp.3	Tropical Brazil	E	unpubl. data

A, anatomical; E, external; H, histological; \*, own examination.

supplemented with results from several recent reviews and phylogenetic studies (Thompson & Brown, 1984; Wägele & Willan, 2000; Schrödl, 2003; Fahey & Valdés, 2005; Martynov & Schrödl, 2008). All available original or secondary literature on corambids was considered (e.g. Verrill, 1870; Bergh, 1871; Fischer, 1891; MacFarland & O'Donoghue, 1929; Marcus, 1955, 1958; Marcus & Marcus, 1967; Lance, 1962; Millen & Nybakken, 1991; Martynov, 1994a). Literature data was supplemented or corrected by our own examinations of most species (Table 1); micromorphological data from semi-thin histological slides was used to confirm and supplement results from dissections, especially of small specimens.

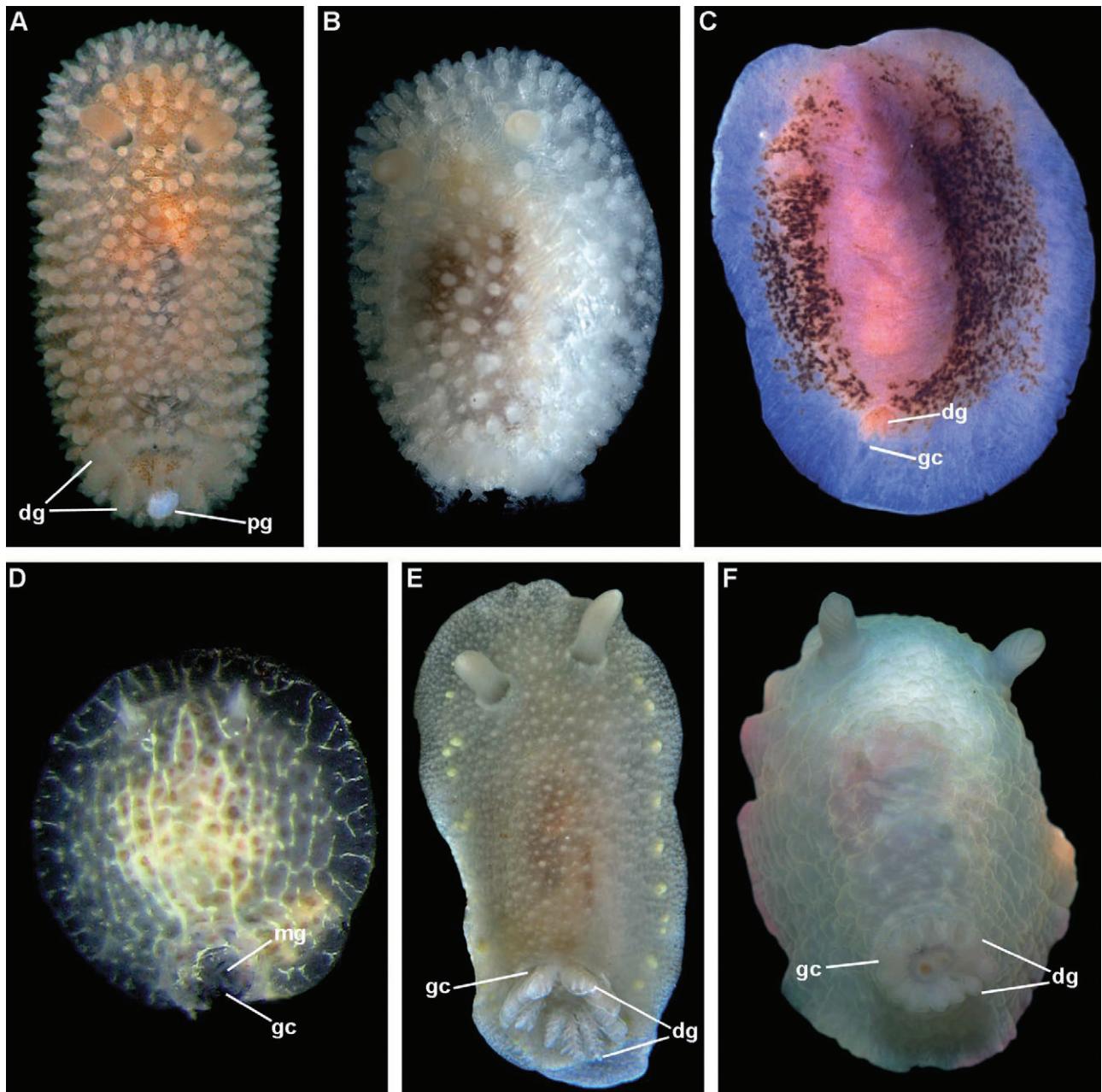
The following 73 characters (Table 2) were used for parsimony analysis (PAUP 4.0b10; Swofford, 2001). Missing information and non-applicable characters were coded as unknown.

1. Body shape. The body of *Cadlina*, *Onchimira*, *Calycidoris*, *Acanthodoris falklandica*, *Adalaria proxima*, and *Onchidoris* (Figs 1E, F and 2B) is more or less highly elevated (0), whereas the body is more flattened (Fig. 1A–D) in most corambids and in *Adalaria jannae* (1).
2. Notum. In *Cadlina*, *Onchimira*, *Calycidoris*, *Acanthodoris falklandica*, *Adalaria proxima*, *Onchidoris*, and some *Corambe* species the notum is more or less regularly convex in cross section (0), omega-like shaped with elevated central notum in *Adalaria jannae* and *Loy* (1), or just slightly convex in most *Corambe* species (2).
3. Body outline. In dorsal view, the (living) body outline of out-group taxa is oval or rounded (Figs 1A–B; E–F; 2B) but variable according to the state of activity (0), whereas it is subrectangular (Fig. 1C) in *Loy* species (1), and invariably rounded (Fig. 1D) in *Corambe* (2).
4. Body size. *Cadlina*, *Calycidoris guentheri* Abraham, 1876, *Adalaria proxima*, and *Onchidoris bilamellata* (Linnaeus, 1767) reach 30 mm (0). *Adalaria jannae*, *Onchidoris muricata* (Müller, 1776), and all corambids are smaller than 15 mm (1).
5. Notal tubercles. Large tubercles (Figs 1A–B; 2A–B) are present in *Calycidoris*, *Acanthodoris*, *Adalaria*, and *Onchidoris* (0), whereas the notum of *Cadlina*, *Onchimira*, and corambids is smooth (Fig. 1C–F) or shows low bumps (1).
6. Posterior notal rim. The posterior mantle margin is entire (Figs 1A–B, E–F; 2B, D) in most adult dorids, including *Cadlina*, *Onchimira*, *Calycidoris*, *Adalaria*, *Onchidoris*, and some *Corambe* (0), whereas the posterior notum is bilobed (Figs 1D and 2E–G) in *Loy* and several *Corambe* (1).
7. Symmetry of notal lobes. Lobes are asymmetrical (with a larger right lobe) (Fig. 1C) in adult *Loy* and, though less developed (Fig. 1D), in *Corambe evelinae* and *Corambe mancorensis* (0), but are symmetrical (Fig. 2E–F) in other *Corambe* with lobes (1).
8. Notal notch. In species with notal lobes, *Loy meyeri* (Martynov, 1994) (Fig. 1C) shows a superficial furrow and a slight posterior incision (0), whereas the posterior notum has a deep notch (Figs 1D and 2E–G) in other *Loy* and *Corambe* (1).
9. Notch shape. The notal notch is narrow in *Loy millenae* Martynov, 1994 (0), whereas it is broad in *Loy thompsoni* (Millen & Nybakken, 1991) and several *Corambe* (1).
10. Connective tissue of notum. The layer of notum connective tissue is thin in comparison with the height of the body cavity in cryptobranch dorids, *Calycidoris*, *Acanthodoris*, *Adalaria*, *Onchidoris*, and *Loy* (0), whereas a thick layer (Schrödl & Wägele, 2001) is present in *Corambe* (1).
11. Notal cuticle. Most dorids, including *Loy*, lack any significant dorsal cuticle (0). A cuticle (Schrödl & Wägele, 2001) is present in all other corambids (1).
12. Cuticle dimension. The dorsal cuticle of *Corambe evelinae*, *Corambe mancorensis*, *Corambe obscura*, *Corambe burchi*, and *Corambe carambola* is a relatively thin layer (0), whereas the cuticle of other corambids is thick and consists of some more or less distinct shedding layers (1).
13. Spicules. Calcareous spicules are present in onchidoridids and *Loy* (0), but are absent in *Corambe* (1).
14. Rhinophores. Rhinophores are transversely lamellate in most cryptobranch dorids and onchidoridids (Figs 1F and 2B) (0), smooth in *Loy* and *Corambe steinbergae* (1), and longitudinally folded in other corambids (2).
15. Longitudinal lamellae. Where present, there may be two (0) or four longitudinal rhinophoral folds (1).
16. Gill cavity. Cryptobranch dorids (except for most Phyllidiidae), and some Suctorina such as *Onchimira*, *Calycidoris*, *Loy*, and some *Corambe* species have a permanent gill cavity (Figs 1C–F; 2A, G) (0), whereas *Acanthodoris*, *Adalaria*, *Onchidoris*, and other corambids have none (Figs 1A, B and 2C–E) (1).
17. Shape of the gill cavity. In cryptobranchs, *Onchimira*, and *Calycidoris* the gill cavity (Fig. 1E–F) is large (0), whereas it is small (Fig. 1C, D) in corambids (1).
18. Closable gill pocket. Cryptobranch dorids and *Onchimira* have a contractile gill sheath, or gill cavity margin that closes over the gill cavity (Fig. 1E–F) and the retracted gills, which is also at

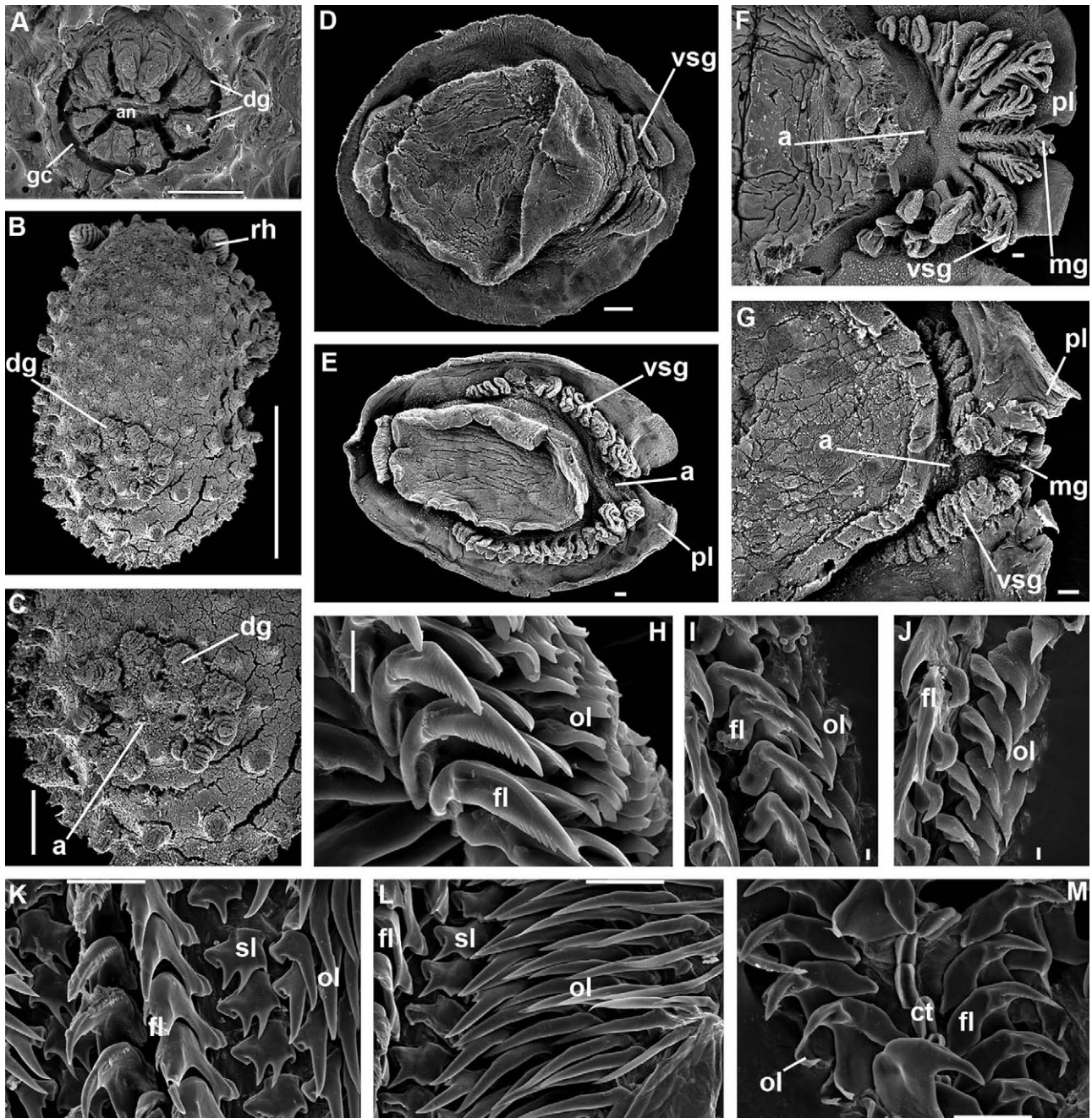
**Table 2.** Data matrix of out-group and corambid in-group taxa with character states 0–4

	1	2	3	4	5	6	7
<i>*Cadiina laevis</i>	000010???	0?00?00000	00000?0000	0000?00000	??001?1100	0001000000	000?0000?0
<i>*Goniodoris castanea</i>	000010???	0?00?1???	000000?000	0000000?00	0011102000	0101000000	000?0010?0
<i>*Onchimidira cavifera</i>	000010???	0?00?00000	000000?000	1000000100	0000100000	0100000100	0010100???
<i>Calycidoris guentheri</i>	000000???	0?00?00000	000000?010	1100000000	0001000000	0001000000	000?0000??
<i>*Diaphorodoris lirulatocauda</i>	000100???	0?00?0100?	000000?000	0000?00101	00111?2010	0101000000	000?0000?1
<i>Acanthodoris falklandica</i>	000000???	0?00?1???	000000?000	000000?000	0001100010	000?000000	000?0000??
<i>Onchidoris bilamellata</i>	000000???	0?00?1???	000010?110	1100000001	2010002010	0101001000	100?0010?0
<i>Onchidoris muricata</i>	000100???	0?00?1???	000010?100	1010000101	2010102010	0101001010	100?0000?0
<i>Adalaria proxima</i>	000000???	0?00?1???	000010?110	1000000011	1000000110	0100011010	100?0000?1
<i>Adalaria loveni</i>	000000???	0?00?1???	000010?100	1000000011	1000000110	0?000?1010	100?0000??
<i>Adalaria slavi</i>	000000???	0?00?1???	000010?100	1000?00111	1000100010	01000?1010	100?0000??
<i>Adalaria jannae</i>	110100???	0?00?1???	000010?1?0	1010000111	1001100110	0100011010	100?0010?1
<i>Loy meyeri</i>	11111100?0	0?01?01111	000120?000	1000101102	0101111110	0100011010	10110010??
<i>Loy millenae</i>	1111110100	0?01?01111	010120?000	2?01101102	0101111110	0100011110	10110010??
<i>Loy thompsoni</i>	1111110110	0?01?01111	010120?000	1001101102	0100100110	0100011010	10100010??
<i>Corambe obscura</i>	002110???	101201???	1?1?411011	1101011112	1001100011	1101111?01	1110101101
<i>Corambe burchi</i>	002110???	101201???	1?1?411011	1101011112	1001100011	1101111101	1110101101
<i>Corambe carambola</i>	002110???	101211???	1?1?411011	11010111?2	1001100011?	1110111001	111010110?
<i>Corambe steinbergae</i>	122110???	1111?1???	1?1?0410?0	1101?11112	1001100011	1110111110	1010111111
<i>Corambe evelinae</i>	1110110110	1110110110	0110210?00	0110210?00	1001100011?	1111?111?021	1010101011??
<i>Corambe lucea</i>	1221111111	111210???	1?1?041010	1101011112	1001100011	1110111010	1110001011
<i>Corambe pacifica</i>	1221111111	1112101111	1?1?0310000	1001011112	1001100011	1110111101	1110001111
<i>Corambe testudinaria</i>	1221111111	111211???	1?1?041010	1?01011112	1001100011	11?1111001	1110111111
<i>Corambe mancorensis</i>	1221101011	1012101111	0110210000	1001011112	1001100011	1110111121	101000111?
<i>*Corambe sp.1 (South Africa)</i>	1221111111?	??2?1???	101?401?00	110101?11?	??2???	??2???	??2???
<i>*Corambe sp.2 (Australia)</i>	12211100???	1?1?1?1?1?1?	1?1?1?41?00	??01?1?1???	??2???	??2???	??2???
<i>*Corambe sp.3 (Brazil)</i>	1110110110???	1?1?2211???	1?1?1?411?11	1110101111?	??2???	??2???	??2???

?, inapplicable characters or missing data; \*taxa not included in the main analysis.



**Figure 1.** Examples of external features used for phylogenetic analyses from living specimens of cryptobranch and phanerobranch Doridoidea. A, *Adalaria jannae* Millen, 1987: showing usual phanerobranch onchidoridid pattern with dorsal gills, but without gill cavity; note the well-defined postbranchial gland; specimen from Western Pacific, Kamchatka, 7 mm in length. B, *Adalaria jannae* Millen 1987: showing omega-shaped notum, 8 mm in length. C, corambid onchidoridid *Loy meyeri* Martynov, 1994a with three dorsal gills in a small cavity; specimen from the Sea of Japan, Peter the Great Bay, 6.5 mm in length. D, corambid onchidoridid *Corambe mancorensis* Martynov *et al.*, 2011: with ventral serial gills and three separate median gills in a semiclosed cavity; specimen from Mancora, Peru, 4 mm in length. E, *Cadlina laevis* (Linnaeus, 1767): showing a 'typical' cryptobranch chromodoridid pattern, with dorsal gills in a well-defined gill cavity; specimen from White Sea, Kandalakshsky Bay, 25 mm in length. F, *Onchimira cavifera* Martynov *et al.* 2009: an onchidoridid with dorsal gills in a well-defined gill cavity; specimen from Western Pacific, Kamchatka, 21 mm in length. Abbreviations: dg, dorsal gills; gc, gill cavity (= gill pocket); mg, median gills; pg, postbranchial gland. Photos: A, E–F, Tanya Korshunova; B, Karen Sanamyan; C, Alexander Martynov; D, Michael Schrödl & Bastian Brenzinger.



- least partially closable (Fig. 2A) in *Calycidoris* (0). Corambid gill pockets (Figs 1C–D and 2F, G) are not closable by contraction of their margin (1); this is also true for *Corambe mancorensis*, which covers its gill cavity by special lobules.
19. Gill retraction. In cryptobranchs, *Onchimira*, and *Calycidoris* gills are completely retractable (Fig. 2A) into the gill cavity (0); this is not the case in corambids with gill pockets (Fig. 2D, F–G) (1).
  20. Joint gill retractor muscle. In cryptobranch dorids, *Onchimira*, and *Calycidoris* the gill muscles join

basally and form a single strong retractor muscle (0), which is not detectable in other onchidorids and corambids (1). Joint muscle bundles along the gill bases of *Corambe carambola* are coded as unknown because of their paired nature and questionable direct homology with the single gill retractor.

21. Dorsal gills. Gills situated on notum tissue are present in cryptobranch dorids, *Onchimira*, *Calycidoris*, *Adalaria*, *Onchidoris*, *Loy*, *Corambe evelinae*, and *Corambe mancorensis* (Figs 1 and 2A–C,



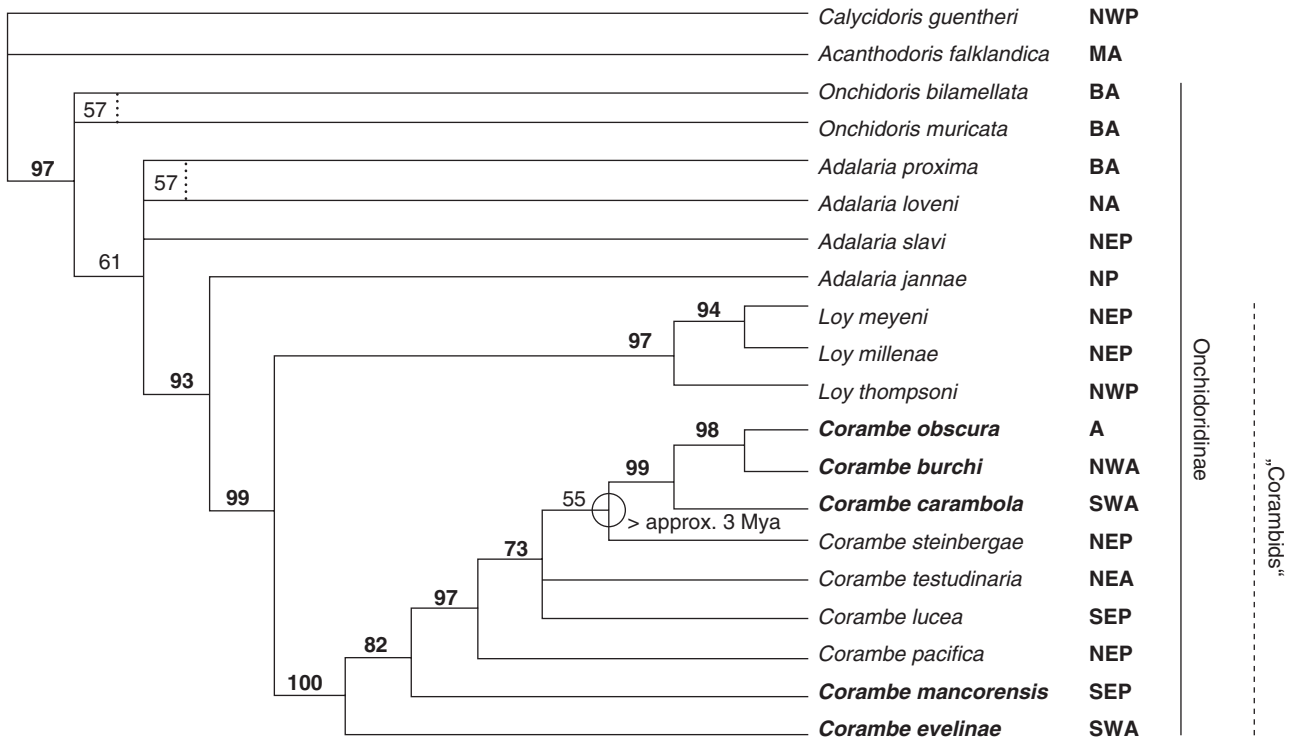
**Figure 2.** Scanning electron micrographs showing examples of the special onchidoridid structures used for phylogenetic analyses. A, *Onchimira cavifera* Martynov *et al.*, 2009: posterior notum showing well-defined dorsal gill cavity; preserved specimen of 10 mm in length, north-west Pacific, Kamchatka. *Onchidoris muricata* (Müller, 1776): B, dorsal overview, Barents Sea, Dalne-Zelenetskaya Bay; C, detail view showing dorsal gills; gill cavity completely lacking, gills inserted directly to the notum. D, *Corambe obscura* (Verrill, 1870): showing few plate-like ventral gills; median gills absent; posterior notal lobes absent; specimen from the Black Sea, Sevastopol region. E, *Corambe lucea* Marcus, 1959: showing numerous ventral serial gills; median gills absent; posterior notal lobes well defined; specimen from central Chile, south-eastern Pacific Ocean; F, *Corambe pacifica* MacFarland & O'Donoghue 1929, showing ventral serial gills and median gills; posterior notal lobes well-defined; specimen from the north-eastern Pacific Ocean. G, *Corambe mancorensis* Martynov *et al.*, 2011: showing ventral serial gills and three dorsally displaced median gills within a semiclosed cavity; posterior notal lobes well defined; specimen from tropical northern Peru. H, *Adalaria jannae* Millen 1987: radular teeth showing large differentiated first laterals and several excavated short outer laterals; specimen from Kamchatka, north-western Pacific. *Corambe mancorensis*: I, radular teeth showing large differentiated first laterals; J, radular teeth showing several short excavated outer laterals. *Loy meyeri* Martynov, 1994a: K, radular teeth showing large differentiated first laterals and fork-shaped second laterals; specimen from Peter the Great Bay, Sea of Japan; L, same, radular teeth showing long needle-shaped outer laterals. M, *Onchidoris muricata* (Müller, 1776): radular teeth showing large differentiated first laterals and single rounded outer laterals; specimen from Dalne-Zelenetskaya Bay, Barents Sea. Scale bars: A, 1 mm; B, 2 mm; C, 500 µm; D–G, 100 µm; H, 20 µm; I, J, 3 µm; K, L, 60 µm; M, 40 µm. Abbreviations: a, anus; ct, central teeth; dg, dorsal gills; fl, first lateral teeth; gc, gill cavity (= gill pocket); mg, median gills; ol, outer lateral teeth; pl, posterior notal lobes; rh, rhinophore; sl, second lateral teeth; vsg, ventral serial gills.

- G) (0), but are absent in other corambids (Fig. 2D–F) (1).
22. Subventral gills. Whereas all out-group taxa and *Loy meyeri* possess normal dorsal gills (Figs 1A–C; E–F; 2A–C) anterior to the mantle margin (0), gills are in a terminal subventral position in *Loy thompsoni*, *Loy millenae*, *Corambe evelinae*, and *Corambe mancorensis* (Figs 1D and 2G) (1).
23. Lateroventral gills. Gills in a lateroventral position are absent in all out-group taxa and *Loy* (0), whereas they are present in all *Corambe* (Figs 2D–G) (1).
24. Gill number. *Onchimira*, *Calycidoris*, *Adalaria*, *Onchidoris*, and most *Corambe* species have more than five gills (Figs 1A, E–F; 2A–C; E–G) (0), *Loy* has three gills (Fig. 1C) (1), and some *Corambe* species have four gills (Fig. 2D) (2).
25. Anal gill arrangement. Gills associated with the anus are present in most dorids. In many cryptobranchs, *Onchimira*, *Calycidoris*, and *Acanthodoris* gills are arranged in a full circle around the anus (Figs 1E, F and 2A) (0). Gills form a semicircle posteriorly completed by the anus in *Adalaria* and *Onchidoris* (Figs 1A and 2B, C) (1). Gills arise close together in *Loy* and (some posterior ones) (Fig. 1C) in *Corambe evelinae* and *Corambe mancorensis* (2). *Corambe pacifica* has a single anal gill (Fig. 2F) (3). Anal gills are absent in other corambids (Fig. 2D–E) (4).
26. Serial gills. Although absent in onchidoridids and *Loy* (0), all *Corambe* species have serial gills (Fig. 2D–G) (1).
27. Serial gill arrangement. Serial gills form rows (Fig. 2E–G) in most *Corambe* species (0), but form transversal pairs (Fig. 2D) in *Corambe burchi*, *Corambe carambola*, and *Corambe obscura* (1).
28. Gill base connection. Gills are connected to adjacent ones (Figs 1C, F and 2A, F) in *Onchimira*, *Calycidoris*, *Acanthodoris*, *Loy*, and several *Corambe* (0), whereas gills are particular (Figs 1A and 2C–D) in *Onchidoris*, *Adalaria*, and some corambids (1).
29. Gill base width. Although the gill base is narrow in most dorids, including *Acanthodoris falklandica*, *Onchidoris muricata*, *Loy*, *Corambe mancorensis*, and *Corambe pacifica* (0), gill bases are broad in other onchidoridids, such as *Calycidoris*, and in several *Corambe* (1).
30. Shape of gill. Gills are more or less elongate (Figs 1 and 2A, C, E–G) in most dorids, onchidoridids, and corambids (0), but are very stout (Fig. 2D) in *Corambe burchi*, *Corambe carambola*, and *Corambe obscura* (1).
31. Gill ramification. Gills are multipinnate (Fig. 1E) in cryptobranchs and *Acanthodoris* (0), unipinnate or slightly bipinnate (Figs 1F and 2A–G) in *Onchimira*, *Calycidoris*, *Adalaria*, *Onchidoris*, most *Loy*, and *Corambe* (1), and not ramified in *Loy millenae* (2).
32. Shape of gill leaflets. Leaflets are delicate in most out-group taxa used herein, *Loy*, and at least *Corambe mancorensis* and *Corambe pacifica* (0), whereas the lamellae are broader in other onchidoridids and corambids (1).

33. Postbranchial gland. Although generally absent (0), *Adalaria jannae* (Fig. 1A) and *Onchidoris muricata* possess a special large glandular tubercle posterior to the gill circle (1).
34. Anus position. The anus opens dorsally (Figs 1A–C, E–F; 2A, C) in all out-group taxa and *Loy meyeri* (0). The anus opens posteroventrally in all other corambids (Fig. 2D–G) (1).
35. Oral veil. Oral tentacles are connected with a veil with an entire anterior margin in all out-group taxa and most *Corambe* species (0). The anterior margin is partly fused with the hyponotum in *Loy* (1), whereas it is completely fused or absent in *Corambe steinbergae* (2).
36. Shape of oral tentacles. Anterolateral margins of oral veils are lobe-like in out-group taxa and *Loy* (0), somewhat elongate triangular (Fig. 2D–E) in most *Corambe* (1), whereas finger-shaped tentacles are present in *Corambe steinbergae* (2).
37. Connection to foot. Oral tentacles or veils are posterolaterally connected to the foot in at least most out-group taxa (0), but not in corambids (Fig. 2D–E) (1).
38. Anterior foot margin. It is bilabiate in most out-group taxa (0), whereas it is unilabiate (Fig. 2D–E) in some *Adalaria* species and corambids (1).
39. Shape of foot margin. The foot is simple rounded in *Onchimira*, *Calycidoris*, *Acanthodoris falklandica*, *Onchidoris*, and *Loy* (0), but is emarginated (i.e. more or less curved backwards or incised medially) (Fig. 2D–E) in most *Adalaria* and *Corambe* (1). In *Adalaria proxima* just the upper lip seems to be notched.
40. Jaw elements. *Calycidoris* and *Acanthodoris* possess well-defined elongate rodlets (0), and *Adalaria* and *Onchidoris* have basally fused and reduced elements (1). Jaw elements are absent in corambids (2).
41. Shape of buccal pump. It is sessile in *Calycidoris*, *Acanthodoris*, and *Loy* (0), on a wide stalk in *Adalaria* and *Corambe* (1), and on a narrow stalk in *Onchidoris* (2).
42. Size of buccal pump. It is large in out-group taxa and *Corambe* (0), but small in *Loy* (1).
43. Number of teeth per half row. Most dorids have many teeth (>20) per half row. *Onchimira*, *Calycidoris*, *Acanthodoris*, *Adalaria*, *Loy*, and *Corambe* have between four and 14 teeth per half row (Fig. 2H–L) (0); *Onchidoris* have only two or three teeth (Fig. 2M) (1).
44. Rachidian tooth. A rachidian tooth is present (Fig. 2M) in *Onchimira*, most *Adalaria*, *Onchidoris*, and in *Loy thompsoni* (0). It is absent (Fig. 2H–K) in *Calycidoris*, *Acanthodoris*, *Adalaria jannae*, and other corambids (1).
45. Denticles. First laterals of *Calycidoris*, *Adalaria proxima*, *Adalaria loveni* (Alder & Hancock, 1862), and *Onchidoris bilamellata* have smooth cusps (0), whereas those of other out-group taxa and corambids have denticles (Fig. 2H, I, K, M) on the cusp (1).
46. Second lateral. Outer laterals are more or less uniformly shaped (Fig. 2H, J, M) in out-group taxa and most corambids (0), but fork-like second laterals are clearly different from outer laterals in *Loy meyeri* and *Loy millenae* (Fig. 2K) (1).
47. Shape of outer laterals. In *Onchimira*, *Calycidoris*, *Acanthodoris*, *Adalaria*, and most corambids the outer laterals are slightly elongated (Fig. 2H, J) (0), in *Loy millenae*, and especially *Loy meyeri*, laterals are considerably elongated (Fig. 2L) (1), and in *Onchidoris* outer laterals are rounded (Fig. 2M) (2).
48. Outer lateral denticles. Outer lateral teeth may lack denticles (0), whereas at least some laterals have denticles in some *Adalaria* species, *Loy*, *Corambe evelinae*, and *Corambe carambola* (1).
49. Salivary glands. They are long in cryptobranchs and *Calycidoris* (0), but short in *Adalaria*, *Onchidoris*, and corambids (1).
50. Dorsoventral muscles. Pairs of dorsoventral muscle bundles are not present in any out-group taxa or *Loy* (0), whereas they are present in *Corambe* (1).
51. Digestive gland lobes. The digestive gland is usually externally compact in dorids, including all out-group taxa and *Loy* (0), whereas it is more or less marginally divided into lobes around the dorsoventral muscles in *Corambe* species (1). In contrast to the original description of digestive gland lobes in *Loy thompsoni* by Millen & Nybakken (1991), examination of serial histological slides of a rehydrated specimen indicates that there are neither dorsoventral muscles nor digestive gland lobes, but instead a thick and folded layer of gonad tissue on the single mass of digestive gland.
52. Caecum. In *Calycidoris* and *Acanthodoris falklandica* a stomachal blind sac is present (0), whereas this is absent in other out-group taxa and corambids (1).
53. Intestinal bulb. Although the intestine narrows gradually in out-group taxa, *Loy*, and several *Corambe* species (0), in other *Corambe* species the proximal intestine is swollen and forms a longitudinally folded bulb (Schrödl & Wägele, 2001) that is clearly separated from the more slender distal intestine portion (1). Such a

structure is present in *Corambe lucea* and *Corambe pacifica*, for example: in the latter species it was previously misinterpreted as a caecum. The same may be true for the 'short folded caecum' mentioned from *Corambe evelinae* and *Corambe carambola*.

54. Central nervous system. The cerebral and pleural ganglia are well separated in basal nudibranchs such as *Bathydoris*, but also in *Adalaria* and most corambids studied in sufficient detail (0); ganglia are fused in most dorids including *Calycidoris*, *Onchidoris*, *Corambe obscura*, *Corambe testudinaria* Fischer, 1889, and *Corambe burchi* (1).
55. Genital opening. The gonopore is dextralateral in all dorids. It is usually situated considerably posterior to the rhinophores at about one-third of the body in dorids (0), but is at the level of, or closely posterior to, the rhinophore in *Corambe* (1).
56. Ampulla. The hermaphroditic ampulla is narrow in most out-group taxa (0), but is widened in at least *Adalaria proxima*, *Adalaria jannae*, and corambids (1).
57. Receptaculum seminis position. In dorids, including *Calycidoris* and *Acanthodoris*, the seminal receptacle usually sits either at the uterine duct or at the vagina (0), whereas it is placed at the proximal oviduct in *Onchidoris*, *Adalaria*, and at least many corambids (1).
58. Receptacle arrangement. The seminal receptacle has one opening (i.e. has a stalk or is sessile) in out-group taxa and several corambids (0), whereas it has two openings forming a more or less tubular flow-through system in some corambids (1).
59. Vagina size. In *Calycidoris*, *Acanthodoris*, *Onchidoris bilamellata*, and several *Corambe* species the vagina is a more or less narrow tube (0). In *Adalaria*, *Onchidoris muricata*, and *Loy* the vagina is widened into a vaginal bursa (1). *Corambe evelinae* and *Corambe mancorensis* have a very long and narrow vagina (2).
60. Bursa. The bursa is stalked or sessile in the out-group taxa and *Loy* (0), whereas it is 'serially arranged' (i.e. has two distinct openings) in *Corambe* (1).
61. Uterine duct. Most dorids including *Calycidoris* and *Acanthodoris falklandica* have a uterine duct entering the female gland mass separately from the oviduct (0), whereas the uterine duct joins the oviduct in other out-group taxa and corambids (1). Re-examination showed the reproductive system of *Corambe pacifica* and *Corambe steinbergae* resembles that of *Corambe lucea* as described by Schrödl & Wägele (2001), thus lacking any separate uterine duct.
62. Vas deferens portions. In out-group taxa, *Loy*, and some *Corambe* the vas deferens is well differentiated into proximal prostatic and distal muscular portions (0), whereas in other *Corambe* species it is not clearly differentiated (i.e. it is prostatic nearly over its entire length) (1).
63. Penis. In all out-group taxa the distal part of the vas deferens is an eversible ejaculatory duct (0), whereas corambids have a permanent penial papilla (1).
64. Penis shape. *Loy thompsoni* and *Corambe* species have a more or less conical penis (0), whereas *Loy meyeri* and *Loy millenae* possess a wide and flattened penis (1).
65. Penial sheath. The sheath of the ejaculatory vas deferens is long in out-group taxa, *Loy*, and some *Corambe* (0), but is short in other *Corambe* species (1).
66. Penial retractor muscle. Although not present in out-group taxa, *Loy*, and several *Corambe* species (0), at least some *Corambe* species possess a strong penial retractor (1).
67. General colour. *Cadlina laevis*, *Onchimira*, *Calycidoris*, *Acanthodoris falklandica*, most *Adalaria*, and *Onchidoris muricata* are quite uniformly whitish or yellowish (Fig. 1A–B, E–F) (0), whereas *Onchidoris bilamellata* and corambids are mottled with dark spots (Fig. 1C–D) (1).
68. Pigment dots. White, red, or brown and black dots are absent (Fig. 1C) in non-uniformly coloured out-group taxa and *Loy* (0), whereas they are present in other corambids (Fig. 1D) (1).
69. Mimic colour pattern. Some corambids such as *Corambe obscura* have differently coloured dots but do not display any bryozoan colony-mimicking colour pattern (0), whereas several other *Corambe* species mimic *Membranipora* spp. and other encrusting bryozoa by a special arrangement of small whitish, reddish, and blackish pigment dots (Fig. 1D) (1).
70. Egg mass. In most dorids including *Onchidoris* the egg mass is a broad band, attached to the substrata by a rib (0), whereas in *Adalaria* and corambids the egg mass is a rather narrow cord, attached to the substrata over much of their surface (1).
71. Habitat. *Calycidoris* and *Loy* inhabit soft bottoms (0), whereas most *Adalaria* and *Onchidoris* inhabit rocky bottoms (1). *Acanthodoris falklandica*, *Adalaria jannae*, and several *Corambe* species such as *Corambe steinbergae* live in epibioses on large brown algae such as



**Figure 3.** Origin and phylogeny of corambids. Strict consensus tree of ten equally parsimonious trees obtained by cladistic analysis (PAUP) of data matrix given in Table 2. All characters were treated as unweighted and unordered. The tree was unrooted. Numbers above branches refer to bootstrap values (BT < 50 not indicated); values over 75 are set in bold face and are considered as significant (Felsenstein, 1985), obtained by a separate analysis (1000 replications, PAUP) with the same settings. Warm-water species are set in bold face. The split between the Eastern Pacific *Corambe steinbergae* and the terminal clade of Atlantic warm-water species occurred before or at the closing of the Isthmus of Panama, and thus dates back at least ~3 My. Abbreviations indicate geographic distributions: A, Atlantic; BA, Boreo-Arctic; MA, Magellanic; NA, Northern Atlantic; NEA, North-Eastern Atlantic, NEP, North-Eastern Pacific; NP, Northern Pacific; NWA, North-Western Atlantic; NWP, North-Western Pacific; SEP, South-Eastern Pacific; SWA, South-Western Atlantic, SWP, South-Western Pacific.

kelp (2). *Corambe evelinae* and *Corambe obscura* may inhabit several types of environments, and are coded as unknown.

72. Salinity. Although usually restricted to marine conditions (0), at least *Corambe obscura* and *Corambe burchi* tolerate brackish water conditions (1).
73. Diet. *Cadlina* preys upon sponges (0). Most other out-group taxa such as *Acanthodoris falklandica* and *Adalaria jannae*, and most *Corambe* species, feed on bryozoans (1). *Onchidoris bilamellata* feeds on barnacles (2). The diet of *Loy* is unknown.

## RESULTS

The main parsimony analysis was performed on 20 taxa (eight out-group and 12 in-group taxa) using 73 characters based on ecology (3) and morphology (70).

All characters were unordered, and all were given equal weight. Nine characters are parsimony uninformative (characters 8, 9, 20, 31, 33, 43, 47, 49, and 73) in the main analysis. The heuristic search produced ten equally parsimonious trees with a length of 131 steps. The consistency index (CI) is 0.6718. The homoplasy index (HI) is 0.3282. The CI excluding uninformative characters is 0.6446, and the HI excluding uninformative characters is 0.3554. The retention index (RI) is 0.8664, and the rescaled consistency index (RC) is 0.5823. Of the 64 parsimony-informative characters, 28 show homoplasies in the strict consensus tree, i.e. character states evolved more than once or show at least one reversal.

In the strict consensus tree (Fig. 3) the onchidoridid *Calycidoris guentheri* and *Acanthodoris falklandica* are basal. All *Onchidoris*, *Adalaria*, and corambid species form a well-supported clade, with a bootstrap value (BT; 1000 replications, PAUP) of 97. The genus

*Onchidoris* is not recovered in the strict consensus tree, but receives low bootstrap support (BT 58); *Adalaria* species plus corambids form a clade in the strict consensus tree (BT 70). With a significant BT of 94, and showing ten synapomorphies (although nine of them are homoplastic), *Adalaria jannae* is the sister group of the clearly monophyletic corambids (BT 99). Corambids share ten synapomorphies (five of them homoplastic) in the main analysis. The basal corambid dichotomy bears one clade (BT 97) comprising the three species of the northern Pacific genus *Loy sensu* Valdés & Bouchet (1998), with six synapomorphies (three of them homoplastic); *Loy thompsoni* is the sister to *Loy millenae* and *Loy meyeri* (BT 93). The other basal corambid clade (BT 100) comprises all extant known *Corambe* species and shows 17 synapomorphies (only four of them homoplastic), with the Brazilian *Corambe evelinae* as the first offshoot. The clade of further *Corambe* species (BT 83) splits off the tropical Peruvian *Corambe mancorensis* as sister to a clade (BT 97; six synapomorphies, three of which are homoplastic) with the north-eastern Pacific temperate species *Corambe pacifica* and a tritomy (BT 78; seven synapomorphies, six of them homoplastic). The latter combines the temperate south-eastern Pacific *Corambe lucea*, the European *Corambe testudinaria*, and a poorly supported clade (BT 59) of the north-eastern Pacific *Corambe steinbergae* and a clearly monophyletic (BT 99; seven synapomorphies, two of them homoplastic) flock of species inhabiting the warm Atlantic. In contrast to former taxonomic approaches (e.g. Swennen & Dekker, 1995) that lumped these species into *Corambe obscura*, the character coding applied herein has already revealed considerable differences: *Corambe carambola* is the sister of a well-supported clade (BT 99; six synapomorphies, four of which are homoplastic) with *Corambe obscura* and *Corambe burchi*. The 50% majority rule bootstrap tree does not contradict the strict consensus tree, but is better resolved: the two *Onchidoris* species group together (BT 58), forming a sister group to a clade of *Adalaria* and corambid species; a clade of *Adalaria proxima* and *Adalaria loveni* has BT 53. Omitting the three ecological characters from the analysis had no influence on the topology of the strict consensus tree.

Including three further, still undescribed, and only externally known corambid species from South Africa, Australia, and tropical Brazil as additional taxa has little influence on the tree. The first forms a polytomy together with *Corambe testudinaria*, *Corambe lucea*, a well-supported clade (BT 91) of the Australian species, and *Corambe steinbergae*, and the Brazilian species (which has to be compared with *Corambe carambola*) as sister (BT 75) to three warm Atlantic species (tree not shown).

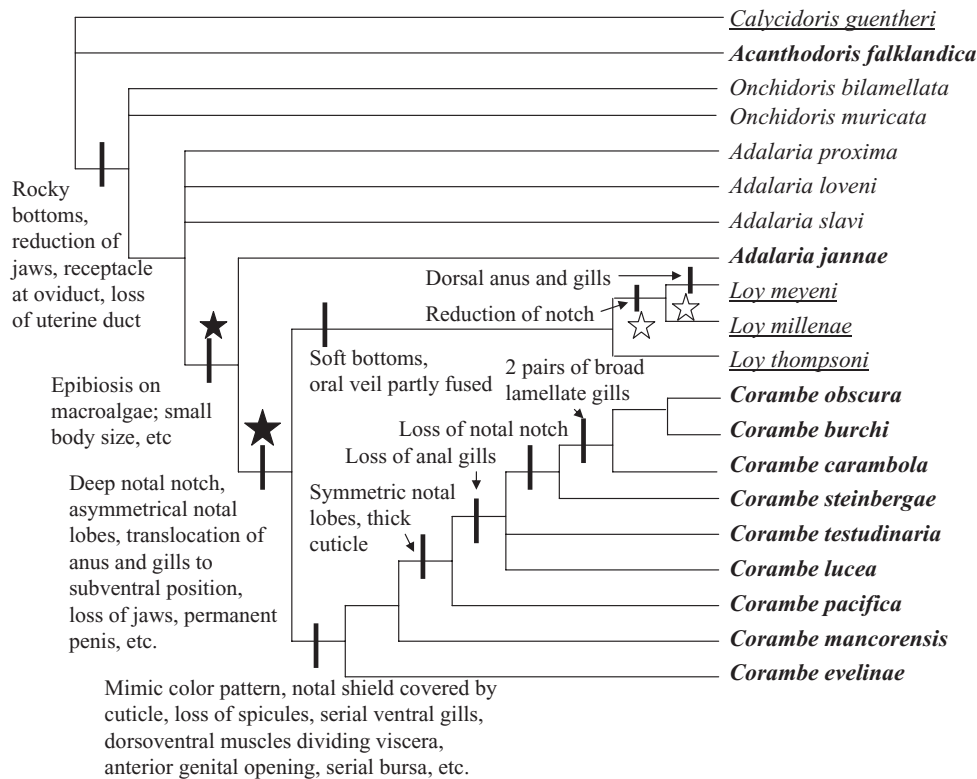
Including the cryptobranch *Cadlina*, and further Suctorina genera (*Goniodoris*, *Diaphorodoris*, and *Onchimira*) into the main analysis led to paraphyletic Onchidorididae (see the Supporting material, with the recently established genus *Onchimira* in a basal position. As in the main analysis, *Onchidoris* is the sister to *Adalaria* including monophyletic corambids, with unchanged internal topology and almost identical support values.

## DISCUSSION

We selected corambid opisthobranch gastropods as a model taxon for reconstructing phylogeny and evolution in detail. Our assumption, that great morphological variation as expressed by corambid species may reflect phylogenetic signal rather than noise, appears to be supported by our results. The strict consensus tree (Fig. 3) resulting from parsimony analysis is well resolved for the in-group, and statistical node support is exceptionally high, especially when compared with other, more general approaches on opisthobranchs and subclades thereof (e.g. Wägele & Willan, 2000; Valdés, 2002; Wägele & Klussman-Kolb, 2005; Martynov & Schrödl, 2008; Martin *et al.*, 2009). Morphology-based cladistic approaches on lower subgroups such as genera or families already may count with a dense taxon sampling, but still a low number of characters, resulting in suboptimal resolution and/or weak node supports (e.g. Pola, Cervera & Gosliner, 2005; Dayrat, 2006). We assume that it is beneficial, or even crucial, to optimize both the coverage of in-group taxa and of structural characters, which also minimizes subjective selection. The corambid tree presented herein basically resembles the topology obtained earlier by Valdés & Bouchet (1998), which was based on a very limited character set, but the nodes are now much better supported (own bootstrap reanalysis, not shown). As our phylogenetic hypothesis is also robust to modifications of taxon sampling (i.e. the inclusion of further species), it is likely to reflect natural relationships. Aspects of the evolutionary history of corambids can thus be reliably reconstructed tracing character state changes on the tree. Mapping available background information such as recent geographical distributions on the tree may give some clue to the geographic origin of certain clades.

## THE ORIGIN OF CORAMBIDS

All taxa included in the main analysis are suctorial dorid nudibranchs, and were considered as members of the Onchidorididae, including the former family Corambidae according to Millen & Martynov (2005). The out-group sampling used herein in the main



**Figure 4.** Evolution of corambids. Strict consensus tree as in Figure 2, showing some selected apomorphies of major groups (indicated by vertical lines). Black star indicates supposed incidents of progenesis in the common ancestor of *Adalaria jannae* and corambids, and, more pronounced, in the stemline of corambids. White star indicates partial reversal of progenesis within the *Loy* lineage. Heterochronic changes correlate with habitat switches from rocky bottoms (species in regular face) to algae epibionts (species in bold face), and towards soft bottom dwellers (species underlined).

and in additional analyses may be dense enough to conclude that *Onchidoris*, *Adalaria*, and corambid species form a thus far unnamed lineage, the monophyly of which is indicated by significant node support (BT 97). One important synapomorphy is the loss (or translocation and fusion) of a separate uterine duct as characteristic for cryptobranch and many other dorids.

The geographic distribution of all but two extant members of *Onchidoris* and of all known *Adalaria* species is limited to cool waters of the northern hemisphere (Martynov *et al.*, 2009; Alvim *et al.*, 2011). Therefore, we can assume that the early radiation of this clade occurred there: dispersal may have occurred along Arctic coasts during warm periods, probably starting prior to the Pleistocene (see below). Corambids thus originated from an *Adalaria*-like ancestor dwelling in cool northern waters. According to our main analysis and an extended analysis that includes all Atlantic and most Pacific *Adalaria* species (Supporting material S1), the northern Pacific *Adalaria jannae* is the direct sister to the clearly monophyletic corambid clade. Plotting geographic distributions on our trees, it is most parsimonious to conclude that the

corambid ancestor occurred in the cool northern Pacific (Fig. 4), as *Adalaria jannae* and all members of the corambid genus *Loy* still do, even though the most basal *Corambe* species occurs in warm western Atlantic waters. The alternative, an Atlantic origin of the ancestor of corambids plus *Adalaria jannae* with independent colonization of cool Pacific waters by *Adalaria jannae* and the ancestor of *Loy* is less likely, based on current knowledge.

Tracing character states, the ancestral corambid already was small, had a depressed body, and was associated with kelp, preying upon encrusting bryozoans of the genus *Membranipora*. As evolutionary novelties, the corambid ancestor lost notal tubercles and rhinophore lamellae, developed a deep posterior notch between asymmetrical notal lobes, re-established a gill cavity, reduced the number of anal gills to three, and translocated gills and anus into a terminal, subventral position, among others (Fig. 4). Hiding the gills in a subventral cavity can be interpreted as protective adaptation to a life on or near to bryozoan-covered fronds of macroalgae that move and rasp on each other because of currents. All

these novelties in adult corambids also occur in early juvenile stages of cryptobranch dorids (Martynov *et al.*, 2011); the aberrant morphology of the corambid ancestor can thus be easily explained by accepting its paedomorphic nature. Other novelties of an ancestral corambid, such as the development of a permanent penis and the loss of jaws, might have evolved independently from heterochronic changes.

#### UNEQUAL SISTERS – EARLY CORAMBID RADIATION

Corambids basally split into two highly supported clades (Fig. 3), which conform to the subfamilies Loyinae and Corambinae according to Martynov (1994a), or the genera *Loy* and *Corambe* as defined by Valdés & Bouchet (1998). The three extant species of the genus *Loy* known at present are the product of a northern Pacific radiation towards inhabiting deeper soft bottoms. The most basal species, *Loy thompsoni*, still possesses a well-developed notal notch, which narrowed in the common ancestor of *Loy millenae* and *Loy meyeri*, and is nearly completely closed in the latter, with anus and gills shifted towards a dorsal position (Fig. 4). This can be explained by a habitat switch towards deeper, low-energy environments where gills do not need special mechanical protection, and might have been caused by a partial reversal of the ancestral corambid paedomorphosis. The habitat shift of *Loy* species towards a soft bottom environment without available *Membranipora* must have occurred along with specializing on different food sources. Although the prey of *Loy* species is still unknown, the elongate lateral radula teeth of at least *Loy meyeri* and *Loy millenae* (Fig. 2K–L) indicate that they may prey upon fleshy, soft-bodied animals, such as sponges, tunicates, or worms.

In terms of extant species numbers, the radiation of *Corambe* was much more successful, and there is a number of apomorphic and partly unique traits (Fig. 4). The ancestor of *Corambe* species further specialized to life on shallow water macroalgae. Calcareous spicules were lost and the notum transformed into a wide, flexible fleshy shield (Fig. 1D) that is covered by a resistant cuticle (Schrödl & Wägele, 2001); large, vacuolated cells within the thick connective tissue (Schrödl & Wägele, 2001) may serve as a hydrostatic bolster. Similarly uniquely within sea slugs, three pairs of dorsoventral muscle bundles evolved, connecting the notum with the foot and separating the viscera peripherically into lobes (Schrödl & Wägele, 2001). Contraction of these muscles further depresses and stabilizes the already flattened body, and may enhance the sucking ability of the foot. *Membranipora*-like pigment patterns on the notum perfectly camouflage specimens when sitting on or

nearby their bryozoan food colonies (Fig. 1D). Within *Corambe*, the small ancestral anal gills and their cavity were successively reduced and replaced by multiplied gills arranged along the posterior body sides (Figs 2E–G; 4). Such serial gills ventral to the notum, plus lacunary systems in the lateral body walls and upper foot layer, provide an extended respiratory surface. This probably evolved to compensate for the thick notum covered by a cuticle that clearly minimizes the dorsal dermal diffusion of oxygen. Cilia on the gills produce a strong water current along the body sides that passes the posteroventral anus and nephroporus, and exits through the notal notch (A. Martynov & M. Schrödl, pers. observ.); the latter is thus used as an exhalent siphon that is shaped and fine-tuned by the notal lobes.

#### EPIBIOSIS ON FLOATING ALGAE – WORLDWIDE DISPERSAL AND RADIATION OF *CORAMBE*

The ancestor of *Corambe* species was thus especially well adapted to life on and from *Membranipora*-covered kelp. But what were the driving forces and mechanisms for multiple speciations? If originating from the cool northern Pacific, the ancestral *Corambe* must have competed for food with *Adalaria jannae*, and dispersed to warm south-eastern Pacific and western Atlantic waters before the original population became extinct or formed the stemline of *Corambe pacifica*. Alternatively, ancestral *Corambe* could have already been adapted to warmer waters and radiated within the Eastern Pacific and Western Atlantic. Extant remainders of this early *Corambe* dispersal and radiation are the Brazilian *Corambe evelinae* and the tropical Peruvian *Corambe mancorensis*. Whatever the scenario, dispersal across central American waters before the closing of the Isthmus of Panama is more likely than dispersal towards, and adaptation to, arctic or subantarctic waters followed by migration and adaptation back to the tropics. Californian kelp forests were (re)colonized by the ancestor of *Corambe pacifica* (plus all further *Corambe*) (Fig. 4), which further elaborated the notal shield by possessing a thick, multilayered, shedding cuticle (MacFarland & O'Donoghue, 1929). From here, temperate waters of the south-eastern Pacific and Eastern Atlantic could have been colonized by ancestral *Corambe lucea* and *Corambe testudinaria*, which are still very similar. According to preliminary data (tree not shown), this radiation also led to the temperate South African water species, and to a clade including an Australian cool-water species. Long-distance dispersal, including crossing oceans, with subsequent speciation works well for other epibiotic gastropods in the southern hemisphere (Donald, Kennedy & Spencer, 2005). *Corambe* specimens, together with their food and

ovipostures, are known to live and raft on floating algae such as the giant kelp; in addition, corambid larvae are pelagic (Perron & Turner, 1977; Yoshioka, 1986b; A. Martynov & M. Schrödl, pers. observ.).

Only then, the ancestral *Corambe steinbergae* appeared as a competitor of resident north-eastern Pacific *Corambe pacifica*; some structural differences, such as the closing of the notal notch and the smaller body size of *Corambe steinbergae* are shared with its sister group, a clade of three Atlantic species, and thus were already genetically fixed. Our tree hypothesis indicates that the smaller size of *Corambe steinbergae* was a pre-adaptation allowing for a more efficient exploitation of limited food sources compared with *Corambe pacifica* (Yoshioka, 1986b). Some other features of *Corambe steinbergae* that appear to be related to food detection and uptake, such as the simple rhinophores and special shaped oral veil and tentacles, are shared with the undescribed Australian species. The evolutionary specialization of cephalic sensoric organs could thus be an ancestral pre-adaptation or the result of fierce competition with *Corambe pacifica*, as was suspected for many ecological and life cycle traits by Yoshioka (1986b), and/or a coevolutionary reaction on prey defense. As assumed by Yoshioka (1986b), there was sufficient time for coevolution: the closing of the Central American land bridge some 3 Mya can be assumed to have separated a Pacific, *Corambe steinbergae*-like ancestor from Atlantic individuals (Fig. 3). This second warm water-related radiation of *Corambe* species started in the eastern American tropics, with three (or four, when considering the northern Brazilian *Corambe* sp.3) extant species still occurring in the Caribbean Sea and Western Atlantic; newly introduced *Corambe obscura* also occurs in the Black Sea (Roginskaya & Grintsov, 1990; Martynov, Korshunova & Grintsov, 2007). The common ancestor of *Corambe carambola*, *Corambe burchi*, and *Corambe obscura* reduced the thick notal cuticle into a single layer, substituted the rows of multiple feather-like gills by two pairs of broad lamellate gills, and lost the ancestral bryozoan mimicking colour pattern (Figs 2D and 4). These species are small and ecologically tolerant; they occur among soft substrata, on rocks, or on algae from intertidal to deeper waters, and *Corambe burchi* and *Corambe obscura* at least have stable populations in brackish water conditions.

#### THE UNDERLYING PROCESS – PROGENETIC SHORTENING OF LIFE CYCLES

Several morphological peculiarities that were established during initial corambid evolution can be plausibly attributed to paedomorphosis (Fig. 4). The

question remains whether paedomorphic traits such as the translocation of anus and gills to a better protected subventral and, later, ventral position in *Corambe* species were the trigger for, or just advantageous consequences of, heterochronic evolutionary processes. Most species of the family Onchidorididae, including close corambid relatives of the genera *Onchidoris* and *Adalaria*, inhabit rocky subtidal substrata covered with encrusting Bryozoa. This environment represents relatively stable conditions, and corresponds to the typical onchidoridid subannual life cycle with specimens growing to approximately 2–3 cm in body length (e.g. in *Adalaria proxima*, see Thompson & Brown, 1984). In contrast *Adalaria jannae*, at least facultatively, occurs on bryozoan-covered kelp, and the ancestral corambid and most *Corambe* species exclusively occur on kelp (*Macrocystis* or other macroalgae) covered with *Membranipora* colonies, and they all remain small in size. Although not exactly known for *Adalaria jannae*, Loy, and most *Corambe* species, the time span from settlement to reproduction of kelp-associated corambids appears to be considerably shorter than that of their distant onchidoridid relatives, ranging from less than a month in, e.g. *Corambe pacifica* and *Corambe steinbergae* (Yoshioka, 1986b), to an extreme of only 2 weeks in *Corambe obscura* (Perron & Turner, 1977). Relatively short generation times and small body sizes correspond well to a life (including settlement, metamorphosis, food uptake, growth, reproduction, placing ovipostures, and hatching of larvae) in ephemeral and unstable kelp environments. We therefore conclude that an abbreviation of the ancestral onchidoridid ontogenetic programme was highly advantageous for individuals that switched towards a life exploiting *Membranipora* colonies on kelp. A progenetic ancestor of corambids (Fig. 4) would have already been reproductive at a small body size, and adults would be expected to have retained some morphological features that are elsewhere characteristic for late larvae or early juveniles. In fact, extant early corambids still retain several postlarval features (Martynov *et al.*, 2011), some of which are relics without any obvious selective advantage, such as the slightly asymmetric shape of notal lobes, or the retention of anal gills in addition to much larger and more numerous serial gills (Figs 1C–D, 2F–G). We therefore propose that the major driving force for the corambid radiation and evolutionary success was progenesis, which allowed a highly efficient colonization of instable kelp habitats and exploitation of fast-growing but short-lived resources. As a consequence, paedomorphic features occurred, of which some were advantageous in the new habitat, such as having a notal notch and gills in a protected



position; these were retained, modified, or even lost during further corambid evolution.

#### CONCLUDING REMARKS

Assembling the animal tree of life, molecular techniques greatly help to assess and reconstruct relationships, especially on a low taxon level by population genetics, or exploring selected representatives of higher clades by, e.g. phylogenomic approaches (e.g. Dunn *et al.*, 2008). However, attempting full species coverage of invertebrate clades that comprise members that are rare or occur in remote places or deeper waters is challenging, because there is no access to specimens or tissues that are adequately preserved for sequence analyses. In contrast, there is usually at least some useful morphological information available for all known members of such clades, and collections may house older or formalin-fixed samples that are still adequate for structural analyses. Some researchers think that structural characters have already been well explored, and are mainly useful when mapped on molecular trees (e.g. Scotland, Olmstead & Bennett, 2003). However, careful morphological and histological study of corambid nudibranchs alone reveals a list of 70 structural characters that are coded for phylogenetic analysis; many of them were never used before for cladistic purposes. As also shown by several recent studies on acochlidian opisthobranchs (e.g. Neusser & Schrödl, 2007; Neusser, Martynov & Schrödl, 2009; Schrödl & Neusser, 2010), our revision of our own and museum material of most corambid and out-group species proved to be crucial to correct mistakes from the literature and supplement our data. Our case-study results in a nicely resolved corambid topology, and most nodes are significantly supported. This is not a trivial result, considering that nudibranchs are famous for their rampant level of evolutionary parallelism, otherwise hindering conventional phylogenetic reconstructions (Gosliner & Ghiselin, 1984). Also, in corambid species, we found a mosaic-like mixture of apparently archaic and highly specialized structures, leading to a high level of homoplasy in our tree. However, there is sufficient signal in the data set to recognize such convergencies and incidents of secondary losses. Even more importantly, some of the most peculiar and apparently archaic similarities, such as the possession of dorsal gills in non-corambid dorids and *Loy meyeri*, or the absence of notal notches in adult dorids and some corambids, in our robust topological framework could be recognized as consequences of heterochronic processes; i.e. these are independently derived features rather than sympleiomorphic ones. We conclude that morphology-based phylogenies, if performed properly, can contribute to

fill the taxon gap that remains elusive to molecular approaches. In our model study, the resulting tree is stable and the taxon sampling (including all valid plus several reinstated or undescribed corambid species) appears dense enough to reconstruct evolutionary history reliably. Considering and integrating information on geographical and bathymetrical distributions, habitat types, character evolution as inferred from the tree, ontogenetic data, and knowledge on lifestyle and general evolutionary processes leads to an evolutionary scenario that we consider remarkably detailed and plausible for a group of marine invertebrates. Although we expect that the general picture will persist, the discovery and detailed structural investigation of additional corambid species and future molecular studies, including potential detection of cryptic species and applying molecular clock approaches on nudibranchs, will allow further refinements and insights into the phylogeny and evolution of corambids.

#### ACKNOWLEDGEMENTS

We are grateful to Tanya Korshunova (Moscow, Institute of Higher Nervous Activity and Neurophysiology) for preparing illustrations; she also helped collecting the specimens for this study under sometimes severe conditions. Our sincere thanks go to Sandra Millen (Vancouver) for collecting and making available specimens of *Corambe pacifica*, *Corambe steinbergae*, and *Loy thompsoni*. David Reid (The Natural History Museum, London) is thanked for loaning corambid material. Bill Rudman (Australian Museum, Sydney) kindly provided material of an undescribed Australian *Corambe* species. Rosana Carvalho (Bavarian State Collection of Zoology, ZSM) helped with collecting specimens in Brazil; Luiz Simone and Carlo Magenta (Museo de Zoología, São Paulo) are thanked for collaboration. Nadya Sanamyan, Karen Sanamyan (Kamchatka Branch of the Pacific Institute of Geography FEB RAS, Petropavlovsk-Kamchatsky), Aleksey M. Tokranov and Vyacheslav Shipilov generously organized SCUBA diving in Kamchatka waters. Georgy N. Davidovich, Anatoly G. Bogdanov, and the staff of the scanning electron microscopic laboratory of the Moscow State University are thanked for providing excellent SEM facilities. Eva Lodde (ZSM) helped preparing histological sections. Two anonymous referees are thanked for improving our article. Diving equipment and funds were contributed by the GeoBioCenter (Ludwig Maximilians-Universität) and the Deutsche Forschungsgemeinschaft (DFG SCHR 667/4 to M.S.); A.M.'s visits to the ZSM were financed by DFG grants SCHR 667/6–1 and SCHR 667/10–1.

## REFERENCES

- Aguinaldo AMA, Turbeville JM, Linford LS, Rivera MC, Garey JR, Raff RA, Lake JA. 1997.** Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* **87**: 489–493.
- Alvim J, Padula V, Dias Pimenta A. 2011.** First record of the genus *Onchidoris* (Gastropoda: Nudibranchia: Onchidorididae) from the South Atlantic Ocean, with the description of a new species from Brazil. *Journal of the Marine Biological Association of the United Kingdom* **91**: 505–511.
- Baranets ON, Minichev YS. 1994.** The evolution of the mantle complex in nudibranchiate molluscs (Gastropoda, Nudibranchia). *Zoologicheskyy Zhurnal* **73**: 29–35.
- Bergh RS. 1871.** Beiträge zur Kenntniss der Mollusken des Sargassomeeres. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien* **21**: 1273–1308.
- Bergh RS. 1880.** On the nudibranchiate gastropod mollusca of the North Pacific Ocean, with special reference to those of Alaska, pt. 2. *Proceedings of the Academy of Natural Sciences Philadelphia* **32**: 40–127.
- Bickell LR, Chia FS. 1979.** Organogenesis and histogenesis in the planktotrophic veliger of *Doridella steinbergae* (Opisthobranchia, Nudibranchia). *Marine Biology* **52**: 291–313.
- Bickell LR, Chia FS, Crawford BJ. 1981.** Morphogenesis of the digestive system during metamorphosis of the nudibranch *Doridella steinbergae* (Gastropoda): conversion from phytoplanktivore to carnivore. *Marine Biology* **62**: 1–16.
- Dayrat B. 2006.** A taxonomic revision of *Paradoris* sea slugs (Mollusca, Gastropoda, Nudibranchia, Doridina). *Zoological Journal of the Linnean Society* **147**: 125–238.
- Donald KM, Kennedy M, Spencer HG. 2005.** Cladogenesis as the result of long distance rafting events in South Pacific topshells (Gastropoda, Trochidae). *Evolution* **59**: 1701–1711.
- Dunn CW, Hejnol A, Matus DQ, Pang K, Browne WE, Smith SA, Seaver E, Rouse GW, Obst M, Edgecombe GD, Sørensen MV, Haddock SH, Schmidt-Rhaesa A, Okusu A, Kristensen RM, Wheeler WC, Martindale MQ, Giribet G. 2008.** Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* **452**: 745–749.
- Edmunds M. 2007.** Opisthobranchiate mollusca from Ghana: Dendrodorididae and Dorambidae. *Journal of Conchology* **39**: 253–264.
- Fahey SJ, Valdés A. 2005.** Review of *Acanthodoris* Gray, 1850 with a phylogenetic analysis of Onchidorididae Alder and Hancock, 1845 (Mollusca, Nudibranchia). *Proceedings of the California Academy of Sciences* Ser. 4 **56**: 213–272.
- Felsenstein J. 1985.** Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–791.
- Fischer H. 1891.** Recherches anatomiques sur un mollusque nudibranche appartenant au genre *Corambe*. *Bulletin Scientifique de la France et de la Belgique, Paris* Ser. 4 **23**: 358–398.
- García FJ, Urgorri V, López González PJ. 1991.** Redescription de *Corambe testudinaria* Fischer, 1889 (Gastropoda, Nudibranchia). *Bolletino Malacologico* **26**: 113–124.
- Giribet G, Okusu A, Lindgren AR, Huff SW, Schrödl M, Nishiguchi MK. 2006.** Evidence for a clade composed of molluscs with serially repeated structures: monoplacophorans are related to chitons. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 7723–7728.
- Gosliner TM. 1987.** *Nudibranchs of southern Africa, a guide to opisthobranch molluscs of Southern Africa*. Los Osos: Sea Challengers.
- Gosliner TM, Ghiselin TM. 1984.** Parallel evolution in opisthobranch gastropods and its implications for phylogenetic methodology. *Systematic Zoology* **33**: 255–274.
- Jörger KM, Stöger I, Kano Y, Fukuda H, Knebelberger T, Schrödl M. 2010.** On the origin of Acochlidia and other enigmatic euthyneuran gastropods and implications for the systematics of Heterobranchia. *BMC Evolutionary Biology* **10**: 323.
- Lance JR. 1962.** A new *Stiliger* and a new *Corambella* (Mollusca: Opisthobranchia) from the northwestern Pacific. *Veliger* **5**: 33–38.
- MacFarland FM. 1966.** Studies of the opisthobranchiate mollusks of the Pacific coast of North America. *Memoirs of the California Academy of Sciences* **6**: 1–546.
- MacFarland FM, O'Donoghue C. 1929.** A new species of *Corambe* from the Pacific coast of North America. *Proceedings of the California Academy of Sciences* Ser. 4 **18**: 1–27.
- Marcus Er. 1955.** Opisthobranchia from Brazil. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoology* **207**: 89–261.
- Marcus Er. 1958.** Notes on Opisthobranchia. *Boletim do Instituto Oceanografico, Universidad de São Paulo* **7**: 31–78.
- Marcus Er. 1959.** Reports from the Lund University Chile Expedition 1948–49, No. 36. Lamellariacea und Opisthobranchia. *Lunds Universitets Årsskrift (Ny Följd)* Avd. 2 **55**: 1–133.
- Marcus Ev, Marcus Er. 1967.** Some opisthobranchs from Sapelo Island, Georgia, U.S.A. *Malacologia* **6**: 199–222.
- Martin R, Hess M, Schrödl M, Tomaschko K-H. 2009.** Cnidosac morphology in dendronotacean and aeolidacean nudibranchs (Mollusca: Opisthobranchia): from expulsion of nematocysts to use in defense? *Marine Biology* **156**: 261–268.
- Martynov AV. 1994a.** Materials for the revision of the nudibranch molluscs of the family Corambidae (Gastropoda, Opisthobranchia) Part 1. Taxonomy. *Zoologicheskyy Zhurnal* **73**: 1–15.
- Martynov AV. 1994b.** Materials for the revision of the nudibranch molluscs of the family Corambidae (Gastropoda, Opisthobranchia). Part II. Origin. *Zoologicheskyy Zhurnal* **73**: 36–43.
- Martynov AV. 1995.** Materials for the revision of the nudibranch family Corambidae (Gastropoda, Opisthobranchia). 2. Origin of the Corambidae. *Hydrobiological Journal* **31**: 59–66.
- Martynov AV. 1999.** Buccal pumps, gills pockets and new understanding of the suctorial phanerobranchial dorids. In:

- Rotolo VG, ed. *Proceedings of the 2nd international workshop of malacology: systematic, phylogeny and biology of opisthobranch molluscs*. 10–14 June 1999. Menfi, Italy, 13–14.
- Martynov AV. 2000.** On the taxonomical position of the genus *Echinocorambe* Valdés et Bouchet, 1998 (Gastropoda: Nudibranchia). In: Egorova EM, ed. *Proceedings of XIV (5) Russian malacological conference*. St.Petersburg: Zoological Institute RAS, 50–52.
- Martynov AV, Brenzinger B, Hooker Y, Schrödl M. 2011.** 3D-anatomy of a new tropical Peruvian nudibranch gastropod species, *Corambe mancorensis*, and novel hypotheses on dorid gill ontogeny and evolution. *Journal of Molluscan Studies* **77**: 129–141.
- Martynov AV, Korshunova TA, Grintsov VA. 2007.** Opisthobranch molluscs of the Northern Black Sea. I. Short history of studies and the first record of a non-indigenous nudibranch species *Trinchesia perca* (Er. Marcus, 1958) (Nudibranchia: Tergipedidae). *Ruthenica* **17**: 43–54.
- Martynov AV, Korshunova TA, Savinkin OV. 2006.** Shallow-water opisthobranch molluscs of the Murman coast of the Barents Sea, with new distributional data and remarks on biology. *Ruthenica* **16**: 59–72.
- Martynov AV, Korshunova TA, Sanamyan NP, Sanamyan KE. 2009.** Description of the first cryptobranch onchidoridid *Onchimira cavifera* gen. et sp. nov. and of three new species of the genera *Adalaria* and *Onchidoris* (Nudibranchia: Onchidorididae) from Kamchatka waters. *Zootaxa* **2159**: 1–43.
- Martynov AV, Schrödl M. 2008.** The new Arctic side-gilled sea slug genus *Boreoberthella* (Gastropoda, Opisthobranchia): pleurobranchoidean systematics and evolution revisited. *Polar Biology* **32**: 53–70.
- Millen SV. 1985.** The nudibranch genera *Onchidoris* and *Diaphorodoris* (Mollusca, Opisthobranchia) in the north-eastern Pacific. *Veliger* **28**: 80–93.
- Millen SV. 1987.** The nudibranch genus *Adalaria*, with a description of a new species from the Northeastern Pacific. *Canadian Journal Zoology* **65**: 2696–2702.
- Millen SV, Martynov AV. 2005.** Redescriptions of the nudibranch genera *Akiodoris* Bergh, 1879 and *Armodoris* Minichev, 1972 with description of a new species of *Akiodoris* and description of new family Akiodorididae. *Proceedings of the California Academy of Sciences* Ser. 4 **56**: 1–22.
- Millen SV, Nybakken JW. 1991.** A new species of *Corambe* (Nudibranchia: Doridoidea) from the northeastern Pacific. *Journal of Molluscan Studies* **57** (suppl. 4): 209–215.
- Neusser TP, Martynov A, Schrödl M. 2009.** Heartless and primitive? Computer-based 3D reconstruction of the polar acochlidian gastropod *Asperspina murmanica*. *Acta Zoologica* **90**: 228–245.
- Neusser TP, Schrödl M. 2007.** *Tantulum elegans* reloaded: a computer-based 3D-visualization of the anatomy of a Caribbean freshwater acochlidian gastropod. *Invertebrate Biology* **126**: 18–39.
- Perron FE, Turner FD. 1977.** Development, metamorphosis, and natural history of the nudibranch *Doridella obscura* Verrill (Corambidae: Opisthobranchia). *Journal Experimental Marine Biology and Ecology* **27**: 171–185.
- Pola M, Cervera L, Gosliner MT. 2005.** Review of the systematics of the genus *Roboastra* Bergh, 1877 (Nudibranchia, Polyceridae, Nembrothinae) with the description of a new species from the Galápagos Islands. *Zoological Journal of the Linnean Society* **144**: 167–189.
- Richardson KC, Jarett L, Finke EH. 1960.** Embedding in epoxy resins for ultrathin sectioning in electron microscopy. *Stain Technology* **85**: 313–323.
- Roginskaya IS, Grintsov VA. 1990.** The nudibranch *Doridella obscura*, a new immigrant into the Black Sea. *Okeanologiya* **30**: 633–634.
- Rudman WB. 1984.** The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. *Zoological Journal of the Linnean Society* **81**: 115–273.
- Rudman WB. 1998.** Suborder doridina. In: Beesley PL, Graham JB, Wells R, Wells A, eds. *Mollusca: the southern synthesis. Fauna of Australia. Volume 5, part B*. Melbourne, Vic.: CSIRO Publishing, 990–1001.
- Schrödl M. 2003.** *Sea slugs of southern South America*. ConchBooks.
- Schrödl M, Neusser TP. 2010.** Towards a phylogeny and evolution of Acochlidia (Mollusca: Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society* **158**: 124–154.
- Schrödl M, Wägele H. 2001.** Anatomy and histology of *Corambe lucea* Marcus, 1959 (Gastropoda, Nudibranchia, Doridoidea), with a discussion of the systematic position of Corambidae. *Organisms Diversity & Evolution* **1**: 3–16.
- Scotland RW, Olmstead RG, Bennett JR. 2003.** Phylogeny reconstruction: the role of morphology. *Systematic Biology* **52**: 539–548.
- Spurr AR. 1969.** A low viscosity epoxy resin embedding medium for electron microscopy. *Journal of Ultrastructure Research* **26**: 31–43.
- Swennen C, Dekker R. 1995.** *Corambe batava* Kerbert, 1886 (Gastropoda: Opisthobranchia), an immigrant in the Netherlands, with a revision of the family Corambidae. *Journal of Molluscan Studies* **61**: 97–107.
- Swofford DL. 2001.** PAUP\*. *Phylogenetic analysis using parsimony (\*and other methods)*. Version 4. Sunderland, MA: Sinauer Associates.
- Thompson TE. 1958.** The natural history, embryology, larval biology and post-larval development of *Adalaria proxima* (Alder and Hancock) (Gastropoda Opisthobranchia). *Philosophical Transactions of the Royal Society London (B)* **242**: 1–58.
- Thompson TE. 1967.** Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *Journal of the Marine Biological Association of United Kingdom* **47**: 1–22.
- Thompson TE, Brown GH. 1984.** *Biology of opisthobranch molluscs*. Vol. 2. London: Ray Society.
- Valdés A. 2002.** A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Zoological Journal of the Linnean Society* **136**: 535–636.

- Valdés Á, Bouchet P. 1998.** A blind abyssal Corambidae (Mollusca, Nudibranchia) from the Norwegian Sea, with a reevaluation of the systematics of the family. *Sarsia* **83**: 15–20.
- Verrill AE. 1870.** Contributions to zoology from the Museum of Yale College. No.8. – Descriptions of some New England Nudibranchiata. *American Journal of Science & Arts Ser. 2* **50**: 405–408.
- Wägele H, Cervera JL. 2001.** Histological study of *Goniodoris castanea* Alder and Hancock, 1845 (Nudibranchia, Doridoidea, Goniodorididae). *Journal of Morphology* **250**: 61–69.
- Wägele H, Klussmann-Kolb A. 2005.** Opisthobranchia (Mollusca, Gastropoda) – more than just slimy slugs. Shell reduction and its implications on defence and foraging. *Frontiers in Zoology* **2**: 1–18.
- Wägele H, Willan RC. 2000.** Phylogeny of the Nudibranchia. *Zoological Journal of the Linnean Society* **130**: 83–181.
- Wägele J-W, Letsch H, Klussmann-Kolb A, Mayer C, Misof B, Wägele H. 2009.** Phylogenetic support values are not necessarily informative: the case of the Serialia hypothesis (a mollusk phylogeny). *Frontiers in Zoology* **6**: 12.
- Wägele J-W, Mayer C. 2007.** Visualizing differences in phylogenetic information content of alignments and distinction of three classes of long branch effects. *BMC Evolutionary Biology* **7**: 147.
- Yoshioka PM. 1986a.** Competitive coexistence of the dorid nudibranchs *Doridella steinbergae* and *Corambe pacifica*. *Marine Ecology Progress Series* **33**: 81–88.
- Yoshioka PM. 1986b.** Life history patterns of the dorid nudibranchs *Doridella steinbergae* and *Corambe pacifica*. *Marine Ecology Progress Series* **31**: 179–184.

### SUPPORTING MATERIAL

Origin and phylogeny of corambids, extended out-group sampling (all onchidoridid genera, plus one member of Goniodorididae and Cryptobranchia included). Strict consensus tree of two equally parsimonious trees (152 steps) obtained by cladistic analysis (PAUP) of the data matrix given in Table 2. All characters were treated as unweighted and unordered. The tree was unrooted. Three characters were parsimony uninformative. Numbers above branches refer to bootstrap values (BT < 50 not indicated); values over 75 are set in bold face and are considered as significant (Felsenstein, 1985), obtained by a separate analysis (1000 replications, PAUP) with the same settings. The cryptobranch dorid *Cadlina laevis* and the suctorial onchidoridid *Onchimira cavifera* are basal. The only Goniodorididae included, *Goniodoris castanea*, nestles within onchidoridid taxa and renders Onchidorididae paraphyletic; the data sampling is too poor to be conclusive on this issue. As in the main analysis, *Onchidoris*, *Adalaria*, and corambids form a clade; the first two taxa are fully resolved but paraphyletic. *Adalaria jannae* is the sister to corambids; the inner corambid topology is also identical to the main analysis.